PD

Biogeography, population and trophic ecology of cetaceans in a warm-temperate habitat

DOCTORAL PROJECT

Rita Borges Ferreira

DOCTORAL DEGREE IN BIOLOGICAL SCIENCES

UNIVERSIDADE da MADEIRA

A Nossa Universidade

www.uma.pt

julho | 2024

Biogeography, population and trophic ecology of cetaceans in a warm-temperate habitat

DOCTORAL PROJECT

Rita Borges Ferreira

DOCTORAL DEGREE IN BIOLOGICAL SCIENCES

SUPERVISION
Manfred Kaufmann

CO-SUPERVISION
Filipe Marco Andrade Alves

Quando eu morrer voltarei para buscar

Os instantes que não vivi junto do mar.

Sophia de Mello Breyner Andresen

Acknowledgements

As with all endeavors in life, this work would not have been possible without the support of many people. To all, I extend my deepest gratitude.

To Professor Doutor Manfred Kaufmann, for his invaluable support and guidance throughout the course of this thesis, and for the detail-oriented inputs, suggestions, and orientations.

To Doutor Filipe Alves, whose encouragement inspired me to pursue this odyssey, for the long years of friendship, guidance, shared knowledge, and unwavering support. For the good memories of long hours spent at sea, the constant availability, and the never-ending optimism, especially when pursuing alternative plans when the initial ones failed (as they always do). For valuing me and ensuring I knew it. Additionally, for securing the necessary funding for this study to be successful.

To Doutor Marc Fernandez, who unknowingly accepted the role of an unofficial supervisor, for the patience and encouragement, constant availability to help, and contagious enthusiasm for my work. For the many hours spent debating science and always having a kind word in difficult moments.

To Doutora Ana Dinis, for the long years of mentoring, shared wisdom and knowledge, supportive words during challenging moments, and the constant availability to help and provide support. Additionally, for securing the necessary funding for this study to be successful.

To Doutor João Clode, for believing in me and providing me with an opportunity many years ago, for his support and attention, and for making me feel a valuable asset to the team.

To the MARE-Madeira, ARDITI and University of Madeira institutions, for the logistical and financial support. Also, to the teams of MARE-Madeira and ARDITI, for the excellent work environment and shared knowledge.

To the Whale Team, for the companionship either at sea or in the office, the fantastic work environment that made coming to work every day a pleasure, the shared laughter, and the immense support. To Eliette, for helping with the Blainville's. To Raquel, for helping with the final formatting of the thesis. A special acknowledgment to Annalisa, who patiently guided me through all the small details of the logistics of the thesis.

To all the photographers and whale-watching companies that provided the necessary data for this study, for sharing their passion.

To the sisterhood of women who supported me throughout this journey, whether by leading by example, providing good advice, sharing laughter, or just lending a listening ear when needed: Anita, Cátia, Inês, Eva, Catarina, Petra, Anja, Agnes, Maria João.

To my family. To Luis, for always believing in me and encouraging all my pursuits. To Eva, for the emotional support in the form of post-it notes with inspirational quotes, random hugs, and for lending me the most fantastic unicorn headphones that brought the much-needed magic to help conclude this thesis. To Gonçalo, for the flute playing to keep me company while writing, and for the browser's tabs on Pokémon that alternated with research papers. Above all, to both, for the constant reminder of what is truly important in life.

And finally, though unconventionally, to Rugas and Nina, integral members of the family and the best of companions, that left in the course of completing this work.

Funding

This work was supported by several sources of funding. The doctorate candidate was financially supported by Fundação para a Ciência e Tecnologia (FCT) through the doctoral grant SFRH/BD/147225/2019. The work was partially supported by the INTERREG MAC projects MARCET (MAC/1.1b/149) and MARCET II (MAC2/4.6c/392), by the Ocean Conservation Fund through the Whale Tales Project, by the Project Observatório Oceânico da Madeira (M1420-01-0145-FEDER-000001), and by FCT, through the strategic projects UIDB/04292/2020, granted to MARE, and LA/P/0069/2020, granted to the Associate Laboratory ARNET.

Abstract

Cetaceans play a crucial role in marine ecosystems by maintaining their structure and function, providing essential ecosystem services, and acting as sentinel species. Despite the inherent challenges, research efforts to document the distribution and movements of pelagic cetacean populations have increased. Oceanic islands present strategic advantages for studying pelagic cetaceans and integrating datasets from multiple sources is a valuable approach to obtaining the long-term datasets necessary for ecological studies on these long-lived mammals. Ultimately, such integration provides insights into cetacean populations' connectivity and migration patterns across various territories and international borders. The present study aims to elucidate the distribution, movements, and ecological interactions of eight cetacean species, for which limited information exists in the Macaronesia region (Eastern North Atlantic), thereby providing crucial insights for their conservation. This study focuses on understanding the movement patterns and site fidelity of Bryde's whale, sperm whale, and Blainville's beaked whale in the archipelagos of the Madeira, Azores, and Canaries through photographic-identification methods. Additionally, in Madeira, it examines the social structure of the Blainville's beaked whale through photographic identification and analyzes the dietary habits and ecological roles of six odontocete species through stable isotopes. Research findings indicate that Bryde's whales exhibit high site fidelity to the Madeira Archipelago during their seasonal presence, with first-time documented inter-archipelago movements between Madeira and the Canaries. This reflects the species' wide habitat range in the Macaronesia region, including international waters. For sperm whales, the study supports the existence of a pelagic population in Macaronesia, with a subset regularly using the Azores and Madeira Archipelagos. Preliminary data from the Canaries suggest a need for further research to evaluate a population significantly impacted by ship strikes. Blainville's beaked whales demonstrate female defense polygyny in the Madeira Archipelago, with strong associations between females and immatures, who exhibit the highest site fidelity rates. These findings underscore the significance of the Macaronesia region in providing essential habitats for these species. The study also highlights variations in dietary preferences and foraging strategies among different species, enhancing our understanding of marine biodiversity and ecosystem dynamics. It emphasizes the need for international collaboration when addressing the conservation challenges of these highly dynamic species. By combining long-term datasets with innovative methodologies, this research significantly contributes to the understanding and protection of cetaceans, underscoring the critical role of oceanic islands in marine conservation efforts.

KEYWORDS: Bryde's whale, sperm whale, Blainville's beaked whale, site fidelity, residency times, network analysis, stable isotopes.

Resumo

Os cetáceos desempenham um papel crucial nos ecossistemas marinhos, mantendo a sua estrutura e função, fornecendo serviços ecossistémicos essenciais e actuando como espécies sentinelas. Apesar dos desafios inerentes ao estudo de populações pelágicas de cetáceos, os esforços na investigação da sua distribuição e movimentos têm aumentado. As ilhas oceânicas apresentam vantagens estratégicas para o estudo destes cetáceos e a integração de dados de várias plataformas é uma abordagem valiosa na obtenção dos dados a longo prazo necessários para os estudos ecológicos destes mamíferos longevos. Mais, essa integração fornece conhecimento sobre a conectividade e padrões de migração das populações de cetáceos em várias regiões e cruzando fronteiras internacionais. Este estudo investiga a distribuição, movimentos e interações ecológicas de oito espécies de cetáceos, cuja informação existente na Macaronésia (Atlântico Nordeste) é limitada, providenciando conhecimentos cruciais para a sua conservação. Este estudo investiga os padrões de movimento e de fidelidade ao local da baleia de Bryde, do cachalote e da baleia-de-bico-de-Blainville nos arquipélagos da Madeira, Açores e Canárias através de métodos de foto-identificação. Além disso, na Madeira, examina a estrutura social da baleia-de-bico-de-Blainville através de foto-identificação e analisa os hábitos alimentares e papéis ecológicos de seis espécies de odontocetes através de isótopos estáveis. Os resultados indicam que as baleias de Bryde exibem uma grande fidelidade na Madeira durante a sua presença sazonal, com movimentos inter-arquipélagos documentados pela primeira vez com as Canárias, reflectindo o amplo habitat desta espécie, que inclui águas internacionais. Este estudo suporta igualmente a existência de uma população pelágica de cachalotes na Macaronésia, com uma parte a usar regularmente os Arquipélagos dos Açores e da Madeira. Os dados preliminares das Canárias indicam a necessidade de mais estudos para avaliar uma população significativamente impactada por colisões com navios. As baleias-de-bico-de-Blainville apresentam poliginia de defesa feminina na Madeira, com associações fortes entre fêmeas e imaturos, que exibem as maiores taxas de fidelidade. Os resultados obtidos realçam a importância da Macaronésia para estas espécies relativamente a habitats essenciais, destacando também variações nas estratégias de alimentação entre as diferentes espécies, aumentando a nossa compreensão sobre a dinâmica dos ecossistemas marinhos. Este estudo realça também a necessidade de colaboração internacional para ultrapassar os desafios da conservação de espécies dinâmicas como estas. Ao combinar estudos de longo prazo com metodologias inovadoras, esta investigação contribui significativamente para a compreensão e proteção dos cetáceos, realçando o papel crítico das ilhas oceânicas nos esforços de conservação marinha.

PALAVRAS-CHAVE: baleia de Bryde, cachalote, baleia-de-bico-de-Blainville, fidelidade ao local, residência, análise social, isótopos estáveis.

Thesis Objectives and Outline

The present thesis aims to advance the understanding of cetacean ecology within the Macaronesian archipelagos, with a particular focus on the Madeira Archipelago. This research addresses critical gaps in existing knowledge, by i) investigating the movement patterns of three lesser-studied species in the area; ii) exploring the social structure of a cryptic species; and iii) exploring the dietary behaviors of six key cetacean species. This study leverages extensive long-term datasets and employs innovative analytical techniques to provide a comprehensive picture of how these marine mammals use their habitats and interact within their ecosystems. Additionally, this research emphasizes the importance of international collaboration for species with wide home ranges, setting a precedent for future studies aimed at preserving marine megafauna.

The present thesis is organized into one introductory chapter, four data chapters and a final discussion chapter.

In Chapter I, the main themes related to the biogeography and population ecology of cetaceans are presented, along with insights into the trophic ecology of this taxonomic group. The study area of Macaronesia is described, with a focus on the Madeira Archipelago. Among the eight cetacean species included in this study, there is a brief presentation of the three main species focused, within the context of their presence in the Madeira Archipelago.

Chapters II to V consist of distinct research studies.

Chapter II aims to investigate the site fidelity and residency patterns of Bryde's whales (*Balaenoptera edeni*) in the oceanic archipelago of Madeira and the migratory connectivity to the neighboring archipelago of the Canaries. This study aims to fill the knowledge gaps regarding the occurrence, geographical connectivity, and movement patterns of this species within this region, which is critical for their conservation and management. For that, a comprehensive 14-year photographic dataset was used to elaborate a photo-identification catalogue, with data collected from platforms of opportunity and scientific surveys, with which site fidelity and residency times in the

Madeira Archipelago were assessed. The comparison of this photo-identification catalogue with an open-access catalogue from the Canaries allowed to shed light into the connectivity between these archipelagos. This innovative study aims to provide critical baseline data on the movement ecology of an enigmatic baleen whale species in a pelagic habitat while emphasizing the importance of transborder collaborations.

Chapter III also focuses on investigating site fidelity and residency patterns, but of an iconic toothed whale species, the sperm whale (*Physeter macrocephalus*), and on a wider area comprising the three archipelagos of Macaronesia – Azores, Madeira, and the Canaries. For that, long-term photographic datasets of each archipelago were used to analyze site fidelity, using a composite index and residency times to inform on the movements in and out of these areas. Since the dataset from the Canaries presented a limited temporal coverage, analysis in this archipelago is preliminary. This study is the first to aggregate quantitative data from the three archipelagos to provide a broader image of the habitat use of this frequent species in the Macaronesian basin, where it was heavily targeted during the whaling period and now faces other anthropogenic threats.

Chapter IV is dedicated to a cryptic species in the Madeira Archipelago, the Blainville's beaked whale (*Mesoplodon densirostris*), to investigate this species' site fidelity and social structure. For that, a nine-year photographic dataset from Madeira Archipelago was used, with data from both platforms of opportunity and scientific surveys, to analyze site fidelity, residency times, and social networks to test the hypothesis of female defense polygyny. This study contributes to a deeper understanding of the social structure of an oceanic and less-known species and can be used as a model for future research in other elusive and deep-diving species.

Chapter V aims to investigate the trophic ecology of six odontocete species in the Madeira Archipelago: short-beaked common dolphin (*Delphinus delphis*), Atlantic spotted dolphin (*Stenella frontalis*), common bottlenose dolphin (*Tursiops truncatus*), false killer whale (*Pseudorca crassidens*), short-finned pilot whale (*Globicephala macrorhynchus*), and sperm whale (*Physeter macrocephalus*). The study explores their trophic positions, isotopic niche sizes, foraging habitats, and sex-based differences by analyzing the stable isotope ratios of carbon $\delta^{13}C$ and nitrogen $\delta^{15}N$. This study provides new and relevant data regarding dietary preferences and foraging behaviors of several species of cetaceans that forage in different pelagic layers, contributing to a better understanding of biodiversity and ecological dynamics in oceanic ecosystems.

Finally, Chapter VI consists of a general discussion, where the main conclusions of each chapter are summarized and debated. It also includes a section on future steps, offering recommendations on the direction of future studies in these thematic areas.

Contents

List of figures

List of tables

CHAPTER I – General Introduction

CHAPTER I – General Introduction

Biogeography and Population Ecology of Cetaceans

Cetaceans (whales, dolphins, and porpoises) are a highly diversified marine megafauna group, exhibiting a large range of sizes, occupying virtually all habitats in the world's oceans, lakes, and rivers, and displaying a wide array of life history strategies. Belonging to the order Cetacea, this group encompasses more than 90 recognized species, with new species being recognized and others going extinct in the last few years. Cetaceans are divided into two suborders, Mysticeti and Odontoceti. The mysticetes (large baleen whales), including the largest extant marine megafauna, are typically migratory, alternating high-latitude feeding grounds during summer with low-latitude breeding grounds during winter. They feed mainly on schooling crustaceans or fish (Bannister, 2018). The odontocetes (toothed whales) are more diverse in body size and foraging ecology. They may range from less than 1m long for some newborn dolphins to 18m for an adult male sperm whale and are diverse foragers, which, depending on species and individual preferences, may consume prey as small as krill and as large as blue whales (Hooker, 2018). Odontocetes occur throughout the world's oceans and, unlike mysticetes, even in large rivers (Estes et al., 2016).

Understanding the biogeography of cetaceans offers valuable insights into their spatial distribution, habitat preferences, and the factors influencing their movements, while also uncovering significant ecological processes and interactions with their environment (Gideran et al., 2023). Animal movement impacts nearly all ecological levels, influencing individuals, shaping populations' distribution and structure, affecting inter- and intraspecific interactions, and facilitating the flow of nutrients across ecosystems (Nathan et al., 2008). It manifests in various forms, including small-scale foraging movements, larger one-way dispersive movements, seasonally predictable round-trip migrations, and erratic nomadic movements (Mueller and Fagan, 2008; Shaw, 2020). Although most individuals move at some point in their lives, movement patterns can vary significantly within the same species, differing over time within an individual (intra-individual), among individuals within the same population (inter-individual), or among different populations (inter-population) (Shaw 2020).

In recent years, there has been considerable effort to better document what is known about the distribution and movements of cetaceans (Bräger and Bräger, 2019), specifically for oceanic populations, since most of the existing knowledge comes from nearshore species and/or populations (e.g., Rosel, Hansen and Hohn, 2009; Bilgmann, Parra and Möller, 2018; Lodi, Tardin and Maricato, 2020). Recent research has revealed a high degree of connectivity between essential areas for many oceanic species, highlighting the existence of preferential migration corridors (Figure I.1; Johnson et al., 2022).

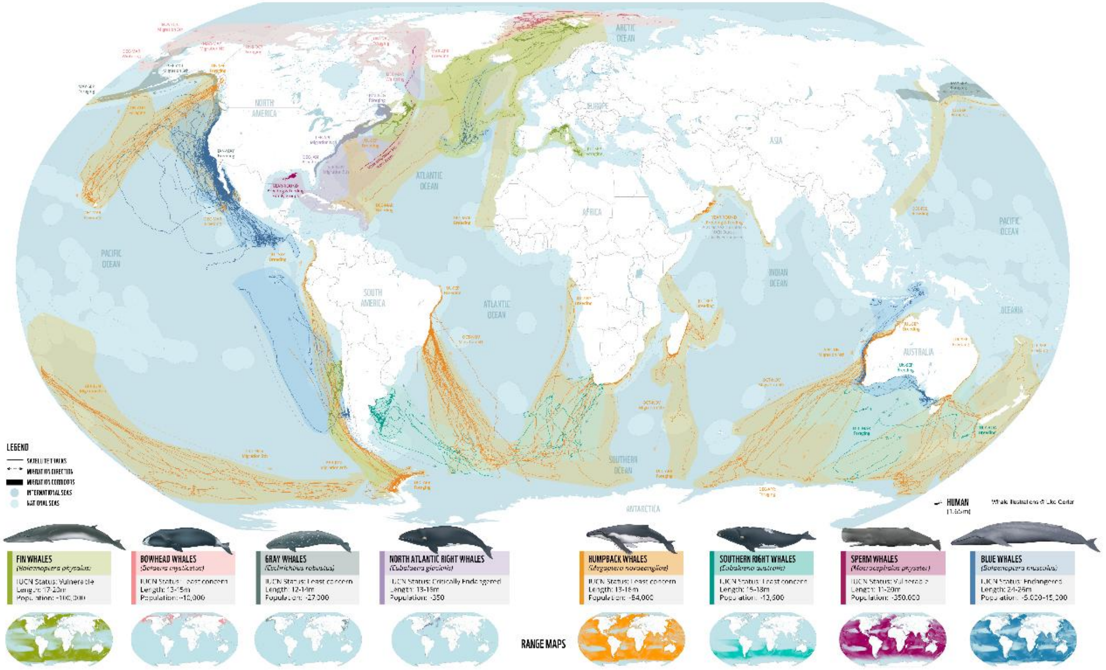

Figure I.1 Global view of blue corridors of migration for several species of whales obtained through satellite telemetry. These species of whales move among different but ecologically interconnected areas, in and out of international and national waters, conducting migrations essential to their survival. Image: Johnson et al. (2022).

Studying the biogeographical patterns of cetaceans presents multiple logistical and financial constraints, particularly for species that inhabit the vast and open oceans. Their high mobility in areas of difficult access and the long periods they spend underwater make the assessment of their presence and identification challenging, leading to knowledge gaps regarding both their contemporary and historical distributions (Alves, Queiroz and Jodice, 2023a). This impacts our understanding of their fundamental ecology, distribution, and abundance (LeDuc, 2018; Laran et al., 2024). Despite some marine areas being well-surveyed, most of the ocean lacks essential baseline data needed for a comprehensive understanding of species diversity and distribution patterns, such as population trends, ecological functions, and species interactions within marine communities (Kaschner et al., 2012; Estes et al., 2016; Correia et al., 2020). This is reflected in the conservation status of many oceanic cetacean species, according to the International Union of Conservation of Nature (IUCN) Red List, where most species are listed as "Data Deficient" (Figure I.2; Braulik et al., 2023).

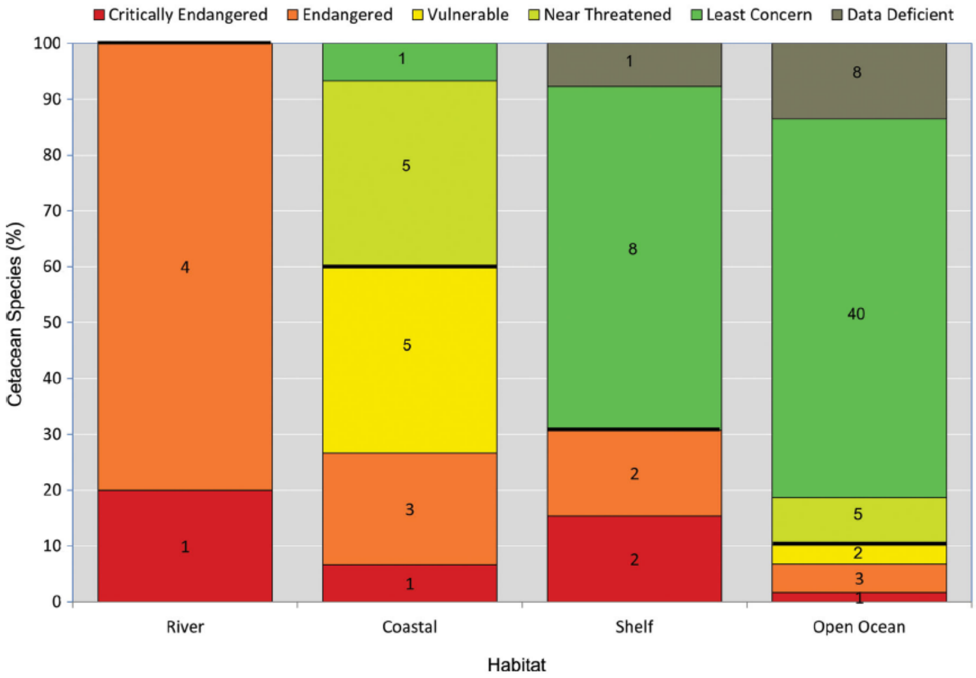

Figure I.2 Percentage of cetacean species in each International Union for the Conservation of Nature (IUCN) Red List category according to their primary habitat. Number in bars represent species numbers. Image: Braulik et al. (2023).

Understanding the spatiotemporal patterns of cetaceans is an important tool when addressing ecological and conservation issues (Parra, Corkeron and Marsh, 2006). Cetaceans, like many vertebrate taxa, can optimize resource utilization either by remaining within a general area or by returning to previously occupied regions, a behavior known as site fidelity (Greenwood, 1980). This behavior is believed to offer evolutionary advantages through familiarity, enhancing effective habitat use (Bose et al., 2017). Site fidelity is also linked to geographic structuring, suggesting that fidelity at fine scales may influence demography and population dynamics (Morrison and Bolger, 2012; van Beest et al., 2013; Bose et al., 2017).

The effects of these movement patterns on population dynamics are interconnected with the social structure of animal populations, which is a vital aspect influencing population growth, dispersal, and gene flow (Sutherland, 1998; Whitehead, 2009). Cognitively advanced mammals exhibit complex social structures that vary significantly within and between species (Costa and Fitzgerald, 1996) and are shaped by interactions and relationships, requiring detailed analysis of their content, quality, and temporal patterns (Hinde, 1976). Social organization, which includes the size and composition of social units, is influenced by factors such as sex, age, and kin relations, often requiring genetic analysis for precise descriptions (Kappeler, 2019). The variability in social structures across species and populations has profound implications for reproductive skew and genetic population structure (Koenig et al., 2013).

Research on cetacean species inhabiting mainly oceanic waters is facilitated in oceanic islands due to their unique geographical position and lack of or reduced shelf compared to continental coasts. This proximity to the pelagic realm facilitates the logistics of data collection, reducing the need for extensive maritime expeditions and allowing for more frequent and regular observations. Consequently, researchers can gather comprehensive data on various aspects of cetacean ecology (Baird et al., 2008a). Furthermore, oceanic islands significantly contribute to pelagic habitats by increasing biodiversity in their surrounding waters. This phenomenon, known as the "island-mass effect" (Doty and Oguri, 1956), arises from the disruption of oceanic currents due to the islands' topography, generating various oceanographic features, such as wakes and eddies (Caldeira et al., 2002), which play a crucial role in enhancing local and regional marine productivity (Barton et al., 2000; Fernandez et al., 2021).

Additionally, the type of platform used for data collection significantly impacts the volume of data gathered. Though ideal for obtaining detailed information, independent research vessels are expensive (Davidson et al., 2014). Consequently, the use of opportunistic platforms, such as large shipping vessels, ferries, cruise ships, and commercial tour vessels, has gained recognition as a viable alternative for scientific data collection over extensive regions (e.g., Evans and Hammond, 2004; Moura, Sillero and Rodrigues, 2012; Hupman et al., 2014; Correia et al., 2020). However, using opportunistic platforms introduces several limitations in data collection and interpretation due to inherent biases. These biases may originate from biological factors, platform constraints, observer variability, and platform-specific issues, such as prior knowledge of species locations or the absence of GPS tracking. Despite these challenges, studies have demonstrated that data collected from these platforms generally correspond with those obtained from independent research platforms conducted by experienced researchers using standardized methods (Hupman et al., 2014).

Trophic Ecology

As apex predators, cetaceans are pivotal in sustaining the structure and functional integrity of marine ecosystems through bottom-up and top-down processes (Roman et al., 2014; Estes et al., 2016; Martin et al., 2021). In bottom-up processes, cetaceans enhance nutrient cycling and primary productivity via several mechanisms, such as excretion and whale falls (Teixeira et al., 2022). Additionally, cetaceans significantly influence the trophic dynamics of marine ecosystems through direct predation and the induction of risk effects, characterizing the top-down processes that help regulate marine populations and ecological balance (Kiszka et al., 2015).

Information on the foraging ecology of cetaceans is crucial to better understand the diverse functional roles within ecosystems (Kiszka, Woodstock and Heithaus, 2022). The dietary ecology of cetaceans can be determined through various methods, with stomach content analysis being one of the most historically used. This traditional approach relies on the examination of the stomach contents of dead animals to identify consumed prey species. However, this method is often biased toward the individual’s last meal, which may not represent the overall diet, especially in by-caught or stranded specimens (Sekiguchi, Klages and Best, 1992; Gibbs, Harcourt and Kemper, 2011). Additionally, stomach content analysis tends to underrepresent soft-bodied or small prey that lacks distinguishable hard parts, such as otoliths or squid beaks, leading to over- or underestimation of the importance of specific prey species (Harvey and Antonelis, 1994; Bisi et al., 2013; Plint et al., 2023).

Stable isotope analysis uses naturally occurring stable isotopes to infer dietary information over longer time scales and from various tissue types, which can be collected from both live and dead animals (Ben-David and Flaherty, 2012; Teixeira et al., 2022). Several tissues may be used for this analysis, each exhibiting a specific turnover rate, which is the rate at which stable isotopes are incorporated into an organism's tissue (Figure I.3). Some of these tissues can be obtained from free-ranging individuals with small invasive techniques that do not require the individual's death for sampling, increasing the number of samples that can be obtained. Biopsy sampling is a commonly used technique in cetaceans to obtain skin and blubber tissue, to which most species exhibit only low to moderate levels of response and wounds that heal quickly with no signs of infection (Noren and Mocklin, 2012).

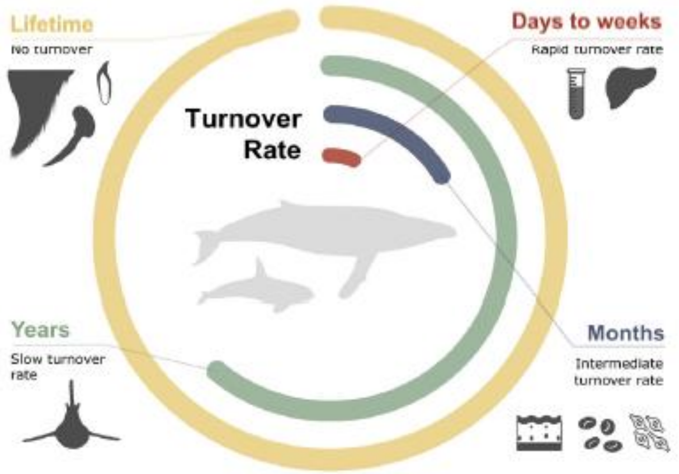

Figure I.3 Turnover rates differ between tissues. In cetaceans, these rates can range from a few days, such as in the liver (Tieszen et al., 1983), to months, as seen in skin and blubber (Abend & Smith, 1995; Giménez et al., 2016), to years in bone collagen (Dalerum and Angerbjörn, 2005), and even to a lifetime with no turnover, as in tooth dentin (Koch, 2007). Image: Teixeira et al. (2022).

Stable isotope analysis is based on the assumption that the isotopic composition of a consumer's tissues reflects the isotopic composition of its assimilated food sources, with minor differences due to diet-to-tissue discrimination factors (Gannes, O'Brien and del Rio, 1997; del Rio et al., 2009). The stable isotope ratios of carbon ($\delta^{13}C$: $^{13}C/^{12}C$) and nitrogen ($\delta^{15}N$: $^{15}N/^{14}N$) are the most used to analyze diet composition and trophic pathways (Park et al., 2018). In dietary analysis, there is a slight enrichment of the heavier isotope between producer/prey and consumer due to the preferential metabolism of lighter isotopic forms of carbon and nitrogen (DeNiro and Epstein, 1981; Post, 2002; McCutchan et al., 2003). The $\delta^{13}C$ ratio enrichment between trophic levels is generally small (0-1‰), which makes it insufficient for precise trophic level determination but useful for assessing diet, feeding habits, and habitat use (Cherel and Hobson, 2007; Torniainen et al., 2017). The $\delta^{15}N$ ratio, in contrast, increases by 3.4-3.8‰ with each trophic level, allowing for more accurate determination of trophic positions (Fry and Sherr, 1984; Hobson and Welch, 1992). This dual isotopic approach is typically visualized using biplots, representing the isotopic niche, and offers valuable ecological insights about the individual, population, or community represented (Jackson et al., 2011).

Although cetacean species occupy a variety of environments, their distributions often overlap despite different habitat requirements and foraging behaviors. To reduce interspecific competition, predators in the same habitat typically engage in resource partitioning by exploiting prey differently or segregating spatially or temporally (Peters et al., 2022). These strategies are reflected in their isotopic niches; however, it is important to note that while differences in isotopic signatures are informative, overlap in isotopic values does not necessarily indicate identical feeding habits or diets. Different prey species with similar isotopic values can produce comparable $\delta^{13}C$ and $\delta^{15}N$ isotope values in their consumers' tissues (Kiszka et al., 2010; Parra et al., 2022). Additionally, predator isotopic composition varies depending on the range of isotopic values and the relative proportions of ingested prey (Phillips, 2001; Newsome et al., 2007). Intrapopulation variability should also be considered, as generalist populations may consist of specialist individuals, leading to a wider range of isotopic values (Bolnick et al., 2002). This variability could also indicate the presence of different ecotypes of the same species with distinct feeding behaviors (de Bruyn, Tosh and Terauds, 2013).

Careful consideration should be given to the fact that, for highly mobile predators, bulk-tissue stable isotope ratios struggle to distinguish between diet differences, foraging regions, and types of organic sources at the food web's base. Unlike traditional methods, such as examining stomach contents, isotope analyses often cannot identify specific prey species unless they have distinct isotope values (Santos et al., 1999). However, stable isotope analyses offer significant advantages in studying cetacean foraging ecology, especially for examining large subsets of populations in their natural environment and providing information on feeding patterns over extended timescales (i.e., months vs. hours/days) (Guerra et al., 2020). This technique is particularly beneficial for offshore species, which rarely strand and often have empty stomachs when they do, or in regions where access to carcasses is challenging (Palacios, Salazar and Day, 2004; Barros and Clarke, 2009). Stable isotope analyses complement stomach content studies by providing a time-integrated view of assimilated prey, offering a more comprehensive understanding of cetacean diets (McCluskey et al., 2021).

Study Area

The Macaronesia region, located in the Eastern North Atlantic (figure I.4), is a complex system regarding its oceanographic and topographic features, including several archipelagos that emerged from deep waters and various seamounts. This region is influenced by the North Atlantic subtropical gyre, which encompasses the Canary Current, North Equatorial Current, and Azores Current. The North Atlantic subtropical gyre is bounded to the north by the Azores Front, which separates the anticyclonic eastern subtropical gyre from the cyclonic subpolar gyre, and to the south by the Cape Verde Frontal Zone, which separates the nutrient-rich South Atlantic Central Waters from the cooler North Atlantic Central Waters (Zenk, Klein and Schroder, 1991; Mason, 2009; Correia et al., 2020). The north-easterly trade winds drive the strong upwelling system off Northwest Africa with marked seasonality, extending their influence northward to the western Iberian Peninsula in summer and southward to Cape Verde in winter (Dave et al., 2015). This intricate oceanographic context, combined with diverse topography, creates a dynamic environment in Macaronesia where oceanic fronts, eddies, meanders, and filaments significantly influence the distribution of primary production and biomass across trophic levels, including top predators (Caldeira and Sangrà, 2012; Sala et al., 2013).

Although the definition of Macaronesia traditionally includes four archipelagos – Azores, Madeira, the Canaries, and Cape Verde –, several studies found no support for this classification on the marine realm and suggested the exclusion of the Cape Verde archipelago due to its high tropical affinity and endemisms (Spalding et al., 2007; Tuya and Haroun, 2009; Freitas et al., 2019;). Spalding et al. (2007) used the "Marine Ecoregions" concept and classified the Azores, Madeira, Selvagens, and Canary Islands as a single ecoregion within the Lusitanian province.

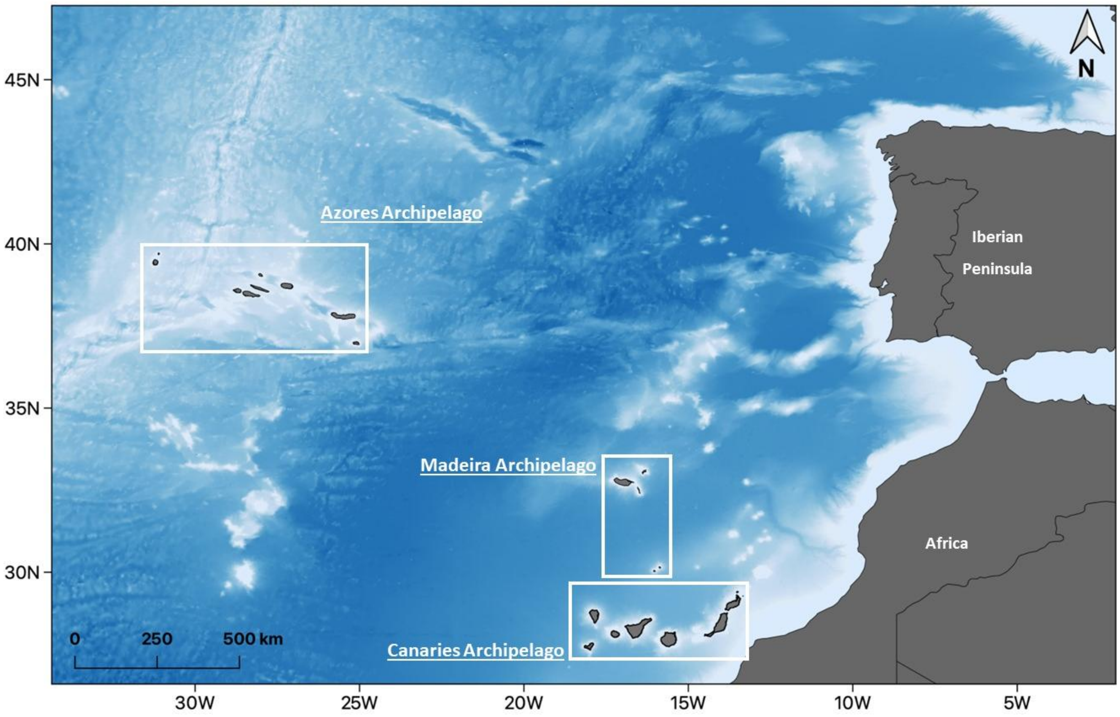

Figure I.4 Location of the study area, Macaronesia, in the Eastern North Atlantic, formed by the archipelagos of the Azores, Madeira, and the Canaries. Bathymetry ranging from approximately 1 000 to 4 000 m, from white to blue, respectively.

The geological age of Macaronesia's extant islands and islets ranges from less than 35 000 years for Alegranza in the Canary Islands to 25.7 million years for Selvagem Grande. However, seamounts around Madeira and the Canary Islands are as old as 67 million years (e.g., Gettysburg), which indicates that Macaronesia is at least twice or three times older than its oldest emerged land (Fernández-Palacios et al., 2015; Ávila et al., 2016). Furthermore, these islands show contrasting levels of geographical isolation from the mainland, varying from 96 km off North Africa (Fuerteventura, Canary Islands) to more than 1 500 km (Flores, Azores) off the Iberian Peninsula (Fernandez-Palacios, 2015).

Around 30 cetacean species inhabit and travel in these oceanic waters (Pérez-Vallazza et al., 2008; Carrillo et al., 2010; Freitas et al., 2012; Silva et al., 2014; Tobeña et al., 2016; Ferreira et al., 2017), making the region a hotspot of cetacean abundance and diversity and a crucial biological corridor for these species due to their significant dispersal capabilities.

Several studies have identified connectivity between populations in the Azores, Madeira, and the Canaries, some of which challenge the definition of site fidelity, such as the sighting in the Azores of a pod of short-finned pilot whales (*Globicephala macrorhynchus*) classified as residents in Madeira archipelago (Alves et al., 2018b). Matches of individuals of this species between Madeira and the Canaries have also been demonstrated (Figure I.5; Alves et al., 2019). Currently, the hypothesis of a preferential migratory corridor between Madeira Island and the most western islands of the Canaries is being investigated through satellite telemetry (Weyn et al., 2024). This species presents no genetic population differentiation within Macaronesia, suggesting the existence of a meta-population in this area (Alves et al., 2013; Miralles et al., 2016).

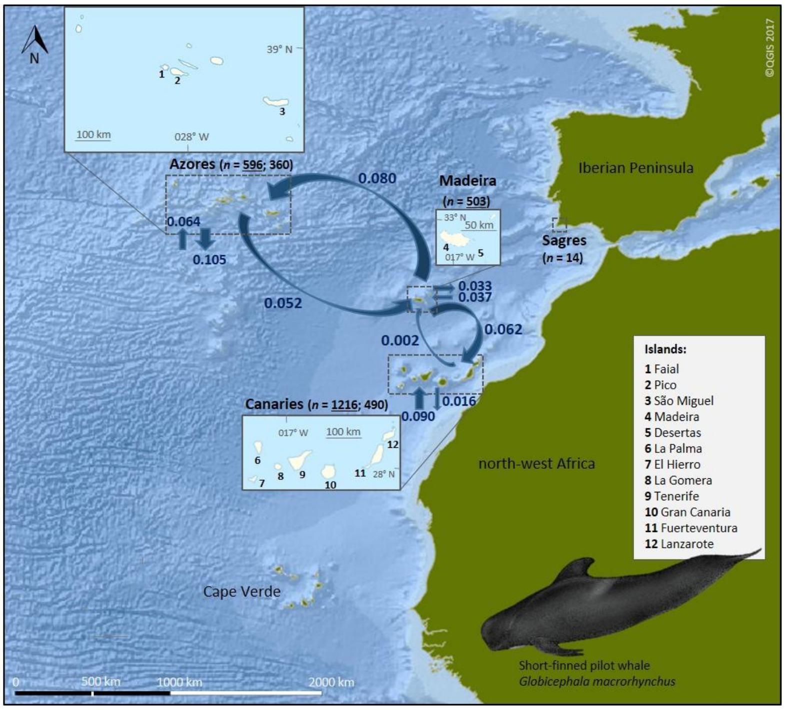

Figure I.5 Location of the areas analyzed in Alves et al. (2019) through photographic and sighting data. *n* (underlined and nonunderlined) indicates the number of catalogued individuals used for two separate analyses, while the arrows (widths and values) indicate transition probabilities between the areas. Image: Alves et al. (2019).

Connectivity patterns of common bottlenose dolphins (*Tursiops truncatus*) in this area were also identified. Although this species is highly abundant in shallower coastal waters, it extends over a wide range of depths and is frequently reported in the high seas (Silva et al., 2008; Dinis et al., 2016; Correia et al., 2020). Previous studies of pelagic bottlenose dolphin populations in the Northeastern Atlantic area suggested that these populations have a high gene flow and are genetically less differentiated, with the absence of fine-scale genetic structure (Quérouil et al., 2007; Fernández et al., 2011; Louis et al., 2014). Dinis et al. (2021) demonstrated movements of individuals between the archipelagos through photo-identification (Figure I.6), and island-associated groups / oceanic ecotypes may be part of a large population in the Eastern North Atlantic (Quérouil et al., 2007; Louis et al., 2014).

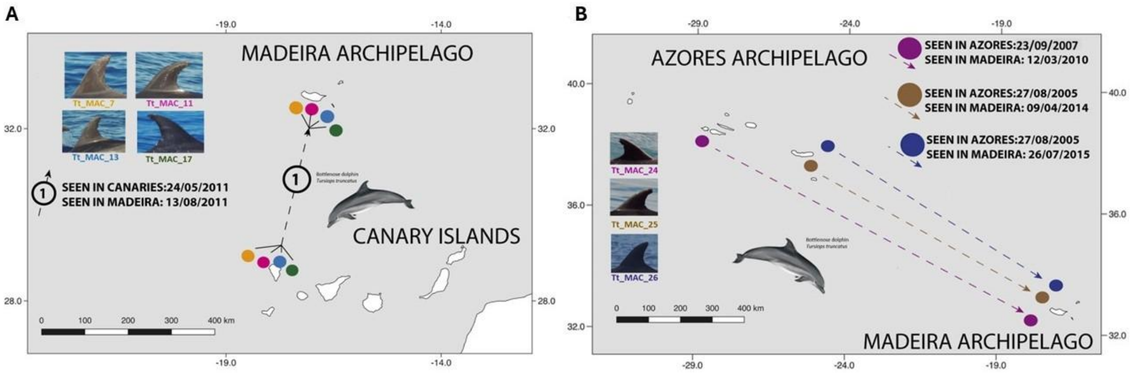

Figure I.6 Maps showing the movement of bottlenose dolphins between archipelagos. The dots are figurative and do not reflect the exact location of the individuals. Illustration by E. Berninsone © ARDITI. **(A)** Movements of four individuals between the island of La Palma, in the Canaries, and Madeira. **(B)** Movements of three individuals between the Azores (Pico and São Miguel Islands) and Madeira Archipelago. Image: Dinis et al. (2021).

Marine connectivity in smaller species of dolphins was also studied; however, due to the difficulty of photographically identifying species such as short-beaked common dolphins (*Delphinus delphis*) and Atlantic spotted dolphins (*Stenella frontalis*), only genetic studies were conducted. Quérouil et al. (2010) found no genetic difference between spotted and common dolphins of the Azores and Madeira, and therefore suggest they belong to the same populations.

Madeira Archipelago

This study has a particular focus on the Madeira Archipelago, which comprises three main islands and a series of islets, all of volcanic origin. This archipelago lies in a warm temperate latitude, approximately 1 000 km off the European continent and 500 km off the West African coast, and is characterized by a narrow shelf, steep submarine canyons, and deep waters (Geldmacher et al., 2000). The oceanographic patterns are influenced by the Portuguese, the Azores, and the Canary Currents, as well as by African filaments and regional dynamics (Caldeira et al., 2002; Caldeira & Sangrà, 2012; Sala et al., 2013). These oceanographic conditions lead to productive cyclonic eddies and fronts (Caldeira et al., 2002), resulting in high salinity, high temperature, and low-nutrient regime waters (Johnson and Stevens, 2000). The obstruction caused by a high mountain ridge (c. 1 800 m altitude) to the prevailing northeast trade winds (Tomczak and Godfrey, 1994) leads to calmer sea state conditions in the southern and southeastern waters of Madeira Island, where most of the data collection took place, in an area of approximately 800 km^2, up to 20 km off the coast (Alves et al., 2018a).

A high number of cetacean species use these waters, some of them regularly, with five species being present between approximately 25% and 50% of the year: the Atlantic spotted dolphin, the bottlenose dolphin, the short-beaked common dolphin, Bryde's whale, and the short-finned pilot whale (Alves et al., 2018a). Madeira Archipelago is also a calving ground for many species, with the observation of births and/or neonates in Atlantic spotted dolphins (Alves et al., 2015), short-finned pilot whales (Reggente et al., 2016), Bryde's whale (Rita Ferreira, personal communication), sperm whales (Correia-Fagundes & Romano, 2013) and minke whales (Rita Ferreira, personal communication). Other vital activities, such as feeding, resting, and socializing, were also recorded for several other species, supporting the importance of these waters for the life cycle of cetaceans (Alves et al., 2018a).

This study has a particular focus on three species of cetaceans: the Bryde's whale, sperm whale and Blainville's beaked whale.

Bryde’s Whale

Bryde's whale (*Balaenoptera edeni*) is one of the least known species of large mysticetes, and consensus on the number of species or subspecies, as well as the correct nomenclature for each, is yet to be established (Rice and SMM, 1998; Kato and Perrin, 2018). The recent identification of two new species that used to be classified as *B. edeni*, Omura's whale *Balaenoptera omurai* (Wada, Oishi and Yamada, 2003) and Rice's whale *Balaenoptera ricei* (Rosel et al., 2021), only adds to the evidence of the doubts that remain regarding the systematics of Bryde's whale. Although globally, this species has an IUCN status of "Least Concern" (Cooke and Brownell, 2018), in the Madeira Archipelago, it presents a regional "Vulnerable" status (Gauffier and Freitas, 2023).

Its occurrence has been reported from all tropical and temperate waters in the North and South Pacific, Indian Ocean, and South and North Atlantic between 40°N and 40°S. Bryde's whales do not undertake the long-range seasonal migrations typically associated with most other baleen whales. Still, they may travel widely throughout ocean basins as they move through tropical and warm-temperate waters (Kato and Perrin, 2018; Freitas and Penry, 2021). This may be related to Bryde's whales having undefined or disparate reproductive cycles and feeding intensively and opportunistically throughout the year. These characteristics, unusual for baleen whales, lessen the need for these animals to migrate to particular feeding or breeding areas (Best, 1977; Kato and Perrin, 2018). Although oceanographic, physical, and biological variables influence Bryde's whales' movements, it is not possible to identify patterns across populations (Corkeron et al., 2011; Weir, MacLeod and Pierce, 2012; Tardin et al., 2017). Nevertheless, studies show that prey dynamics seem to be one of this species' main drivers of movement (Thershy, 1992; Zerbini et al., 1997; Wiseman et al., 2011). Bryde's whales are considered opportunistic feeders, mainly of pelagic schooling fishes such as pilchard, anchovy, sardine, mackerel, herring, and others (Kato and Perrin, 2008).

In the Madeira Archipelago, Bryde's whales were first identified in 2003 (Freitas et al., 2012). However, they may have been present before and gone unnoticed due to their similarity to sei whales (*Balaenoptera borealis*), from which they can only be distinguished with a good view of the head – Bryde's whales present three longitudinal ridges on the rostrum, while sei whales present only one. The species is present in the area mainly during Summer and Autumn, from June to November, and is usually seen alone or in pairs, often of mother and calf, although long-term associations between adults have been recorded (Alves et al., 2010; Alves et al., 2018a; Fernandez et al., 2021). Madeira Archipelago seems to be an essential area for the species, where they have been recorded displaying vital activities such as feeding, resting, and calving, with 15% of the sightings including calves (Alves et al., 2018a). Despite presenting a high occurrence rate, this species presents a very high interannual variation, which has also been reported for the Canaries (Ritter and Newmann, 2006; Alves et al., 2018a). This species was first recorded in the Azores in 2004 (Steiner et al., 2008). Bryde's whales seem to move sequentially between the archipelagos of Macaronesia, being seen more frequently at the beginning of the year in the Canaries, in the middle of the year in Madeira and Azores, and at the end of the year in Madeira and the Canaries again (Freitas, 2024).

Sperm Whale

The sperm whale (*Physeter macrocephalus*), the largest of the odontocetes, exhibits a global distribution, inhabiting all the world's oceans and ranging over thousands of kilometers (Whitehead, 2018; Cantor et al., 2019). Sperm whales are classified as "Endangered" by the IUCN (Taylor et al., 2019), with their populations still slowly recovering from whaling, which caused an estimated 57% decline. Currently, the population is estimated at 850 000 individuals (Whitehead and Shin, 2022).

Sperm whales are deep divers, and although they can be considered generalist foragers, consuming a wide variety of fish and cephalopods, their preferred prey are gelatinous cephalopods from the Histioteuthidae family, with males showing a greater variation in foraging strategies (Clarke, 1980; Cantor et al., 2019).

There are distinct sexual differences in the distribution of sperm whales. Mature females, their calves, and immature whales of both sexes live in matrilineal social groups in warm temperate to tropical waters, maintaining long-term associations and regional ranging patterns. As males mature, they leave these groups to form bachelor groups in temperate and polar waters. Upon reaching sexual and social maturity, males typically live solitary or in small groups, periodically returning to warmer waters to mate (Whitehead, 2018). Studies have documented individual whale movements within warm habitats (e.g., Gero et al., 2007; Whitehead et al., 2008) and the extensive movement patterns of males, primarily in the Atlantic (e.g., Mullin et al., 2022; Steiner et al., 2012). Atlantic populations form smaller groups, consisting of 5-18 individuals, with a higher calves prevalence than the Pacific (Gero et al., 2007). Females show fidelity to coastal basins on both sides of the Atlantic, while males migrate across these regions for breeding (Engelhaupt et al., 2009).

In Macaronesia, this species is common in the waters surrounding the archipelagos (Carrillo et al., 2010; Freitas et al., 2012; Silva et al., 2014) and moves regularly between them (Steiner et al., 2015). Sperm whales in the North Atlantic are considered a single stock (Pinela et al., 2009), and there is no apparent connection between female groups within the west and east North Atlantic Ocean (Alexander et al., 2016), as well as with the Mediterranean Sea (Violi et al., 2023). In the Canaries, there is a high mortality of this species associated with ship strikes, with at least two sperm whales killed per year (Carrillo and Ritter, 2010), which could be causing a decrease in the Macaronesian population since it likely exceeds the reproduction rate of this population (Fais et al., 2016).

In the Madeira Archipelago, sperm whales were first recorded in the logbooks of American whaleships between 1761 and 1920 (Townsend, 1935). Shore-based whaling began in 1941 and continued until the 1980s (Freitas et al., 2012). Presently, they are a frequently sighted species in the archipelago, with group sizes varying between 1 and 30 individuals and calves present in 25% of the groups (Alves et al., 2018a). Although they are present throughout the year, Fernandez et al. (2021) demonstrated a preference for water temperatures around 23˚C, which occur from June to November, with a preference for waters deeper than 1 000 m in the proximity of submarine canyons areas. Their habitat extends towards the open ocean and reaches middle latitudes (Correia et al., 2015).

Blainville’s Beaked Whale

Blainville's beaked whales *Mesoplodon densirostris* belong to the family Ziphiidae, the second largest in cetaceans, which represent around one-quarter of all existing species of cetaceans. Nonetheless, it is among the least studied due to its cryptic biology, deep dives, and remote offshore habitat (Li and Rosso, 2021; Feyer, Stanistreet and Moors-Murphy, 2024). This species is thought to be the most widely distributed *Mesoplodon* species, with a continuous distribution throughout the tropical, sub-tropical, and warm-temperate waters of the world's oceans, with occasional occurrences in cold-temperate areas (MacLeod and Zuur, 2005; MacLeod et al., 2006), except in the Mediterranean Sea (Mead, 1989). In the Eastern North Atlantic, they range from Iceland to the Canaries (Mead, 1989; Ritter and Brederlau, 1999).

Blainville's beaked whales are deep divers, with foraging dives recorded to depths between 1 500 and 2 000 meters and up to 90 minutes long (Baird et al., 2008b). They prey on mesopelagic and deep-water benthic cephalopods and fish (Clarke, 1996), in areas of complex topography (Whitehead et al., 1997).

Historically, most biological information collected on beaked whales is through stranded individuals (Pitman, 2018). Over the last two decades, prompted by mass strandings and a recognition of the adverse effects of military sonar, expanding research efforts and long-term studies have increased our knowledge of beaked whale populations around the world (Hooker et al., 2019). Despite that, ecological data have only been collected in a few areas worldwide, such as the Bahamas, Hawai'i, and the Canary Islands (Shallenberger, 1981; Mead, 1989; Claridge and Balcomb, 1995; Carrillo and Lopez-Jurado, 1998; Macleod, 2000; Aguilar de Soto et al., 2011).

Blainville's beaked whales live in apparently small populations with site fidelity (McSweeney et al., 2007; Baird et al., 2009), forming small groups that often dive synchronously and reappear synchronously at the surface even after long foraging dives (Aguilar de Soto, 2006; Claridge, 2006). Despite the scarce information regarding the social organization of Blainville's beaked whale, this species appears to exhibit female defense polygyny, with a social group of females accompanied by one male who may deny access to the group by other males, and intermale combat is thought to produce the extensive scarring on adult males (Mead, 1989; MacLeod, 1998; Claridge, 2006; McSweeney et al., 2007; Alves et al., 2023b).

The Blainville's beaked whale was first described in the Madeira Archipelago in 1917 (Harmer, 1924), and nowadays it is the most frequently sighted species of beaked whale in the area, using these waters for vital activities and being sighted with calves on more than 40% of the sightings (Alves et al., 2018a). Dinis et al. (2017) conducted the only dedicated research of this species in this area and suggested long-term site fidelity for some individuals, mainly adult females, with some degree of association among them. Fernandez et al. (2021) identified good habitat suitability for Blainville's beaked whales in the Madeira Archipelago, supporting the high site fidelity patterns.

List of Scientific Publications

In peer-reviewed journals, included within the thesis:

- **Chapter II:**

Rita Ferreira, Ana Dinis, Anja Badenas, Annalisa Sambolino, Jacobo Marrero-Pérez, Ana Crespo, and Filipe Alves. 2021. "Bryde's whales in the North-East Atlantic: New insights on site fidelity and connectivity between oceanic archipelagos". *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31(10), 2938-2950. https://doi.org/10.1002/aqc.3665

As the leading author of this publication, I conceptualized the study, conducted fieldwork, analyzed the data, produced the visualizations, composed the initial manuscript, and conducted the reviews and edits.

- **Chapter III:**

Rita Ferreira, Lisa Steiner, Vidal Martín, Francesca Fusar Poli, Ana Dinis, Manfred Kaufmann, Marc Fernandez, and Filipe Alves. 2022. "Unraveling site fidelity and residency patterns of sperm whales in the insular oceanic waters of Macaronesia". *Frontiers in Marine Science,* 9, 1021635. https://doi.org/10.3389/fmars.2022.1021635

As the leading author of this publication, I conceptualized the study, conducted fieldwork, analyzed the data, produced the visualizations, composed the initial manuscript, and conducted the reviews and edits.

- **Chapter IV:**

Anja Badenas, Ana Dinis, Rita Ferreira, Annalisa Sambolino, Eliette Hamard, Leonardo Berninsone, Marc Fernandez, and Filipe Alves. 2022. "Behavioural ecology traits of elusive deep-diver whales unravel a complex social structure influenced by female philopatry and defence polygyny". *Frontiers in Marine Science*, 9, 809902. https://doi.org/10.3389/fmars.2022.809902

As a co-author, I contributed to data collection and organization, assisted with the methodologies, and reviewed and edited the final manuscript.

Submitted manuscript, included within the thesis:

- **Chapter V:**

Rita Ferreira, Ester Dias, Manfred Kaufmann, Marc Fernandez, and Filipe Alves. "Revealing trophic interactions among sympatric odontocetes with oceanic ecosystem traits". Submitted to Journal of Zoology.

Published in July 2025 with the following DOI: 10.1111/jzo.70053

As the leading author of this publication, I co-conceptualized the study, conducted fieldwork, analyzed the data, produced the visualizations, composed the initial manuscript, and conducted the reviews and edits.

References

Abend, Alan G., and Tim D. Smith. 1995. "Differences in Ratios of Stable Isotopes of Nitrogen in Long-Finned Pilot Whales (*Globicephala melas*) in the Western and Eastern North Atlantic". *ICES Journal of Marine Science*, 52, 837–841. https://doi.org/10.1006/jmsc.1995.0080

Aguilar De Soto, Natacha, Peter T. Madsen, Peter Tyack, Patricia Arranz, Jacobo Marrero, Andrea Fais, Eletta Revelli, and Mark Johnson. 2011. "No Shallow Talk: Cryptic Strategy in the Vocal Communication of Blainville's Beaked Whales". *Marine Mammal Science*, 28(2), 75-92. https://doi.org/10.1111/j.1748-7692.2011.00495.x

Alexander, Alana, Debbie Steel, Kendra Hoekzema, Sarah L. Mesnick, Daniel Engelhaupt, Iain Kerr, Roger Payne, and C. Scott Baker. 2016. "What Influences the Worldwide Genetic Structure of Sperm Whales (*Physeter macrocephalus*)?". *Molecular Ecology*, 25(12), 2754-2772. https://doi.org/10.1111/mec.13638

Alves, Filipe, Ana Dinis, Irma Cascão, and Luís Freitas. 2010. "Bryde's Whale (*Balaenoptera brydei*) Stable Associations and Dive Profiles: New Insights into Foraging Behavior". *Marine Mammal Science*, 26(1), 202-212. https://doi.org/10.1111/j.1748-7692.2009.00333.x

Alves, Filipe, Anita Alessandrini, Antonella Servidio, Ana Sofia Mendonça, Karin L. Hartman, Rui Prieto, Simon Berrow, et al. 2019. "Complex Biogeographical Patterns Support an Ecological Connectivity Network of a Large Marine Predator in the Northeast Atlantic". *Diversity and Distributions*, 25(2), 269–284. https://doi.org/10.1111/ddi.12848

Alves, Filipe, Anita Alessandrini, Marc Fernandez, Karin L. Hartman, and Ana Dinis. 2018a. "Home Sweet Home? Wide-Ranging Movements of Socially Stable Resident Delphinids (*Globicephala macrorhynchus*)". *Revista Scientia Insularum*, 1, 37-49. https://doi.org/10.25145/j.SI.2018.01.004

Alves, Filipe, Cátia Nicolau, Ana Dinis, Claúdia Ribeiro, and Luis Freitas. 2015. "Supportive Behavior of Free-Ranging Atlantic Spotted Dolphins (*Stenella frontalis*) Toward Dead Neonates, with Data on Perinatal Mortality". *Acta Ethologica*, 18, 301–304. https://doi.org/10.1007/s10211-014-0210-8.

Alves, Filipe, Nuno Queiroz, and Patrick G. R. Jodice. 2023a. "Editorial: Ecological and Behavioral Traits of Apex Predators in Oceanic Insular Ecosystems: Advances and Challenges in Research and Conservation". *Frontiers in Marine Science*, 10:1252360. https://doi.org/10.3389/fmars.2023.1252360

Alves, Filipe, Rita Ferreira, Miguel Fernandes, Zofia Halicka, Luís Dias, and Ana Dinis. 2018b. "Analysis of Occurrence Patterns and Biological Factors of Cetaceans Based on Long-Term and Fine-Scale Data from Platforms of Opportunity: Madeira Island as a Case Study". *Marine Ecology*, 39(2), e12499. https://doi.org/10.1111/maec.12499

Alves, Filipe, Sarah L. Mesnick, Massimiliano Rosso, and Robert L. Pitman. 2023b. "Beaked Whale Sexual Dimorphism, Mating Strategies, and Diversification". In *Sex in Cetaceans*. Edited by Bernd Würsig, and Dara N. Orbach, 385-413. Springer eBooks. https://doi.org/10.1007/978-3-031-35651-3

Alves, Filipe, Sophie Quérouil, Ana Dinis, Cátia Nicolau, Cláudia Ribeiro, Luís Freitas, Manfred Kaufmann, and Caterina Fortuna. 2013. "Population Structure of Short-Finned Pilot Whales in the Oceanic Archipelago of Madeira Based on Photo-Identification and Genetic Analyses: Implications for Conservation". *Aquatic Conservation: Marine and Freshwater Ecosystems*, 23, 758–776. https://doi.org/10.1002/aqc.2332

Ávila, Sérgio P., Carlos Melo, Björn Berning, Ricardo Cordeiro, Bernard Landau, and Carlos Marques da Silva. 2016. "*Persististrombus coronatus* (Mollusca: Strombidae) in the Early Pliocene of Santa Maria Island (Azores: NE Atlantic): Palaeoecology, Palaeoclimatology and Palaeobiogeographic Implications on the NE Atlantic Molluscan Biogeographical Provinces". *Palaeogeography, Palaeoclimatology, Palaeoecology*, 441, 912–923. https://doi.org/10.1016/j.palaeo.2015.10.043

Baird, Robin W., Daniel L. Webster, Gregory S. Schorr, Daniel J. McSweeney, and Jay Barlow. 2008b. "Diel Variation in Beaked Whale Diving Behavior". *Marine Mammal Science*, 24(3), 630-642. https://doi.org/10.1111/j.1748-7692.2008.00211.x

Baird, Robin W., Daniel L. Webster, Sabre D. Mahaffy, Daniel J. McSweeney, Gregory S. Schorr, and Allan D. Ligon. 2008a. "Site fidelity and association patterns in a deep-water dolphin: Rough-toothed dolphins (*Steno bredanensis*) in the Hawaiian Archipelago". *Marine Mammal Science*, 24(3), 535-553. https://doi.org/10.1111/j.1748-7692.2008.00201.x

Baird, Robin W., Sabre D. Mahaffy, Daniel L. Webster, Jay Barlow, M. Bradley Hanson, Jason P. Turner, and Russel D. Andrews. 2009. "Studies of Beaked Whales in Hawaii: Population Size, Movements, Trophic Ecology, Social Organization and Behavior". *ECS Special Publication Series*, 51, 23–25.

Bannister, John L. 2018. "Baleen whales (Mysticeti)". In *Encyclopedia of Marine Mammals*, 3rd Edition. Edited by Bernd Würsig, J. G. M. Thewissen and Kit M. Kovacs 62-69. London, UK: Academic Press.

Barros, Nélio B., and Malcom R. Clarke. 2009. "Diet". In *Encyclopedia of Marine Mammals*, 2nd Edition. Edited by Bernd Würsig, William Perrin, J.G.M. Thewissen, 311-316. London, UK: Academic Press.

Barton, Eric D., Gotzon Basterretxea, Pierre Flament, E. Gay Mitchelson-Jacob, Bethan Jones, Javier Arístegui, and Felix Herrera. 2000. "Lee Region of Gran Canaria". *Journal of Geophysical Research,* 105, 17173–17193. https://doi.org/10.1029/2000jc900010

Ben-David, Merav, and Elizabeth A. Flaherty. 2012. "Stable Isotopes in Mammalian Research: A Beginner's Guide". *Journal of Mammalogy*, 93(2), 312-328. https://doi.org/10.1644/11-MAMM-S-166.1

Best, Peter B. 1977. "Two Allopatric Forms of Bryde's Whale off South Africa". *Reports of the International Whaling Commission, Special Issue,* 1, 10–38.

Bilgmann, Kerstin, Guido J. Parra, and Luciana M. Möller. 2018. "Occurrence, Distribution and Abundance of Cetaceans off the Western Eyre Peninsula in the Great Australian Bight". *Deep Sea Research. Part II, Topical Studies in Oceanography*, 134-145. https://doi.org/10.1016/j.dsr2.2017.11.006

Bisi, Tatiana Lemos, Paulo Renato Dorneles, José Lailson-Brito, Gilles Lepoint, Alexandre de Freitas Azevedo, et al. 2013. "Trophic Relationships and Habitat Preferences of Delphinids from the Southeastern Brazilian Coast Determined by Carbon and Nitrogen Stable Isotope Composition". *PLoS One*, 8(12), e82205. https://doi.org/10.1371/journal.pone.0082205

Bolnick, Daniel I., Louie H. Yang, James A. Fordyce, Jeremy M. Davis, and Richard Svanbäck. 2002. "Measuring Individual-Level Resource Specialization". *Ecology*, 83(10), 2936–2941. https://doi.org/10.1890/0012-9658(2002)083[2936:MILRS]2.0.CO;2

Bose, Samhita, Tavis D. Forrester, Jennifer L. Brazeal, Benjamin N. Sacks, David S. Casady, and Heiko U. Wittmer. 2017. "Implications of Fidelity and Philopatry for the Population Structure of Female Black-Tailed Deer". *Behavioral Ecology*, 28(4), 983-990. https://doi.org/10.1093/beheco/arx047

Bräger, Stefan, and Zsuzsanna Bräger. 2019. "Movement Patterns of Odontocetes Through Space and Time". In *Ethology and Behavioral Ecology of Odontocetes.* Edited by Bernd Würsig, 117-143. Springer Nature Switzerland AG. https://doi.org/10.1007/978-3-030-16663-2

Braulik, Gill T., Barbara L. Taylor, Gianna Minton, Giuseppe Notarbartolo Di Sciara, Tim Collins, Lorenzo Rojas-Bracho, Enrique A. Crespo, et al. 2023. "Red-List Status and Extinction Risk of the World's Whales, Dolphins, and Porpoises". *Conservation Biology*, 37(5), e14090. https://doi.org/10.1111/cobi.14090

Caldeira, Rui M. A., and Pablo Sangrà. 2012. "Complex Geophysical Wake Flows. Madeira Archipelago Case Study". *Ocean Dynamics*, 62, 683–700. https://doi.org/10.1007/s10236-012-0528-6

Caldeira, Rui M. A., S. Groom, P. Miller, D. Pilgrim, and N. P. Nezlin. 2002. "Seasurface Signatures of the Island Mass Effect Phenomena around Madeira Island, Northeast Atlantic". *Remote Sensing of Environment*, 80, 336–360. https://doi.org/10.1016/s0034-4257(01)00316-9

Cantor, Mauricio, Shane Gero, Hal Whitehead, and Luke Rendell. 2019. "Sperm Whale: The Largest Toothed Creature on Earth". In *Ethology and Behavioral Ecology of Marine Mammals*. Edited by Bernd Würsig, 261–80. Springer Nature Switzerland AG. https://doi.org/10.1007/978-3-030-16663-2

Carrillo, Manuel, Claudia Pérez-Vallazza, and Rosana Álvarez-Vázquez. 2010. "Cetacean Diversity and Distribution off Tenerife (Canary Islands)". *Marine Biodiversity Records*, 3. https://doi.org/10.1017/s1755267210000801

Carrillo, Manuel, and Fabian Ritter. 2010. "Increasing Numbers of Ship Strikes in the Canary Islands: Proposals for Immediate Action to Reduce Risk of Vessel-Whale Collisions". *Journal of Cetacean Research and Management*, 11, 131–138. https://doi.org/10.47536/jcrm.v11i2.618

Carrillo, Manuel, and L. F. López-Jurado. 1998. "Structure and Behaviour of a Blainville's beaked whale (*Mesoplodon densirostris*) group in Tenerife (Canary Islands)". The World Marine Mammal Science Conference, Monaco, January.

Cherel, Yves, and Keith A. Hobson. 2007. "Geographical Variation in Carbon Stable Isotope Signatures of Marine Predators: a Tool to Investigate their Foraging Areas in the Southern Ocean". *Marine Ecology Progress Series*, 329, 281–287. https://doi.org/10.3354/meps329281

Claridge, Diane E. 2006. “Social Structure of Blainville’s Beaked Whale in Bahamas”. M.Sc. thesis, University of Aberdeen, Aberdeen, Scotland.

Claridge, Diane E., and K. C. Balcomb. 1995. “Photo-identification of Dense-Beaked Whales (*Mesoplodon densirostris*) in the North-Eastern Bahamas”. 11th Biennial Conference on the Biology of Marine Mammals, Orlando, USA, December.

Clarke, Malcom R. 1980. “Cephalopods in the Diet of sperm whales of the Southern Hemisphere and their Bearing on Sperm Whale Biology”. *Discovery Reports*, 37, 1–324.

Clarke, Malcom R. 1996. “Cephalopods as Prey. III. Cetaceans”. *Philosophical Transactions of the Royal Society,* 351, 1053-1063.

Cooke, J.G., and R. L. Brownell Jr. 2018. *Balaenoptera edeni*. The IUCN Red List of Threatened Species 2018: e.T2476A50349178. https://dx.doi.org/10.2305/IUCN.UK.2018-1.RLTS.T2476A50349178.en

Corkeron, P. J., G. Minton, T. Collins, K. Findlay, A. Wilson, and R. Baldwin. 2011. “Spatial Models of Sparse Data to Inform Cetacean Conservation Planning: an Example from Oman”. *Endangered Species Research*, 15, 39–52. https://doi.org/10.3354/esr00367

Correia, Ana Mafalda, Ágatha Gil, Raul Valente, Massimiliano Rosso, Isabel Sousa-Pinto, and Graham John Pierce. 2020. “Distribution of Cetacean Species at a Large Scale: Connecting Continents with the Macaronesian Archipelagos in the Eastern North Atlantic”. *Diversity and Distributions*, 26(10), 1234-1247. https://doi.org/10.1111/ddi.13127

Correia, Ana Mafalda, Paola Tepsich, Massimiliano Rosso, Rui Caldeira, and Isabel Sousa-Pinto. 2015. “Cetacean Occurrence and Spatial Distribution: Habitat Modelling for Offshore Waters in the Portuguese EEZ (NE Atlantic)”. *Journal of Marine Systems*, 143, 73–85. https://doi.org/10.1016/j.jmarsys.2014.10.016

Correia-Fagundes, Catarina, and Hugo Romano. 2013. “Observation of a Birth of a Sperm Whale *Physeter macrocephalus* at Madeira (NE Atlantic)”. *Bocagiana*, 236, 1–3.

Costa, James T., and Terrence D. Fitzgerald. 1996. “Developments in Social Terminology: Semantic Battles in a Conceptual War”. *Trends in Ecology & Evolution*, 11, 285–289. https://doi.org/10.1016/0169-5347(96)10035-5

Dalerum, F., A. Angerbjörn. 2005. “Resolving Temporal Variation in Vertebrate Diets using Naturally occurring Stable Isotopes”. *Oecologia*, 144, 647–658. https://doi.org/10.1007/s00442-005-0118-0

Dave, Apurva C., Andrew D. Barton, M. Susan Lozier, and Galen A. McKinley. 2015. “What Drives Seasonal Change in Oligotrophic Area in the Subtropical North Atlantic?”. *Journal of Geophysical Research: Oceans*, 120, 3958–3969. https://doi.org/10.1002/2015jc010787

Davidson, E.H., Jens Currie, Stephanie Stack, Greg Kaufman, and Emmanuelle Martinez. 2014. “Whale and Dolphin Tracker, a Web-Application for Recording Cetacean Sighting Data in Real-Time: Example Using Opportunistic Observations Reported in 2013 from Tour Vessels off Maui, Hawaii”. *Report to the International Whaling Commission,* 65b, 1–17.

De Bruyn, P. J. N., Cheryl A. Tosh, and Aleks Terauds. 2013. “Killer Whale Ecotypes: Is There a Global Model?”. *Biological Reviews of the Cambridge Philosophical Society,* 88(1), 62–80. https://doi.org/10.1111/j.1469-185X.2012.00239.x

DeNiro, Michael J., and Samuel Epstein. 1981. “Influence of Diet on the Distribution of Nitrogen Isotopes in Animals”. *Geochimica Et Cosmochimica Acta*, 45, 341–351. https://doi.org/10.1016/0016-7037(81)90244-1

del Rio, Carlos Martínez, Nathan Wolf, Scott A. Carleton, and Leonard Z. Gannes. 2009. “Isotopic Ecology Ten Years After a Call for More Laboratory Experiments”. *Biological Reviews of the Cambridge Philosophical Society*, 84(1), 91–111. https://doi.org/10.1111/j.1469-185x.2008.00064.x

Dinis, Ana, Carlota Molina, Marta Tobeña, Annalisa Sambolino, Karin Hartman, Marc Fernandez, Sara Magalhães. 2021. “Large-scale Movements of Common Bottlenose Dolphins in the Atlantic: Dolphins with an International Courtyard”. *PeerJ*, 9:e11069. https://doi.org/10.7717/peerj.11069

Dinis, Ana, Filipe Alves, Cátia Nicolau, Claúdia Ribeiro, Manfred Kaufmann, Ana Cañadas, and Luis Freitas. 2016. “Bottlenose dolphin *Tursiops truncatus* group Dynamics, Site Fidelity, Residency and Movement Patterns in the Madeira Archipelago (North-East Atlantic)”. *African Journal of Marine Science*, 38(2), 151–160. https://doi.org/10.2989/1814232x.2016.1167780

Dinis, Ana, Raquel Marques, Luís Dias, Dinarte Sousa, Claudia Gomes, Nicolau Abreu, and Filipe Alves. 2017. “Site Fidelity of Blainville’s Beaked Whale (*Mesoplodon densirostris*) off Madeira Island (Northeast Atlantic)”. *Aquatic Mammals,* 43(4), 387–90. https://doi.org/10.1578/am.43.4.2017.387

Doty, M. S., and M. Oguri. 1956. “The Island Mass Effect”. *ICES Journal of Marine Science,* 22, 33–37. https://doi.org/10.1093/icesjms/22.1.33

Engelhaupt, Daniel, A. Rus Hoelzel, Colin Nicholson, Alexandros Frantzis, Sarah Mesnick, Shane Gero, Hal Whitehead, et al. 2009. “Female Philopatry in Coastal Basins and Male Dispersion Across the North Atlantic in a Highly Mobile Marine Species, the Sperm Whale (*Physeter macrocephalus*)”. *Molecular Ecology*, 18(20), 4193-4205. https://doi.org/10.1111/j.1365-294X.2009.04355.x

Estes, James A., Michael Heithaus, Douglas J. McCauley, Douglas B. Rasher, and Boris Worm. 2016. “Megafaunal Impacts on Structure and Function of Ocean Ecosystems”. *Annual Review of Environment and Resources*, 41(1), 83-116. https://doi.org/10.1146/annurev-environ-110615-085622

Evans, Peter G. H., and Philip S. Hammond. 2004. “Monitoring Cetaceans in European Waters”. *Mammal Review*, 34: 131–156. https://doi.org/10.1046/j.0305-1838.2003.00027.x

Fais, Andrea, Tim P. Lewis, Daniel P. Zitterbart, Omar Álvarez, Ana Tejedor, and Natacha Aguilar De Soto. 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. https://doi.org/10.1371/journal.pone.0150660

Fernandez, Marc, Filipe Alves, Rita Ferreira, Jan-Christopher Fischer, Paula Thake, Nuno Nunes, Rui Caldeira, and Ana Dinis. 2021. “Modeling Fine-Scale Cetaceans’ Distributions in Oceanic Islands: Madeira Archipelago as a Case Study”. *Frontiers in Marine Science,* 8. https://doi.org/10.3389/fmars.2021.688248

Fernández, Ruth, M. Begoña Santos, Graham John Pierce, Ángela Llavona, Alfredo López, Mónica A. Silva, Manuel Carrillo, et al. 2011. “Fine-scale Genetic Structure of Bottlenose Dolphins, *Tursiops truncatus*, in Atlantic Coastal Waters of the Iberian Peninsula”. *Hydrobiologia,* 670, 111–125. https://doi.org/10.1007/s10750-011-0669-5

Fernández-Palacios, José María, Kenneth F. Rijsdijk, Sietze J. Norder, Rüdiger Otto, Lea De Nascimento, Silvia Fernández-Lugo, et al. 2015. “Towards a Glacial-Sensitive Model of Island Biogeography”. *Global Ecology and Biogeography,* 25(7), 817–830. https://doi.org/10.1111/geb.12320

Ferreira, Rita, Filipe Alves, Claudia Gomes, Daniel Jardim, Judith Kok, and Ana Dinis. 2017. “First Confirmed Record of Northern Bottlenose Whale (*Hyperoodon ampullatus*) in Madeira Archipelago, Northeast Atlantic”. *Aquatic Mammals,* 43 (5), 474–478. https://doi.org/10.1578/AM.43.5.2017.474

Feyrer, Laura J., Joy E. Stanistreet, and Hilary B. Moors-Murphy. 2024. “Navigating the Unknown: Assessing Anthropogenic Threats to Beaked Whales, Family Ziphiidae”. *Royal Society Open Science,* 11(4), 240058. https://doi.org/10.1098/rsos.240058

Freitas, Luis. 2024. “The Ecological Importance of Oceanic Islands for Cetaceans: the Case Study of Madeira Archipelago”. PhD dissertation, University of St Andrews.

Freitas, Luis, Ana Dinis, Cátia Nicolau, Cláudia Ribeiro, and Filipe Alves. 2012. “New Records of Cetacean Species for Madeira Archipelago with an Updated Checklist”. *Boletim Do Museu Municipal Do Funchal*, 62, 25–43.

Freitas, Luis, and G. S. Penry. 2021. “Bryde’s whale *Balaenoptera edeni*, Anderson, 1878”. In *Cetacea, One*. Edited by Caroline R. Weir, Peter G.H. Evans, and Marianne Helene Rasmussen, 1-32. Springer Nature Switzerland AG.

Freitas, Rui, Maria Romeiras, Luís Silva, Ricardo Cordeiro, Patrícia Madeira, José Antonio González, Peter Wirtz, et al. 2019. “Restructuring of the ‘Macaronesia’ Biogeographic Unit: A Marine Multi-taxon Biogeographical Approach”. *Scientific Reports*, 9, 15792. https://doi.org/10.1038/s41598-019-51786-6

Fry, B., and E. B. Sherr. 1984. “δ^{13}C Measurements as Indicators of Carbon Flow in Marine and Freshwater Ecosystems”. In *Stable Isotopes in Ecological Research, Volume 68, Ecological Studies*. Edited by P. W. Rundel, J. R. Ehleringer, K. A. Nagy, 196-229. New York: Springer. https://doi.org/10.1007/978-1-4612-3498-2_12

Gannes, Leonard Z., Diane M. O'Brien, and Carlos Martínez Del Rio. 1997. “Stable Isotopes in Animal Ecology: Assumptions, Caveats, and a Call for More Laboratory Experiments”. *Ecology*, 78, 1271–1276. https://doi.org/10.1890/0012-9658(1997)078[1271:SIIAEA]2.0.CO;2

Gauffier, Pauline, and Luis Freitas. 2023. “*Balaenoptera edeni* (Europe assessment)”. *The IUCN Red List of Threatened Species* 2023: e.T2476A225016607.

Geldmacher, Jörg, Paul Van Den Bogaard, Kaj Hoernle, and Hans-Ulrich Schmincke. 2000. "The 40Ar/39Ar Age Dating of the Madeira Archipelago and Hotspot Track (Eastern North Atlantic)". *Geochemistry, Geophysics, Geosystems,* 1(2), 1999GC000018. https://doi.org/10.1029/1999gc000018

Gero, Shane, Jonathan Gordon, Carole Carlson, Peter Evans, and Hal Whitehead. 2007. "Population Estimate and Inter- Island Movement of Sperm Whales, *Physeter macrocephalus*, in the Eastern Caribbean Sea". *Journal of Cetacean Research and Management,* 9(2), 143-150. https://doi.org/10.47536/jcrm.v9i2.682

Gibbs, Susan E., Robert G. Harcourt, and Catherine M. Kemper. 2011. "Niche Differentiation of Bottlenose Dolphin Species in South Australia Revealed by Stable Isotopes and Stomach Contents". *Wildlife Research,* 38(4), 261–270. https://doi.org/10.1071/wr10108

Gideran, Chuznun N., Muhammad Taswin Munier, M. Luthfi Dhaifullah, Prima Reksa Tama, and Alda Awayan Banjarsari. 2023. "Biogeography of Indonesia Migratory Marine Megafauna". *Journal of Oceanography and Aquatic Science*, 2(1), 6-12. https://doi.org/10.56855/joane.v2i1.9501-3

Giménez, Joan, Francisco Ramírez, Javier Almunia, Manuela G. Forero, and Renaud De Stephanis. 2016. "From the Pool to the Sea: Applicable Isotope Turnover Rates and Diet to Skin Discrimination Factors for Bottlenose Dolphins (*Tursiops truncatus*)". *Journal of Experimental Marine Biology and Ecology,* 475, 54–61. https://doi.org/10.1016/j.jembe.2015.11.001

Greenwood, P. 1980. "Mating Systems, Philopatry and Dispersal in Birds and Mammals". *Animal Behaviour*, 28, 1140–62.

Guerra, Marta, Lucy Wing, Stephen Dawson, and William Rayment. 2020. "Stable Isotope Analyses Reveal Seasonal and Inter-individual Variation in the Foraging Ecology of Sperm Whales". *Marine Ecology. Progress Series*, 638, 207-219. https://doi.org/10.3354/meps13255

Harmer, S. F. 1924. "On Mesoplodon and other Beaked Whales". *Proceedings of the Zoological Society of London*, 36, 541-587.

Harvey, James T., and George A. Antonelis. 1994. "Biases Associated with Non-Lethal methods of Determining the Diet of Northern Elephant Seals". *Marine Mammal Science*, 10, 178–187. https://doi.org/10.1007/s00300-002-0447-y

Hinde, R. A. 1976. "Interactions, Relationships and Social Structure". *Man New Series*, 11(1), 1-17. https://doi.org/10.2307/2800384

Hobson, Ka, and He Welch. 1992. "Determination of Trophic Relationships Within a High Arctic Marine Food Web Using δ^{13}C and δ^{15}N Analysis". *Marine Ecology. Progress Series*, 84, 9–18. https://doi.org/10.3354/meps084009

Hooker, Sasha K. 2018. "Toothed whales (Odontoceti)". In *Encyclopedia of Marine Mammals*, 3rd Edition. Edited by Bernd Würsig, J. G. M. Thewissen and Kit M. Kovacs, 1004-1010. London, UK: Academic Press.

Hooker, Sascha K., Natacha Aguilar De Soto, Robin W. Baird, Emma L. Carroll, Diane Claridge, Laura Feyrer, Patrick J. O. Miller, et al. 2019. "Future Directions in Research on Beaked Whales". *Frontiers in Marine Science*, 5, 411237. https://doi.org/10.3389/fmars.2018.00514

Hupman, Krista, Ingrid N. Visser, E. Martinez, and Karen A. Stockin. 2014. "Using Platforms of Opportunity to Determine the Occurrence and Group Characteristics of Orca (*Orcinus orca*) in the Hauraki Gulf, New Zealand". *New Zealand Journal of Marine and Freshwater Research*, 49(1), 132–149. https://doi.org/10.1080/00288330.2014.980278

Jackson, Andrew L., Richard Inger, Andrew C. Parnell, and Stuart Bearhop. 2011. "Comparing Isotopic Niche Widths Among and Within Communities: SIBER - Stable Isotope Bayesian Ellipses in R". *Journal of Animal Ecology*, 80(3), 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Johnson, Chris, Ryan Reisinger, Daniel Palacios, Ari Friedlaender, Alex Zerbini, Andrew Willson, Melanie Lancaster, et al. 2022. "Protecting Blue Corridors, Challenges and Solutions for Migratory Whales Navigating International and National Seas". WWF, Oregon State University, University of California, Santa Cruz. WWF International, Switzerland.

Johnson, John, and Ian Stevens. 2000. "A Fine Resolution Model of the Eastern North Atlantic Between the Azores, the Canary Islands and the Gibraltar Strait". *Deep Sea Research Part I: Oceanographic Research Papers*, 47(5), 875–899. https://doi.org/10.1016/S0967-0637(99)00073-4

Kappeler, Peter M. 2019. "A Framework for Studying Social Complexity". *Behavioral Ecology and Sociobiology*, 73(13). https://doi.org/10.1007/s00265-018-2601-8

Kaschner, Kristin, Nicola J. Quick, Rebecca Jewell, Rob Williams, and Catriona M. Harris. 2012. "Global Coverage of Cetacean Line-Transect Surveys: Status Quo, Data Gaps and Future Challenges". *PLoS One*, 7(9), e44075. https://doi.org/10.1371/journal.pone.0044075

Kato, Hidehiro, and William F. Perrin. 2018. "Bryde's whale *Balaenoptera edeni*". In *Encyclopedia of Marine Mammals*, 3rd Edition. Edited by Bernd Würsig, J. G. M. Thewissen and Kit M. Kovacs, 143-145. London, UK: Academic Press.

Kiszka, Jeremy, Marc Oremus, Pierre Richard, Michael Poole, and Vincent Ridoux. 2010. "The Use of Stable Isotope Analyses from Skin Biopsy Samples to Assess Trophic Relationships of Sympatric Delphinids off Moorea (French Polynesia)". *Journal of Experimental Marine Biology and Ecology*, 395(1–2), 48–54. https://doi.org/10.1016/j.jembe.2010.08.010

Kiszka, Jeremy J., Mathew S. Woodstock, and Michael R. Heithaus. 2022. "Functional Roles and Ecological Importance of Small Cetaceans in Aquatic Ecosystems". *Frontiers in Marine Science*, 9, 803173. https://doi.org/10.3389/fmars.2022.803173

Kiszka, Jeremy J., Michael R. Heithaus, and Aaron J. Wirsing. 2015. "Behavioural Drivers of the Ecological Roles and Importance of Marine Mammals". *Marine Ecology Progress Series*, 523, 267–81. https://doi.org/10.3354/meps11180

Koch, Paul L. 2007. "Isotopic Study of the Biology of Modern and Fossil Vertebrates". In *Stable isotopes in ecology and environmental science*. Edited by Robert Michener, and Kate Lajtha, 99-154. Blackwell Publishing. https://doi.org/10.1002/9780470691854.ch5

Koenig, Andreas, Clara J. Scarry, Brandon C. Wheeler, and Carola Borries. 2013. “Variation in Grouping Patterns, Mating Systems and Social Structure: What Socio-ecological Models Attempt to Explain”. *Philosophical Transactions - Royal Society. Biological Sciences,* 368(1618), 20120348. https://doi.org/10.1098/rstb.2012.0348

Laran, Sophie, Olivier Van Canneyt, Ghislain Dorémus, Claire Garrigue, Tristan Berr, Hugo Bourgogne, Mathieu Genu, et al. 2024. “Who Lives in the Open Sea? Distribution and Densities of Surfacing Marine Megafauna in Three Subregions of the South Pacific (New Caledonia, Wallis and Futuna, and French Polynesia)”. *Pacific Conservation Biology*, 30, PC23023. https://doi.org/10.1071/pc23023

LeDuc, R. (2018) “Biogeography”. In *Encyclopedia of Marine Mammals*, 3rd Edition. Edited by B. Würsig, J. G. M. Thewissen, K. M. Kovacs., 99-103. London, UK: Academic Press.

Li, Songhai, and Massimiliano Rosso. 2021. “Lack of knowledge threatens beaked whales”. *Science*, 371(6531), 791-791. https://doi.org/10.1126/science.abg8922

Lodi, Liliane, Rodrigo Tardin, and Guilherme Maricato. 2020. “Modeling Cetacean Habitat Use in an Urban Coastal Area in Southeastern Brazil”. *Marine Ecology Progress Series*, 642, 227–40. https://doi.org/10.3354/meps13313

Louis, Marie, Amélia Viricel, Tamara Lucas, Hélène Peltier, Eric Alfonsi, Simon Berrow, Andrew Brownlow, et al. 2014. “Habitat-driven Population Structure of Bottlenose Dolphins, *Tursiops truncatus*, in the North-East Atlantic”. *Molecular Ecology*, 23(4), 857–874. https://doi.org/10.1111/mec.12653

MacLeod, Colin D. 1998. “Intraspecific Scarring in Odontocete Cetaceans: An Indicator of Male ‘Quality’ in Aggressive Social Interactions?”. *Journal of Zoology*, 244, 71–77. https://doi.org/10.1111/j.1469-7998.1998.tb00008.x

Macleod, Colin. 2000. “Review of the Distribution of Mesoplodon Species (order Cetacea, family Ziphiidae) in the North Atlantic”. *Mammal Review*, 30(1), 1-8. https://doi.org/10.1046/j.1365-2907.2000.00057.x

MacLeod, Colin, and Alan Zuur. 2005. “Habitat Utilization by Blainville’s Beaked Whales off Great Abaco, Northern Bahamas, in Relation to Seabed Topography”. *Marine Biology*, 147(1), 1-11. https://doi.org/10.1007/s00227-004-1546-9

MacLeod, Colin D., William F. Perrin, Robert Pitman, Jay Barlow, Lisa Ballance, Angela D’Amico, Tim Gerrodette, et al. 2006. “Known and Inferred Distributions of Beaked Whale Species (Ziphiidae: Cetacea)”. *Journal of Cetacean Research Management*, 7(3), 271–286.

Martin, Angela Helen, Heidi Christine Pearson, Grace Kathleen Saba, and Esben Moland Olsen. 2021. “Integral Functions of Marine Vertebrates in the Ocean Carbon Cycle and Climate Change Mitigation”. *One Earth,* 4(5), 680–93. https://doi.org/10.1016/j.oneear.2021.04.019

Mason, Evan. 2009. “High-resolution Modeling of the Canary Basin Oceanic Circulation”. PhD dissertation, University of Las Palmas of Gran Canaria.

McCluskey, Shannon M., Kate R. Sprogis, Josh M. London, Lars Bejder, and Neil R. Loneragan. 2021. “Foraging Preferences of an Apex Marine Predator Revealed Through Stomach Content and Stable Isotope Analyses”. *Global Ecology and Conservation,* 25, e01396. https://doi.org/10.1016/j.gecco.2020.e01396

McCutchan, James H., William M. Lewis, Carol Kendall, and Claire C. McGrath. 2003. “Variation in Trophic Shift for Stable Isotope Ratios of Carbon, Nitrogen, and Sulfur”. *Oikos*, 102(2), 378–90. https://doi.org/10.1034/j.1600-0706.2003.12098.x

McSweeney, Daniel J., Robin W. Baird, and Sabre D. Mahaffy. 2007. “Site Fidelity, Associations and Movements of Cuvier’s (*Ziphius cavirostris*) and Blainville’s (*Mesoplodon densirostris*) Beaked Whales off the Island of Hawai’i”. *Marine Mammal Science,* 23, 666–687. https://doi.org/10.1111/j.1748-7692.2007.00135.x

Mead, James G. 1989. “Beaked Whales of the Genus Mesoplodon”. In *Handbook of Marine Mammals, Volume 4, River dolphins and the larger toothed whales*. Edited by S. H. Ridgeway, and R. Harrison*,* 349–430. London: Academic Press Ltd.

Miralles, Laura, Marc Oremus, Mónica A. Silva, Serge Planes, and Eva Garcia-Vazquez. 2016. “Interspecific Hybridization in Pilot Whales and Asymmetric Genetic Introgression in Northern *Globicephala melas* Under the Scenario of Global Warming”. *PloS One,* 11(8), e0160080. https://doi.org/10.1371/journal.pone.0160080

Morrison, Thomas A., and Douglas T. Bolger. 2012. “Wet Season Range Fidelity in a Tropical Migratory Ungulate”. *Journal of Animal Ecology,* 81(3), 543–52. https://doi.org/10.1111/j.1365-2656.2011.01941.x

Moura, André E., Neftalí Sillero, and Ana Rodrigues. 2012. “Common Dolphin (*Delphinus delphis*) Habitat Preferences Using Data from Two Platforms of Opportunity”. *Acta Oecologica*, 38, 24–32. https://doi.org/10.1016/j.actao.2011.08.006

Mueller, Thomas, and William F. Fagan. 2008. "Search and Navigation in Dynamic Environments - From Individual Behaviors to Population Distributions". *Oikos*, 117, 654–664. https://doi.org/10.1111/j.2008.0030-1299.16291.x

Mullin, Keith D., Lisa Steiner, Charlotte Dunn, Diane Claridge, Laura González García, Jonathan Gordon, and Tim Lewis. 2022. “Long-Range Longitudinal Movements of Sperm Whales (*Physeter macrocephalus*) in the North Atlantic Ocean Revealed by Photo-Identification”. *Aquatic Mammals*, 48(1), 3–8. https://doi.org/10.1578/am.48.1.2022.3

Nathan, Ran, Wayne M. Getz, Eloy Revilla, Marcel Holyoak, Ronen Kadmon, David Saltz, and Peter E. Smouse. 2008. “A Movement Ecology Paradigm for Unifying Organismal Movement Research”. *Proceedings of the National Academy of Sciences of the United States of America*, 105(49), 19052–59. https://doi.org/10.1073/pnas.0800375105

Newsome, Seth D., Carlos Martinez Del Rio, Stuart Bearhop, and Donald L. Phillips. 2007. “A Niche for Isotopic Ecology”. *Frontiers in Ecology and the Environment*, 5(8), 429–36. https://doi.org/10.1890/060150.1

Noren, Dawn P., and Julie A. Mocklin. 2011. “Review of Cetacean Biopsy Techniques: Factors Contributing to Successful Sample Collection and Physiological and Behavioral Impacts”. *Marine Mammal Science*, 28(1), 154–99. https://doi.org/10.1111/j.1748-7692.2011.00469.x

Palacios, Daniel M., S. K. Salazar, and D. Day. 2004. “Cetacean Remains and Strandings in the Galápagos Islands, 1923-2003”. *Latin American Journal of Aquatic Mammals*, 3(2), 127-150. https://doi.org/10.5597/lajam00058

Park, Hyun Je, Tae Hee Park, Chung-Il Lee, and Chang-Keun Kang. 2018. “Ontogenetic Shifts in Diet and Trophic Position of Walleye Pollock, *Theragra chalcogramma*, in the Western East Sea (Japan Sea) Revealed by Stable Isotope and Stomach Content Analyses”. *Fisheries Research*, 204, 297–304. https://doi.org/10.1016/j.fishres.2018.03.006

Parra, Guido J., Peter J. Corkeron, and Helene Marsh. 2006. “Population Sizes, Site Fidelity and Residence Patterns of Australian Snubfin and Indo-Pacific Humpback Dolphins: Implications for Conservation”. *Biological Conservation*, 129(2), 167–80. https://doi.org/10.1016/j.biocon.2005.10.031

Parra, Guido J., Zachary Wojtkowiak, Katharina J. Peters, and Daniele Cagnazzi. 2022. “Isotopic Niche Overlap Between Sympatric Australian Snubfin and Humpback Dolphins”. *Ecology and Evolution*, 12(5), e8937. https://doi.org/10.1002/ece3.8937

Pérez-Vallazza, Claudia, Rosana Álvarez-Vázquez, Laura Cardona, Clara Pintado, and Joaquín Hernández-Brito. 2008. “Cetacean Diversity at the West Coast of La Palma Island (Canary Islands)”. *Journal of the Marine Biological Association of the United Kingdom*, 88(6), 1289–1296. https://doi.org/10.1017/s0025315408001239

Peters, Katharina J., Sarah J. Bury, Bethany Hinton, Emma L. Betty, Déborah Casano-Bally, Guido J. Parra, and Karen A. Stockin. 2022. “Too Close for Comfort? Isotopic Niche Segregation in New Zealand’s Odontocetes”. *Biology*, 11(8), 1179. https://doi.org/10.3390/biology11081179

Phillips, Donald L. 2001. “Mixing Models in Analyses of Diet Using Multiple Stable Isotopes: A Critique”. *Oecologia*, 127(2), 166–70. https://doi.org/10.1007/s004420000571

Pinela, Ana M., Sophie Quérouil, Sara Magalhães, Mónica A. Silva, Rui Prieto, J. A. Matos, and Ricardo S. Santos. 2009. “Population Genetics and Social Organization of the Sperm Whale (*Physeter macrocephalus*) in the Azores Inferred by Microsatellite Analyses”. *Canadian Journal of Zoology*, 87(9), 802–13. https://doi.org/10.1139/z09-066

Pitman, Robert. 2018. “Mesoplodon Beaked Whales”. In *Encyclopedia of Marine Mammals*, 3rd Edition. Edited by Bernd Würsig, J. G. M. Thewissen and Kit M. Kovacs, 595-602. London, UK: Academic Press.

Plint, Tessa, Mariel T.I. ten Doeschate, Andrew C. Brownlow, Nicholas J. Davison, Georg Hantke, Andrew C. Kitchener, Fred J. Longstaffe, et al. 2023. “Stable Isotope Ecology and Interspecific Dietary Overlap Among Dolphins in the Northeast Atlantic”. *Frontiers in Marine Science*, 10, 1111295. https://doi.org/10.3389/fmars.2023.1111295

Post, David M. 2002. “Using Stable Isotopes to Estimate Trophic Position: Models, Methods and Assumptions”. *Ecology*, 83, 703-718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Quérouil, Sophie, Luís Freitas, Irma Cascão, Filipe Alves, Ana Dinis, Joana R. Almeida, Rui Prieto, et al. 2010. “Molecular Insight into the Population Structure of Common and Spotted Dolphins

Inhabiting the Pelagic Waters of the Northeast Atlantic”. *Marine Biology*, 157(11), 2567–80. https://doi.org/10.1007/s00227-010-1519-0

Quérouil, Sophie, Mónica A. Silva, Luis Freitas, Rui Prieto, Sara Magalhães, Ana Dinis, Filipe Alves, et al. 2007. “High Gene Flow in Oceanic Bottlenose Dolphins (*Tursiops truncatus*) of the North Atlantic”. *Conservation Genetics*, 8, 1405-1419. https://doi.org/10.1007/s10592-007-9291-5

Reggente, Melissa A. L., Filipe Alves, Cátia Nicolau, Luís Freitas, Daniele Cagnazzi, Robin W. Baird, and Paolo Galli. 2016. “Nurturant Behavior Toward Dead Conspecifics in Free-Ranging Mammals: New Records for Odontocetes and a General Review”. *Journal of Mammalogy*, 97(5), 1428–34. https://doi.org/10.1093/jmammal/gyw089

Rice, Dale W., and Society for Marine Mammalogy. 1998. *Marine Mammals of the World: Systematics and Distribution*. Lawrence, KS: Society for Marine Mammalogy.

Ritter, Fabian, and B. Brederlau. 1999. “Abundance, Distribution and Behaviour of Dense Beaked Whales (*Mesoplodon densirostris*) off La Gomera (Canary Islands) and their Interactions with Humans”. *Aquatic Mammals*, 25(2), 55-61.

Ritter, Fabian, and K. Neumann. 2006. “The year of the whale: extraordinary occurrence of Bryde's whales off La Gomera (Canary Islands) in 2005”. Poster presented at the 20th Conference of the European Cetacean Society, Gdynia, Poland, April.

Roman, Joe, James A. Estes, Lyne Morissette, Craig Smith, Daniel Costa, James McCarthy, J. B. Nation, et al. 2014. “Whales as Marine Ecosystem Engineers”. *Frontiers in Ecology and Environment*, 12, 3771–385. https://doi.org/10.1890/130220

Rosel, Patricia E., L. Hansen, and A. A. Hohn. 2009. “Restricted Dispersal in a Continuously Distributed Marine Species: Common Bottlenose Dolphins *Tursiops truncatus* in Coastal Waters of the Western North Atlantic”. *Molecular Ecology*, 18(24), 5030-5045. https://doi.org/10.1111/j.1365-294X.2009.04413.x

Rosel, Patricia E., Lindsey A. Wilcox, Tadasu K. Yamada, and Keith D. Mullin. 2021. “A New Species of Baleen Whale (Balaenoptera) from the Gulf of Mexico, with a Review of its Geographic Distribution”. *Marine Mammal Science*, 37(2), 577-610. https://doi.org/10.1111/mms.12776

Sala, Iria, Rui M. A. Caldeira, Sheila N. Estrada-Allis, Elsa Froufe, and Xavier Couvelard. 2013. “Lagrangian Transport Pathways in the Northeast Atlantic and their Environmental Impact”. *Limnology and Oceanography: Fluids and Environments*, 3, 40–60. https://doi.org/10.1215/21573689-2152611

Santos, M. B., Graham J. Pierce, P. R. Boyle, R. J. Reid, H. M. Ross, I. A. P. Pattersson, C. C. Kinze, et al. 1999. “Stomach Contents of Sperm Whales *Physeter macrocephalus* Stranded in the North Sea 1990-1996”. *Marine Ecology Progress Series*, 183, 281-294. https://doi.org/10.3354/meps183281

Sekiguchi, K., N. T. W. Klages, and Peter B. Best. 1992. “Comparative Analysis of the Diets of Smaller Odontocete Cetaceans along the Coast of Southern Africa”. *South African Journal of Marine Science,*12(1), 843–886. https://doi.org/10.2989/02577619209504746

Silva, Monica, Ricardo Prieto, Inês Cascão, Marta Seabra, Miguel Machete, Mark Baumgartner, Sofia Santos, and José M. Gonçalves. 2014. "Spatial and Temporal Distribution of Cetaceans in the Mid-Atlantic Waters around the Azores". *Marine Biology Research*, 10(2), 123–137. https://doi.org/10.1080/17451000.2013.793814.

Silva, Mónica A., Rui Prieto, Sara Magalhães, Maria I. Seabra, Ricardo S. Santos, and Phillip S. Hammond. 2008. “Ranging Patterns of Bottlenose Dolphins Living in Oceanic Waters: Implications for Population Structure”. *Marine Biology*, 156, 179–192. https://doi.org/10.1007/s00227-008-1075-z

Shallenberger, E.W. 1981. “The Status of Hawaiian Cetaceans”. Final report for MMC contract MM7AC028. NTIS PB82-109398.

Shaw, Allison K. 2020. “Causes and Consequences of Individual Variation in Animal Movement”. *Movement Ecology*, 8, 12. https://doi.org/10.1186/s40462-020-0197-x

Spalding, Mark D., Helen E. Fox, Gerald R. Allen, Nick Davidson, Zach A. Ferdaña, Max Finlayson, Benjamin S. Halpern, et al. 2007. “Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas”. *Bioscience*, 57(7), 573–583. https://doi.org/10.1641/B570707

Steiner, Lisa, Luca Lamoni, Marta Acosta Plata, Silje-Kristin Jensen, Erland Lettevall, and Jonathan Gordon. 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. https://doi. org/10.1017/S0025315412000793

Steiner, Lisa, Mónica A. Silva, Jasmine Zereba, and Maria João Leal. 2008. “Bryde's Whales, *Balaenoptera edeni*, Observed in the Azores: A New Species Record for the Region”. *Marine Biodiversity Records*, 1, e66, 1–6. https://doi.org/10.1017/S1755267207007282

Steiner, Lisa, Monica Pérez, Miranda van der Linde, Luis Freitas, Raul Peres dos Santos, Vidal Martin, and Jonathan Gordon. 2015. “Long Distance Movements of Female/Immature Sperm Whales in the North Atlantic”. Poster presented at the 21st Biennial Conference of Society of Marine Mammalogy, San Francisco, USA, December.

Sutherland, William J. 1998. “The Importance of Behavioural Studies in Conservation Biology”. *Animal Behavior*, 56, 801–809. https://doi. org/10.1006/anbe.1998.0896

Tardin, Rodrigo H., Yongwan Chun, Sheila M. Simão, and Maria Alice S. Alves. 2017. “Modeling Habitat Use by Bryde’s Whale *Balaenoptera edeni* off Southeastern Brazil”. *Marine Ecology Progress Series*, 576, 89–103. https://doi. org/10.3354/meps12228

Taylor, B.L., Robin Baird, J. Barlow, S. M. Dawson, J. Ford, J. G. Mead, G. Notarbartolo di Sciara, P. Wade, and R. L. Pitman. 2019. *Physeter macrocephalus* (amended version of 2008 assessment). The IUCN Red List of Threatened Species 2019: e.T41755A160983555. https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T41755A160983555.en

Teixeira, Clarissa R., Genyffer C. Troina, Fabio G. Daura-Jorge, Paulo C. Simões-Lopes, and Silvina Botta. 2022. “A Practical Guide on Stable Isotope Analysis for Cetacean Research”. *Marine Mammal Science*, 38(3), 1200-1228. https://doi.org/10.1111/mms.12911

Tershy, Bernie R. 1992. “Body Size, Diet, Habitat Use, and Social Behavior of *Balaenoptera* Whales in the Gulf of California”. *Journal of Mammalogy*, 73, 477–486. https://doi.org/10.2307/1382013

Tieszen, Larry L., Thomas Boutton, K. G. Tesdahl, and Norman A. Slade. 1983. “Fractionation and Turnover of Stable Carbon Isotopes in Animal Tissues: Implications for $\delta^{13}C$ Analysis of Diet”. *Oecologia*, 57(1), 32–37. https://doi.org/10.1007/bf00379558

Tobeña, Marta, Rui Prieto, Miguel Machete, and Mónica A. Silva. 2016. “Modeling the Potential Distribution and Richness of Cetaceans in the Azores from Fisheries Observer Program Data”. Frontiers of Marine Science, 3, 202655. https://doi.org/10.3389/fmars.2016.00202

Tomczak, M., and J. S. Godfrey. 1994. *Regional oceanography: An introduction*. London, UK: Pergamon.

Torniainen, Jyrki, Anssi Lensu, Pekka J. Vuorinen, Eloni Sonninen, Marja Keinänen, Roger I. Jones, William P. Patterson, et al. 2017. “Oxygen and Carbon Isoscapes for the Baltic Sea: Testing their Applicability in Fish Migration Studies”. *Ecology and Evolution*, 7 (7), 2255e2267. https://doi.org/10.1002/ece3.2841

Townsend, C. H. 1935. “The distribution of certain whales as shown by logbook records of American whaleships”. *Zoologica*, 19 (1): 1-50.

Tuya, Fernando, and Ricardo J. Haroun. 2009. “Phytogeography of *Lusitanian* Macaronesia: Biogeographic Affinities in Species Richness and Assemblage Composition”. *European Journal of Phycology*, 44, 405-413. https://doi.org/10.1080/09670260902836246

van Beest, Floris M., Eric Vander Wal, Austrid Vik Stronen, Paul C. Paquet, and Ryan K. Brook. 2013. “Temporal Variation in Site Fidelity: Scale-Dependent Effects of Forage Abundance and Predation Risk in a Non-Migratory Large Herbivore”. *Oecologia*, 173, 409–420. https://doi.org/10.1007/s00442-013-2647-2

Violi, Biagio, Menno J. de Jong, Alexandros Frantzis, Paraskevi Alexiadou, Céline Tardy, Denis Ody, Renaud de Stephanis, et al. 2023. “Genomics Reveals the Role of Admixture in the Evolution of Structure among Sperm Whale Populations within the Mediterranean Sea”. *Molecular Ecology*, 32(11), 2715-2731. https://doi.org/10.1111/mec.16898

Wada, Shiro, Masayuki Oishi, and Tadasu K. Yamada. 2003. “A newly discovered species of living baleen whales”. *Nature*, 426, 278–281. https://doi.org/10.1038/nature02103

Weir, Caroline. R., Colin D. MacLeod, and Graham John Pierce. 2012. “Habitat preferences and evidence for niche partitioning amongst cetaceans in the waters between Gabon and Angola, eastern tropical Atlantic”. *Journal of the Marine Biological Association of the United Kingdom*, 92, 1735–1749. https://doi.org/10.1017/S0025315412000148

Weyn, Mieke, Jacobo Marrero-Pérez, Atenery Sánchez, Ana Pimentel, Rita Ferreira, Annalisa Sambolino, Ana Dinis, et al. 2024. “Integrating satellite tracking and photographic-identification to understand pilot whale connectivity between Madeira and the Canary Islands and support conservation”. Poster presented at the 35th conference of the European Cetacean Society, Catania, Italy, April.

Whitehead, Hal. 2009. “SOCPROG Programs: Analysing Animal Social Structures”. *Behavioral Ecology and Sociobiology*, 63, 765–778. https://doi.org/10.1007/s00265-008-0697-y

Whitehead, Hal. 2018. “Sperm Whale”. In *Encyclopedia of Marine Mammals*, 3rd Edition. Edited by Bernd Würsig, J. G. M. Thewissen and Kit M. Kovacs, 919-924. London, UK: Academic Press.

Whitehead, Hal, Amanda Coakes, Nathalie Jaquet, and Susan Lusseau. 2008. “Movements of Sperm Whales in the Tropical Pacific”. *Marine Ecology Progress Series*, 361, 291-300. https://doi.org/10.3354/meps07412

Whitehead, Hal, and Megan Shin. 2022. “Current Global Population Size, Post-Whaling Trend and Historical Trajectory of Sperm Whales”. *Scientific Reports*, 12(1), 1-12. https://doi.org/10.1038/s41598-022-24107-7

Whitehead, Hal, Shannon Gowans, Annick Faucher, and Stephen W. McCarrey. 1997. “Population Analysis of Northern Bottlenose Whales in the Gully, Nova Scotia”. *Marine Mammal Science*, 13(2), 173-185. https://doi.org/10.1111/j.1748-7692.1997.tb00625.x

Wiseman, Nicky, Stuart Parsons, Karen A. Stockin, and C. Scott Baker. 2011. “Seasonal Occurrence and Distribution of Bryde’s Whales in the Hauraki Gulf, New Zealand”. *Marine Mammal Science*, 27(4), E253-E267. https://doi.org/10.1111/j.1748-7692.2010.00454.x

Zenk, Walter, Birgit Klein, and Michael Schroder. 1991. “Cape Verde frontal zone.” *Deep Sea Research Part A. Oceanographic Research Papers*, 38, S505-S530. https://doi.org/10.1016/S0198-0149(12)80022-7

Zerbini, Alexandre N., Eduardo R. Secchi, Salvatore Siciliano, and Paulo C. Simões-Lopes. 1997. “A review of the occurrence and distribution of whales of the genus Balaenoptera along the Brazilian coast”. *Report of the International Whaling Commission*, 47, 407–417.

CHAPTER II – Bryde's Whales in the North-East Atlantic: New Insights on Site Fidelity and Connectivity between Oceanic Archipelagos

This chapter is published as:

Ferreira, Rita, Ana Dinis, Anja Badenas Krakauer, Annalisa Sambolino, Jacobo Marrero-Pérez, Ana Crespo, and Filipe Alves. 2021. "Bryde's whales in the North-East Atlantic: new insights on site fidelity and connectivity between oceanic archipelagos". *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31(10), 2838-2950. https://doi.org/10.1002/aqc.3665

CHAPTER II - Bryde’s Whales in the North-East Atlantic: New Insights on Site Fidelity and Connectivity between Oceanic Archipelagos

Abstract

1. The conservation of marine megafauna presents numerous difficulties owing to their high mobility over difficult-to-access oceanic areas that impairs the collection of basic, but essential, biological information.

2. The Bryde's whale (*Balaenoptera edeni*) is one of the most elusive species of baleen whales, and although it is known to be a seasonal visitor to several archipelagos in Macaronesia (the Azores, Madeira, and Canaries), there are no studies regarding its occurrence or geographical connectivity in this area of the Atlantic.

3. A 14-year photographic database was used to determine short-term (intraseasonal) and long-term (inter-annual) Bryde's whale site fidelity and to estimate individual residency times in Madeira, whereas photographic catalogues from Madeira and the Canaries were compared in order to assess large-scale movements (i.e. on the scale of hundreds of kilometres).

4. In Madeira, 59 individuals were identified, 27 (45.8%) of which were recaptured. Of these, 10 individuals (37.0%) presented short-term site fidelity and 17 individuals (63.0%) presented long-term site fidelity, with a maximum recapture interval of 12 years. Lagged identification rates showed that five individuals (SE = 2) remained in the area for 32 days (SE = 108 days) before leaving and not returning during the same year. Seven individuals were seen both in Madeira and the Canaries (catalogue comprising 51 individuals), three of which were identified multiple times in both archipelagos, with a minimum of 43 days between consecutive sightings.

5. This information combined with the fact that this species is commonly sighted accompanied by calves and feeding in both archipelagos highlights the ecological importance of this area for Bryde's whales. This should be taken into consideration by policymakers when implementing conservation measures, where coordination of effort among countries is needed. This study also reinforces the value of using data from platforms of opportunity and of making photographic data open access.

KEYWORDS: *Balaenoptera edeni*, Macaronesia, marine megafauna, migratory species, oceanic movements, open access data

Introduction

The study of megafauna has long been relevant for their economic and ecological importance, and the appeal that they present to human societies (Lindsey et al., 2017). Cetaceans are a highly charismatic marine megafauna group whose research and conservation presents numerous challenges (e.g. high mobility and amount of time spent below the surface, low detectability and difficulties associated with their identification, large distribution and seasonal migrations of some species, high economic costs of undertaking assessment studies and difficulty in accessing their oceanic habitats; Mann, 1999; Redfern et al., 2006; Kaschner et al., 2012; Horton et al., 2017; Thums et al., 2018; Afonso et al., 2020). The study of their movement patterns is not only essential for understanding population ecology and biogeographical patterns, but also to assess the conservation status of populations across their entire home range, and evaluate the extent to which they are subjected to increasing anthropogenic impacts (Whitehead, 2001; Sequeira et al., 2018). However, the incorporation of movement data into conservation strategies remains underused (Hays et al., 2016).

Many cetacean species perform long-distance migrations driven by foraging, calf or breeding requirements, or predator avoidance (Corkeron & Connor, 1999), with considerable energetic expenditure. Among cetaceans, baleen whales are the most extensive travellers, with some species moving over 10,000 km between feeding and breeding grounds (Stevick et al., 2011). In the North Atlantic, although some knowledge exists on the movements of some species of baleen whales (e.g. blue *Balaenoptera musculus*, fin *B. physalus*, and sei whales *B. borealis*; Prieto et al., 2014; Pérez-Jorge et al., 2020), the movements and distribution of other species, such as Bryde's whales (*Balaenoptera edeni*), remain poorly understood. There are several exceptions to the traditional Mysticete seasonal migration model from high-latitude feeding grounds to low-latitude breeding grounds, suggesting a wide range of movement strategies between species or populations (Śirović et al., 2013; Geijer, Notarbartolo di Sciara & Panigada, 2016). The Bryde's whale is an elusive large baleen whale species, discovered just over a century ago, for which basic scientific knowledge, such as taxonomy and life cycle, remains under debate (Kato & Perrin, 2018). Although it is currently classified as a single species, different subspecies and forms are presently identified and may, in the future, lead to their classification into different species (Best, 1977; Best, 2001; Kershaw et al., 2013; Rosel & Wilcox, 2014; Pastene et al., 2015; Constantine et al., 2018; Committee on Taxonomy, 2020; Rosel et al., 2021). Bryde's whales remain in tropical and warm temperate waters year-round, between 40˚N and 40˚S in the Atlantic, Pacific, and Indian oceans, and very little is known about their breeding or feeding grounds. Evidence suggests that unlike other baleen whales, Bryde's whales do not make extensive seasonal migrations to high-latitude feeding grounds but instead move across ocean basins throughout their range (Lockyer & Brown, 1981; Weir, 2010; Kato & Perrin, 2018). In the East Atlantic, the species has been identified from the Azores to the African coast as far as South Africa, and in the western Atlantic from the Gulf of Mexico to Argentina (Reiner, dos Santos & Wenzel, 1996; Notarbartolo di Sciara et al., 1998; Hazevoet & Wenzel, 2000; Best, 2001; Steiner et al., 2008; Bastida & Rodriguez, 2009; De Boer, 2010; Weir, 2010; Rosel & Wilcox, 2014; Tardin et al., 2017; Kato & Perrin, 2018). Studies of Bryde's whales in the North-East Atlantic have mainly relied on sighting data in the Macaronesia biogeographic region (Ritter & Neumann, 2006; Steiner et al., 2008; Freitas et al., 2012), except for a foraging behavioural study that gave a brief insight into the dive behaviour and seasonal site fidelity of two individuals across 4 years in the Madeira Archipelago (Alves et al., 2010).

In Macaronesia, no information exists regarding individual movements or residency patterns of Bryde's whales in any of the archipelagos. In the Madeira Archipelago, Bryde's whales were first identified in 2003 and have been seen regularly between late spring and autumn (June to November) ever since, and are one of the five most observed species by the whale-watching industry (Alves et al., 2010; Freitas et al., 2012; Alves et al., 2018b). They are regularly seen feeding on small pelagic schooling fishes (e.g. sardines and mackerel; Rita Ferreira, Ana Dinis, Filipe Alves, pers. obs.) or travelling alone, although they can also be seen with calves (including neonates; Rita Ferreira, Ana Dinis, Filipe Alves, pers. obs.), in pairs of adults, or sporadically in inter-specific associations (Alves et al., 2018b). In the Canaries, Bryde's whales are frequently seen from spring to autumn (Ritter & Neumann, 2006; Pérez-Valazza et al., 2008; Carrillo, Pérez-Vallazza & Álvarez-Vázquez, 2010), whereas in the Azores, they were first identified in 2004 and are rare visitors during the summer months (Steiner et al., 2008; Silva et al., 2014).

Site fidelity, defined as the tendency of an animal to return to a previously occupied place (Baird et al., 2008), has been demonstrated for Bryde's whales through the use of photographic identification (hereafter referred to as photo-id) in some areas of the world, such as the coastal areas of Ecuador, Peru, and Panama (Castro et al., 2017), in Brazil (Figueiredo et al., 2014; Lodi et al., 2015; Athayde et al., 2020), in the Gulf of Mexico (Rosel & Wilcox, 2014; Rosel et al., 2021), in the Gulf of California (Tershy, 1992), and in New Zealand (Tezanos-Pinto et al., 2017). Nevertheless, studies evaluating residency times through the application of lagged identification rates have never been conducted for Bryde's whales, nor have the movements of individuals been detected between distant regions. Photo-id is a technique that uses the natural markings of individuals and is widely used in marine mammal research to study movement patterns (e.g. Würsig & Jefferson, 1990; Baird et al., 2008; Silva et al., 2008; Baird et al., 2009; Alves et al., 2013; Dinis et al., 2016; Alves et al., 2019). This non-invasive technique involves the collection of data from dedicated surveys or platforms of opportunity, such as whale-watching vessels, which are increasingly being used in research for their low cost and high volume of data that can be collected regularly (e.g. Evans & Hammond, 2004; Hauser et al., 2006; Moura, Sillero & Rodrigues, 2012; Hupman et al., 2014).

Connectivity between the Azores, Madeira, and the Canaries has been recorded for three species of cetaceans through photo-id comparison (for sperm whales, *Physeter macrocephalus*; Steiner et al., 2015; for short-finned pilot whales, *Globicephala macrorhynchus*; Alves et al., 2019; and for bottlenose dolphins, *Tursiops truncatus*; Dinis et al., 2021). Additionally, the lack of genetic differentiation between populations in Macaronesia has been shown for: short-finned pilot whales (Alves et al., 2013; Miralles et al., 2016); bottlenose dolphins (Quérouil et al., 2007); Atlantic spotted dolphins, *Stenella frontalis*; and short-beaked common dolphins, *Delphinus delphis* (Quérouil et al., 2010). The connectivity shown by these species, together with the highly mobile nature of all cetacean species (Hoyt, 2005), suggests that Bryde's whales may also move between archipelagos in Macaronesia; however, information on the movement ecology of this species in the North-East Atlantic is lacking.

In this study, long-term photo-id catalogues collected from platforms of opportunity and dedicated scientific surveys were used to investigate the site fidelity and movements of Bryde's whales across Macaronesia. This evaluation was based on the hypotheses that: (i) Bryde's whales demonstrate different degrees of site fidelity within the Madeiran Archipelago; and (ii) that individuals may move between the neighbouring archipelagos of Madeira and the Canaries. Filling these critical knowledge gaps regarding the movement patterns of Bryde's whales will provide novel insights into future coordinated efforts between the relevant countries (i.e. Portugal and Spain) to establish transborder conservation measures.

Material and Methods

Study Site

The present study was conducted within the biogeographic region of Macaronesia, which includes the Azores, Madeira, Canaries and a small area of the north-western African coast (Kim et al., 2008). The work to address the assessment of site fidelity was carried out in the warm-temperate oceanic archipelago of Madeira (33˚N, 17˚W) that consists of several islands, of which only two are inhabited. Being one of the most isolated oceanic habitats of the North Atlantic, it is surrounded by steep submarine canyons and deep waters (approximately 1,500 m in depth) very close to the coast, because of the lack of a continental shelf (Geldmacher et al., 2000). Photo-id data were collected from the southern waters of Madeira Island (Figure II.1).

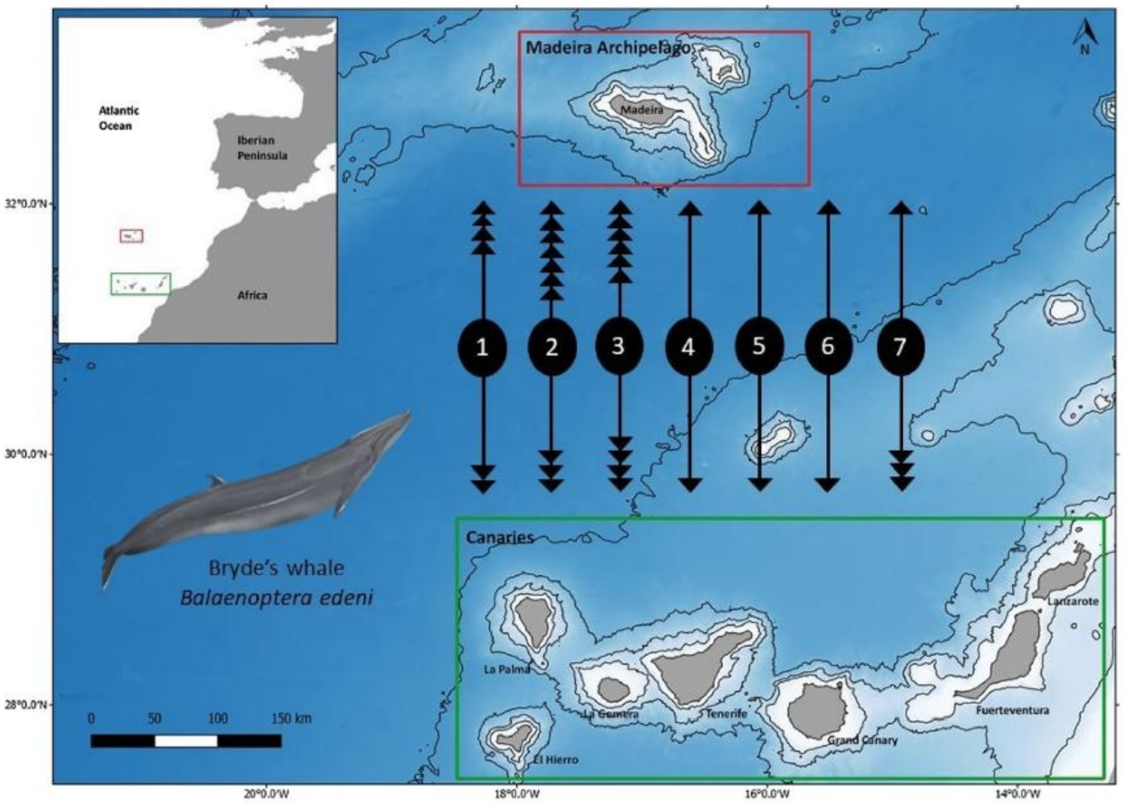

Figure II.1 Location of the study area in the North-East Atlantic, in the Madeira Archipelago and the Canaries, within the Macaronesia region. Map showing bathymetry and contour lines at every 1,000 m. Each vertical line represents one individual of Bryde's whale that was identified in both archipelagos, and the number of arrow tips represents the total number of months the individual was identified in each archipelago during the study period. Illustration by E. Berninsone ©ARDITI.

To assess the connectivity between archipelagos, data from the Canaries, the closest archipelago to Madeira (approx. 500 km; Figure II.1), were analysed. These archipelagos are considered the most similar among Macaronesia, from a marine biogeographical point of view (Freitas et al., 2019), and share similarities in terms of volcanic origin and oceanographic features (Anguita & Hernan, 2000; Spalding et al., 2007).

Photographic identification procedure

Photo-id images were collected between 2005 and 2018 on board platforms of opportunity (i.e. whale-watching vessels) operating in Madeira Island. Whale-watching activity primarily occurs off the south coast of the island owing to favourable meteorological conditions, with a mean of 321 days of trips per year (Alves et al., 2018b). The whale-watching boats search for the highest number of sightings for their clients and are not species orientated, achieving good spatial coverage in terms of offshore and inshore areas. The boat operators provide an optimal search effort, in which the boats leave from the same harbour at nearly the same time and spatially orient themselves to be approximately one nautical mile apart from one another, in order to scan a larger area for cetaceans. Some boats search for animals with onboard binoculars, whereas others rely on land-based lookouts to direct them; the search effort continues during most of the trip and only stops when they are approaching land. Many of the boats share the locations of the sightings via radio or mobile phone. Taking this into consideration, together with the fact that the Bryde's whale is one of the most sighted species and is the most abundant baleen whale in these waters (Alves et al., 2018b), it is considered that most of the individuals present in the area were approached and photographed whenever possible. Photographs were taken by crew members with Reflex cameras (with different specifications used among photographers). The number of whale-watching boats, trips, and photographers, as well as trip duration and departure/arrival point, remained constant throughout the sampling period. Thus, potential variation in sighting opportunities was considered negligible.

Photo-id data collected from dedicated scientific surveys in the same area in 2017 and 2018 were also included. A photo-id catalogue was compiled, and a dataset of capture histories was created following Würsig & Jefferson (1990). ‘Capture’ was defined as the first identification of an individual, and a ‘recapture’ as the subsequent photographic re-identification of the same individual from a separate sampling event. Identifications on the same day were pooled together to avoid repeated sightings of the same individual from different boats or locations. Each individual whale was identified using biological features, such as permanent marks, either natural or acquired, located on the trailing edge of the dorsal fin, that could be identified from both sides (Katona et al., 1979). Secondary features, such as pigmentation patterns, cookie-cutter shark scars or others (such as tumour-like deformities, observed in a few individuals), were only used to confirm matches. The best photograph of the individual in each sampling event was selected and rated 1 through 4 in terms of photographic quality (poor, fair, good and excellent, respectively) and distinctiveness of the individual (non-distinctive, slightly distinctive, distinctive and very distinctive, respectively) (as described by Baird et al., 2009; Alves et al., 2013). To maximize the reliability of the catalogue, the analysis was limited to photographic quality and distinctiveness ratings of 2 to 4. The catalogue was compiled by a single observer (RF) and verified by secondary experienced researchers (AD and FA), to avoid false-positives and false-negatives.

Site fidelity

Site fidelity was evaluated considering the intra- and inter-annual presence of individuals. Short-term site fidelity was assigned when an individual was ‘recaptured’ within a single year (or season, given that Bryde's whales occur in Madeira mainly from late spring to autumn; Freitas et al., 2012; Alves et al., 2018b), whereas long-term site fidelity was assigned when an individual was ‘recaptured’ over multiple years (as described by Alves et al., 2013; Dinis et al., 2017). The resighting rate (RR) was calculated as the number of animals with ‘recaptures’ divided by all of the animals identified during the study period. A discovery curve was created based on the cumulative number of identifications in relation to the number of identified individuals throughout the study period.

Residency in the area

The residency of individuals in Madeira was investigated by calculating lagged identification rates (LIRs). These rates estimate the probability that an individual identified in the study area at any time will be identified again in the study area after some time lag later (Whitehead, 2001). In order to comply with the assumptions of the analysis and considering the migration behaviour of Bryde's whales in the area, the maximum lag (τ) considered was the number of days of the peak season (i.e. from late spring to autumn). Previous studies used a similar criterion to estimate LIRs in other seasonal visitor species, such as migratory humpback whales, *Megaptera novaeangliae*, in Réunion Island (Dulau-Drouot et al., 2012), or took into consideration data collected during limited seasons within a year, e.g. northern bottlenose whales, *Hyperoodon ampullatus*, in Nova Scotia (Gowans et al., 2000). Thus, this analysis was conducted for the 2014 sampling period (i.e. the year with the highest number of ‘recaptures’). The calculated LIR was compared with the expected LIRs from exponential mathematical models of residency established by Whitehead (2001), and fitted using maximum-likelihood methods. The sampling period was defined as a day. The Akaike information criterion (AIC) was used to determine the model of best fit, instead of the quasi-Akaike information criterion (QAIC), as no overdispersion was observed (Whitehead, 2007). The model with the lowest AIC was selected, and although there was a difference of two values in the AIC from the next best model, we followed the principle of parsimony and selected the simplest model and the one with lower standard errors (Burnham & Anderson, 2002). Precision (SE) was estimated using a bootstrap method. The analysis was performed with SOCPROG 2.9 (Whitehead, 2009).

Inter-archipelago movements

Long-distance movements of individual Bryde's whales were assessed through comparison of the photo-id catalogue from Madeira (described above) with an open-access online catalogue from the Canaries provided by Asociación Tonina (https://asociaciontonina.com/portfolio/catalogo-rorcuales-gen-balaenoptera). The open access catalogue provides data from 2005 to February 2020, collected around the islands of Tenerife, La Palma, El Hierro, and Fuerteventura, using both opportunistic platforms and dedicated research surveys, and comprises 51 individual Bryde's whales. This catalogue is periodically updated with new information and currently includes 17 Bryde's whale ‘recaptures’, 15 of which were sighted in different years. For the present comparison, in order to increase the likelihood of matches, the catalogue from Madeira included an additional individual identified only in 2019. Comparisons were made visually (e.g. Robbins et al., 2011; Alves et al., 2019) by the primary researcher (RF), and all matches were subsequently validated by other secondary experienced researchers (AD and FA).

Results

Site fidelity

Approximately 20,000 photographs were taken, which resulted in 190 captures and 59 individuals catalogued (Table II.1).

Table II.1 Total number of captures and individuals (in bold) and percentages of their respective categories for photographic quality and the distinctiveness of the individuals.

Captures (total number)		**190**
Photo quality	fair	8,9%
	good	63,2%
	excellent	27,9%
Individuals (total number)		**59**
Distinctiveness	slighly distinctive	20,3%
	distinctive	45,8%
	very distinctive	33,9%

The number of photographic encounters and individual identifications varied considerably between years, with 2014 and 2017 presenting much higher values (302 and 231 photographic encounters and 62 and 30 identifications, respectively) (Table II.2). The fewest photographic encounters per year were recorded in 2006, 2008, and 2010, corresponding to two, three, and five individual identifications, respectively. However, the fewest identifications occurred in 2016, where although there were some encounters, with poor-quality photos (caused by unfavourable weather conditions or by animals avoiding the boats), most of the encounters comprised good photographs but of non-distinctive animals (i.e. without identifiable marks). Therefore, there were no recaptured animals nor new individuals added to the catalogue during the 2016 sampling period.

Table II.2 Summary of encounters and identifications by year for the Madeira dataset. Encounters refer to the total number (no.) of photographic encounters, independent of photographic quality and individuals' distinctiveness. Number of identifications refers to the number of individuals which were added to the catalogue (captures plus recaptures). Number of new identifications refers only to new individuals added to the catalogue.

Summary of encounters and identifications			
Year	**No. encounters**	**No. identifications**	**No. new identifications**
2005	10	4	4
2006	5	2	1
2007	6	1	1
2008	5	3	2
2009	16	6	3
2010	5	5	2
2011	11	7	3
2012	22	4	3
2013	13	2	1
2014	302	62	16
2015	99	15	2
2016	24	0	0
2017	231	30	12
2018	54	14	7

Thirty-two individuals (54.2%) were captured only once and 27 individuals (45.8%) were recaptured. Most of these individuals were recaptured up to four times (n = 44, 74.6%), seven individuals were recaptured between five and nine times (11.9%), four individuals were recaptured between 10 and 14 times (6.8%), and one individual was recaptured more frequently, with 21 recaptures (1.7%) (Figure II.2).

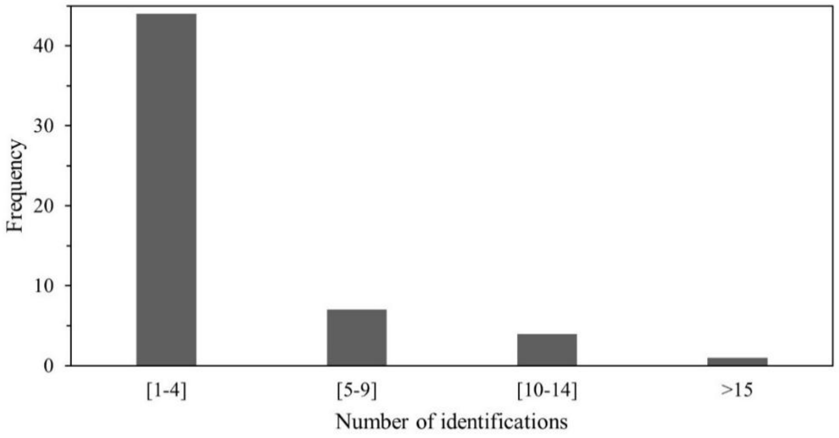

Figure II.2 Capture frequency histogram for individual Bryde's whales (n = 59) for the Madeira dataset between 2005 and 2018. More than half of the individuals (n = 32) were captured only once. Captures were aggregated in categories to facilitate visualization.

The overall resighting rate was 0.46. The absence of a temporal plateau in the discovery curve demonstrated that the number of individuals identified had not yet stabilized, indicating that the whole population has yet to be sampled (Figure II.3).

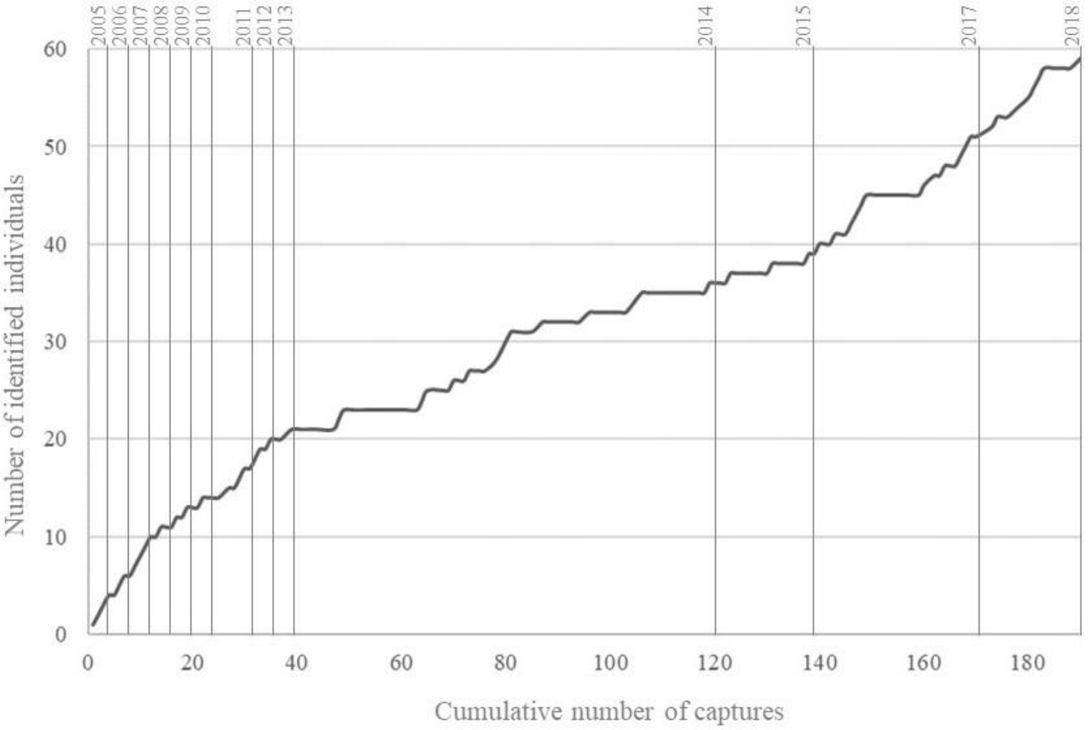

Figure II.3 Discovery curve for individual Bryde's whales (n = 59) for the Madeira dataset between 2005 and 2018. The curve has not yet reached a plateau, indicating that new individuals are still being recruited to the population.

Of the 27 individuals that were recaptured, 10 (37.0%) demonstrated short-term site fidelity and 17 (63.0%) demonstrated long-term site fidelity. For the individuals who demonstrated long-term site fidelity, the median inter-annual interval between the first and the last capture was 5.1 years (SD = 3.7 years, range 1–12 years). Although the largest proportion of individuals were observed in two different years (41.2%), four individuals were observed in three and four different years (23.5% each), and two individuals were observed in five different years (11.8%).

Residency in the area

The residency model that best fitted the LIR for the peak season of 2014 was the emigration/mortality model (goodness of fit χ2 = 18.687, df = 24, P = 0.7685), which indicated that five individuals (SE = 2) out of the 26 used in this analysis spent an average of 32 days (SE = 108) in the area, before leaving and not returning in the same season (Figure II.4; Table II.3).

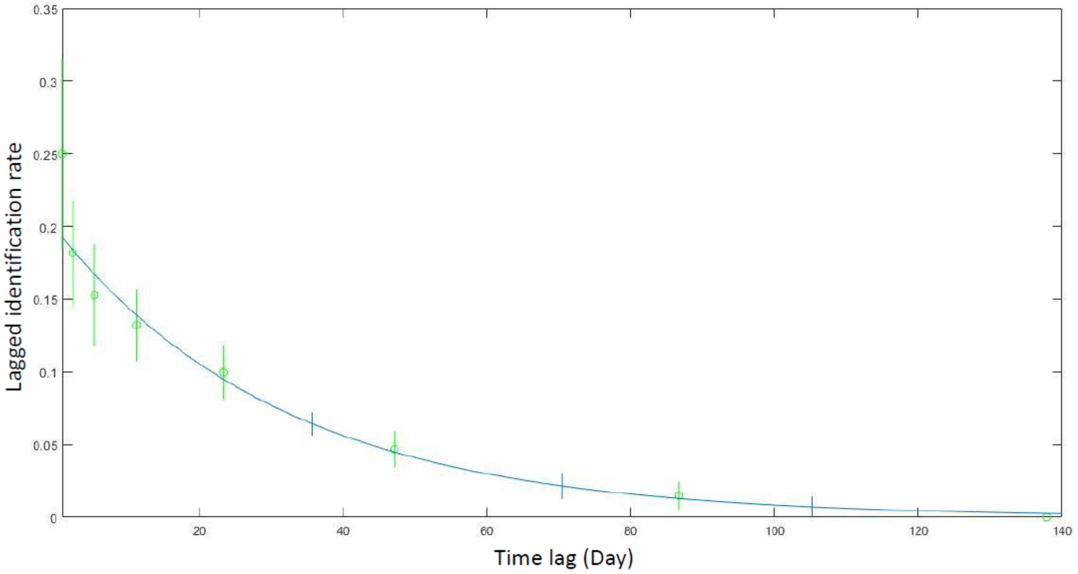

Figure II.4 Lagged identification rates (LIRs) for Bryde's whales during the peak season in 2014. The figure shows the probability that an individual identified in the study area at any time will be identified again in the study area some time lag later. The line represents the best-fitting model according to Table III.3, and the vertical bars indicate SEs calculated using the bootstrap method.

Table II.3 Models fitted to lagged identification rates (LIRs) for Bryde's whales in Madeira in the peak season of 2014, using SOCPROG.

Model	No. of parameters	AIC	Summed log likelihood
Emigration/Mortality	2	1724,592	-860,296
Emigration + Reimmigration	3	1726,592	-860,296
Emigration + Reimmigration + Mortality	4	1727,597	-859,7986
Closed	1	1888,076	-943,0381

* The differences in AIC of the two best fitted models is of two values, which according to Burnham and Anderson (2002) is indicative that both models may offer support. The first model was chosen based on the principle of parsimony recommended by these authors, being the simplest model and the one with the lowest standard errors. From a biological perspective, the chosen model is more adequate taking into consideration the migration behavior of this species and the capture histories observed.

Inter-archipelago movements

Seven Bryde's whales were identified in both archipelagos (Figure II.1; Table II.4). Of these, four individuals were identified only once in Madeira and once or twice in the Canaries. Three individuals were identified multiple times in both archipelagos: one whale, 'Bbr011/Izar', travelled to and from the Canaries in different years, and two individuals 'Bbr015/Scorpio' and 'Bbr032/Draco' were seen in both archipelagos in the same year, with a minimum of 43 days between consecutive inter-archipelago sightings. Six (out of the seven) individuals were captured more often in Madeira than in the Canaries (Figure II.1).

Table II.4 Identification (ID) matches of individuals in the Madeira Archipelago and the Canaries, with reference to the sighting history for each individual in the respective archipelago.

Madeira ID	Sighting history MAD	Canaries ID	Sighting history CAN	Movements between archipelagos
OOM_Bbr011	Jan2008 Sep2009 May2011 Sep2017	IZAR (BE_TS_A_013)	Jul2014 Jan2020	Mad - Mad - Mad - Can - Mad - Can *different years*
OOM_Bbr015	Aug2007 Jan2008 Aug2011 Nov2014 Jan, Aug, Sep2015	SCORPIO (BE_GIG_D_012)	May2014 Jul2015 Mar2017	Mad - Mad - Mad - Can - Mad - Mad - Can - Mad - Can *some in the same year*
OOM_Bbr032	Sep2005 Jul2006 Jul, Aug, Sep2014 Oct2017	DRACO (BE_TS_A_015)	May2005 Jul2007 Apr2014 Mar2015	Can - Mad - Mad - Can - Can - Mad - Can - Mad *some in the same year*
OOM_Bbr038	Nov2014	NORMA (BE_FV_D_030)	Sept2016	Mad - Can
OOM_Bbr040	Nov2014	CORONA (BINI_TS_I_054)	Sept2016	Mad - Can
OOM_Bbr051	Oct2017	SPICA (Bin_TS_I_001)	Jan2019	Mad - Can
New ind_2019	Jun2019	HYDRA (BE_TS_A_018)	May2017 Apr, May2018	Can - Can - Mad

Discussion

This study provides novel information on Bryde's whale site fidelity and movements in the North-East Atlantic. It shows that the Madeira Archipelago represents an important seasonal migration area for Bryde's whales, with some individuals demonstrating long-term site fidelity that may span across decades. The residency times estimated here are indicative of the moderate usage (of about a month) of the area by the species during the peak season. Moreover, this study shows that some individuals move between

Madeira and the Canaries archipelagos and that movements may occur within the same year, demonstrating that this species explores and moves regularly within the Macaronesian basin. To the best of our knowledge, this is the first study evaluating site fidelity and connectivity between archipelagos of a baleen whale species in Macaronesia, which is important for the establishment of conservation measures at both national and transborder levels.

Although site fidelity has been described commonly in migratory cetacean species at either feeding or breeding grounds (e.g. Lockyer & Brown, 1981; Valenzuela et al., 2009; Barendse et al., 2013), Bryde's whales do not undertake such long-range migrations and seem to feed regularly rather than relying on stored reserves (characteristic of income breeders; Constantine et al., 2018). These high energetic requirements may be an important driver of seasonal fluctuations in Bryde's whales (Tardin et al., 2017), although other studies have also described physiographic and oceanographic influences (Corkeron et al., 2011; Weir, MacLeod & Pierce, 2012). The results of this study indicate a large degree of variability in site fidelity for Bryde's whales in the Madeira Archipelago. The majority of the individuals were captured only once, whereas others (resighting rate of 0.46) presented both intra-seasonal or inter-annual site fidelity, even across a decade (two individuals with 10 and 12 years between first and last sightings). Despite the opportunistic nature of the data, there was negligible variability in the sighting effort (i.e. number of boats, trips, or photographers, and in the type of trips and photographic equipment) across the study period, indicating that this large degree of variability in site fidelity can be mainly attributed to the variable migration patterns of Bryde's whales. This is in accordance with Tezanos-Pinto et al. (2017), who also found variable results on site fidelity of Bryde's whales in New Zealand, but with the use of dedicated surveys. The innovative analysis of residency times with lagged identification rates revealed the moderate usage of the area by a few individuals (five, SE = 2) for 32 days (SE = 108 days), after migrating and not returning in the same year. Although the best-fitting model considers that emigration or mortality could be responsible for the absence of the animals, emigration is the most likely ecological explanation (e.g. Lodi et al., 2015; Tezanos-Pinto et al., 2017; Alves et al., 2018a). Cetaceans are long-lived animals and taking the study period into account, annual natural mortality is not a reasonable explanation for this absence. Also, by being a migratory species, they are expected to leave the area, and with individuals being resighted in the following years, this reinforces the ecological explanation of emigration for this analysis. Notwithstanding, anthropogenic causes of mortality pose a threat for many species of large whales (e.g. Constantine et al., 2015; Fais et al., 2016; Dolman & Brakes, 2018; Fossi et al., 2018), and cannot be disregarded.

The connectivity found in this study between neighbouring oceanic archipelagos in Macaronesia for Bryde's whales was expected, taking into consideration the biogeographical similarities between the Madeira Archipelago and the Canaries (Freitas et al., 2019), and the migration behaviour of Bryde's whales within oceanic basins (Kato & Perrin, 2018). These movements are also in accordance with what is observed for other species in the same area (e.g. Steiner et al., 2015; Alves et al., 2019; Dinis et al., 2021). Studies on Bryde's whales have demonstrated movements of individuals between closer areas (e.g. with the maximum of 294 km between Ecuator and Peru; Castro et al., 2017) and with an interval of a few years (e.g. with a maximum of 8 years in Brazil; Lodi et al., 2015), but this is the first study to demonstrate movements across such a large period of time and distance in an open ocean environment. As observed in the Madeira Archipelago, Bryde's whales are also seen feeding in the Canaries and accompanied by young individuals, although there are no birthing records or newborn sightings (Jacobo Marrero, pers. comm.). For oceanic marine mammals such as these, the home ranges tend to be large owing to the lower productivity of such waters (Silva et al., 2008). However, other factors besides energetic requirements, such as reproductive strategies or intraspecific competition (Stevick et al., 2006; Alves et al., 2018a), may play a role in determining their distribution. The described movements of Bryde's whales between archipelagos may be associated with several factors that still require further investigation.

Bryde's whales in the North-East Atlantic appear to have their northernmost limit in the Azores, and range south as far as Cape Verde and Senegal (Reiner, dos Santos & Wenzel, 1996; Hazevoet & Wenzel, 2000; Steiner et al., 2008). Weir (2010) documented Bryde's whales in the Gulf of Guinea, but with no indication of the season, whereas Best (2001) identified the migration of a South African stock to the waters of Gabon from May until July, after which the whales returned south. No information exists on the occurrence of Bryde's whales between the Gulf of Guinea and Cape Verde and Senegal. However, the temporal occurrence of Bryde's whales in Macaronesia (between June and November) and in the Gulf of Guinea (between May and July) suggests that these individuals might not belong to the same population, and therefore reveal the possible presence of two populations in the East Atlantic. Future studies should include satellite telemetry, which provides important information regarding movement and migrations, and genetic studies to investigate population structuring along the East Atlantic.

Although the use of platforms of opportunity for data collection, as in the case of this study, provides cost-effective and regular access to large datasets (e.g. Moura, Sillero & Rodrigues, 2012; Hupman et al., 2014; Vinding et al., 2015; Alves et al., 2018b; Alves et al., 2019), it presents specific limitations and biases: spatial and temporal restrictions of the surveyed area; a lack of data on effort or vessel tracks; species misidentification by inexperienced observers; unequal sampling effort; and inadequate vessel manoeuvring around an individual/group that affects the quality of the photographs (Moura, Sillero & Rodrigues, 2012; Hupman et al., 2014; New et al., 2015; Vinding et al., 2015; Alves et al., 2018b). Even though some of these limitations are unavoidable, others may be easily resolved with the proper training of crew members for data collection (both sighting and photographic data) and the implementation of specific sampling protocols (Hupman et al., 2014), as well as specific analysis to minimize bias (Moura, Sillero & Rodrigues, 2012). The lack of scientific design in sampling trip routes in this study was balanced by the optimized effort in searching for the whales in the study area (i.e. with the use of lookouts and excellent communication between most of the boats) that resulted in a high number of photographs. The overall quality of the photographs used (63.2% of good quality photographs) indicates that, despite the photographs being taken by experienced crew members with good photographic equipment, there is a need for training in order to increase this value. To avoid misidentification errors between Bryde's and sei whales (which are also present in Madeiran waters), photographs were only used if it was possible to confirm the species. Species identification was conducted either on board or a posteriori through photographic analysis (i.e. if the three ridges on the rostrum were visible or if the dive profile was identifiable; Kato & Perrin, 2018). With the spatial restriction of the surveyed area, it is assumed that these outputs are limited to the south coast of Madeira Island. Nevertheless, the size of the covered area (nearly half of the main island of the archipelago), together with the large temporal scale of the study (decadal), allowed for an otherwise difficult and expensive collection of data. Finally, the difference of the two values in the AIC between the best and the second-best model (Table 3), near the limit of offering substantial support (Burnham & Anderson, 2002), is most likely caused by the opportunistic nature of the data and requires caution when interpreting these results (Alves et al., 2018a). Therefore, this study provides baseline information that should be supplemented in future research with dedicated scientific surveys covering a wider area.

The update of the conservation status of the Bryde's whale by the International Union for Conservation of Nature (IUCN) in 2018 from Data Deficient to Least Concern (Cooke & Brownell, 2018) is indicative of the improved knowledge of this species. However, when making management decisions a precautionary approach should be taken, as recommended by Constantine et al. (2018). Caution is warranted because of the uncertainty in the number of species classified as Bryde's whales, which is still under consideration (as recently demonstrated by the establishment of a new species, Rice's whale, *Balaenoptera ricei*, which was previously classified as a Bryde's whale; Rosel et al., 2021), and also because information on the connectivity between populations is still lacking. This study sheds new light on the migratory patterns of this species in the North-East Atlantic and on the range to which conservation measures should be established. In spite of the lack of information regarding anthropogenic causes of death of this species in Macaronesia, Sousa et al. (2019) considers Bryde's whales to be one of the most vulnerable species to climate change in the Madeira Archipelago, and they may also be threatened by marine traffic (Cunha et al., 2017). Ship strikes are one of the main threats that large whales face worldwide, but especially in the Canaries because of the prevalence of fast ferries (Fais et al., 2016). Ingestion of plastic debris or entanglement have been reported in more than 60% of all cetacean species (Fossi et al., 2018) and has been recently documented for Bryde's whales in the Madeira Archipelago, where a whale-watching operator filmed a severely emaciated whale with a net closing its mouth that prevented the animal from feeding (August 2020, see Acknowledgements). This individual (Bbr028) was identified as a female (as it had been observed with calves in the past) and was one of the longest known (recaptured) individuals in the study, but was not seen again following this event. In addition to these direct sources of mortality, the exposure of cetaceans to the whale-watching activity that occurs in both archipelagos cannot be disregarded, and the associated chronic stress, displacement, or change in behaviour may translate into declines in health and vital rates (Wright, Aguilar Soto & Baldwin, 2007; Parsons, 2012).

The knowledge of movement patterns of migratory oceanic species is crucial to better understand the conservation implications at both geographical and geopolitical levels. By moving within the Macaronesian basin, Bryde's whales are subjected to several sources of anthropogenic disturbance, and policymakers must consider this information when establishing conservation measures. In the Canaries, the recent classification of Tenerife as a Whale Heritage Site, the first in European waters, has brought international attention to cetaceans in the area, as well as in the Madeira Archipelago, with the establishment of a Site of Community Importance to a depth of 2,500 m for cetaceans within the exclusive economic zone (EEZ). Both these mechanisms are important steps in the further protection of cetacean species in both areas. The introduction of speed limits for fast ferries or changing their routes in the Canaries, and the prohibition of such ferries in the Madeira Archipelago (where they do not yet exist) are recommended measures to mitigate one of the main causes of high whale mortality. The placement of observers on board these ferries should be encouraged, as is already happening on cargo ships operating in this area (Correia et al., 2020). Observers are an effective way to monitor ship strikes and to aid in the identification of areas where they are more likely to occur. Regarding entanglement, the enforcement of regulations targeting the reduction of ghost nets in the oceanic waters of Macaronesia should be debated both by local authorities and by specialist groups (i.e. IUCN Cetacean Specialist Group), as this area has been shown to be a vital component in the movement ecology of several cetacean species. Finally, the continued monitoring of whale-watching activity is of key importance, for the identification of species and populations that are more sensitive to this source of disturbance. Other platforms of opportunity, such as fishing vessels, should also be taken into consideration for data collection as they regularly travel to more offshore areas (Zhang et al., 2021).

This is the first study analysing the movement patterns of Bryde's whales in the North-East Atlantic, confirming intra- and inter-annual site fidelity to a specific island as well as inter-archipelago movements. Marine oceanic species such as Bryde's whales are increasingly exposed to anthropogenic threats and their conservation is a complex process that requires coordinated actions between several stakeholders (e.g. policymakers, researchers, and whale-watching operators) from all of the countries within their distribution range (Dunn et al., 2019). The fact that the inter-archipelago movements described in this study involve the outermost regions of two European countries requires particular attention for concerted policies towards the conservation of the species.

Acknowledgements

We thank the photographers Nicolau Abreu, Cláudio Martins, Luís Dias, Dinarte Sousa, Filipe Moura, Zofia Halicka, Vanessa Pires, Leonardo Berninsone, Claudia Gomes, Paula Thake, Heather Bodie, and Ágatha Gil. We also thank the whale-watching companies Lobosonda, H2O Madeira, VMT-Madeira, and Ventura|Nature Emotions. We are grateful to Eliette Hamard for helping with the update of the catalogue. We thank Gustavo Silva (OOM) for helping with the map. We thank Ashlie J. McIvor for the English language editing and review, and Marc Fernandez for inputs in the revision process. We are grateful to Hal Whitehead for valuable input confirming the use of the seasonal peak data in the LIR analysis. We thank Francisco do Carmo for sharing the video of the entangled Bryde's whale (available at https://www.facebook.com/groups/CetalFauna/permalink/3187352524718271). RF was supported by the Oceanic Observatory of Madeira (M1420-01-0145-FEDER-000001-OOM) and by Fundação para a Ciência e a Tecnologia (FCT) doctoral grant (SFRH/BD/147225/2019). AB was supported by MARE-ARDITI (ARDITI-MARE-2019-003). AS was financially supported by an FCT doctoral grant (SFRH/BD/141609/2018). FA and

AD acknowledge Madeira's Regional Agency for the Development of Research, Technology and Innovation (ARDITI) for funding their research throughout the project M1420-09-5369-FSE-000002. This study had the support of the FCT throughout the strategic project UID/MAR/04292/2020 granted to MARE.

References

Afonso, P., Fontes, J., Giacomello, E., Magalhães, M.C., Martins, H.R., Morato, T. et al. (2020). The Azores: A mid-Atlantic hotspot for marine megafauna research and conservation. *Frontiers in Marine Science*, 6, 826. https://doi.org/10.3389/fmars.2019.00826

Alves, F., Alessandrini, A., Fernandez, M., Hartman, K.L. & Dinis, A. (2018a). Home sweet home? Wide-ranging movements of socially stable residents delphinids (*Globicephala macrochynchus*). *Scientia Insularum*, 1, 37–49. https://doi.org/10.25145/j.SI.2018.01.004

Alves, F., Alessandrini, A., Servidio, A., Mendonça, A.S., Hartman, K.L., Prieto, R. et al. (2019). Complex biogeographical patterns support an ecological connectivity network of a large marine predator in the northeast Atlantic. *Diversity and Distributions*, 25(2), 269–284. https://doi.org/10.1111/ddi.12848

Alves, F., Dinis, A., Cascão, I. & Freitas, L. (2010). Bryde's whale (*Balaenoptera brydei*) stable associations and dive profiles: New insights into foraging behavior. *Marine Mammal Science*, 26(1), 202–212. https://doi.org/10.1111/j.1748-7692.2009.00333.x

Alves, F., Ferreira, R., Fernandes, M., Halicka, Z., Dias, L. & Dinis, A. (2018b). Analysis of occurrence patterns and biological factors of cetaceans based on long-term and fine-scale data from platforms of opportunity: Madeira Island as a case study. *Marine Ecology*, 39(2), e12499. https://doi.org/10.1111/maec.12499

Alves, F., Quérouil, S., Dinis, A., Nicolau, C., Ribeiro, C., Freitas, L. et al. (2013). Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: Implications for conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 23(5), 758–776. https://doi.org/10.1002/aqc.2332

Anguita, F. & Hernan, F. (2000). The Canary Islands origin: A unifying model. Journal of Volcanology and Geothermal Research, 103(1-4), 1–26. https://doi.org/10.1016/S0377-0273(00)00195-5

Athayde, A., Cardoso, J., Francisco, A. & Siciliano, S. (2020). Bryde's whales (*Balaenoptera brydei*) off the north coast of São Paulo, Brazil: First photo-identification study. *Aquatic Mammals*, 46(5), 488–501. https://doi.org/10.1578/AM.46.5.2020.488

Baird, R.W., Gorgone, A.M., McSweeney, D.J., Ligon, A.D., Deakos, M.H., Webster, D.L. et al. (2009). Population structure of island associated dolphins: Evidence from photo-identification of common bottlenose dolphins (*Tursiops truncatus*) in the main Hawaiian Islands. *Marine Mammal Science*, 25(2), 251–274. https://doi.org/10.1111/j.1748-7692.2008.00257.x

Baird, R.W., Webster, D.L., Mahaffy, S.D., McSweeney, D.J., Schorr, G.S. & Ligon, A.D. (2008). Site fidelity and association patterns in a deepwater dolphin: Rough-toothed dolphins (*Steno bredanensis*) in the Hawaiian Archipelago. *Marine Mammal Science*, 24(3), 535–553. https://doi.org/10.1111/j.1748-7692.2008.00201.x

Barendse, J., Best, P.B., Carvalho, I. & Pomilla, C. (2013). Mother knows best: Occurrence and associations of resighted humpback whales suggest maternally derived fidelity to a Southern Hemisphere coastal feeding ground. *PLoS ONE*, 8(12), e81238. https://doi.org/10.1371/journal.pone.0081238

Bastida, R. & Rodriguez, D. (2009). *Marine mammals of Patagonia and Antarctica*. Buenos Aires, Argentina: Vasquez Mazzini Editores.

Best, P. (1977). Two allopatric forms of Bryde's whale off South Africa. Report of the International Whaling Commission, 10-38.

Best, P.B. (2001). Distribution and population separation of Bryde's whale Balaenoptera edeni off southern Africa. *Marine Ecology Progress Series*, 220, 277–289. https://doi.org/10.3354/meps220277

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information theoretic approach*. New York: Springer Verlag.

Carrillo, M., Pérez-Vallazza, C. & Álvarez-Vázquez, R. (2010). Cetacean diversity and distribution off Tenerife (Canary Islands). *Marine Biodiversity Records*, 3(E97), 1–9. https://doi.org/10.1017/S1755267210000801

Castro, C.A., Rasmussen, K., Pacheco, A.S., Cardenas, D., Carnero-Human, R., Echeverria, G. et al. (2017). Bryde's whale *Balaenoptera edeni* occurrence and movements in coastal areas off Ecuador, Peru and Panama. A preliminary report. (No. SC/67A/SH15). International Whaling Commission.

Committee on Taxonomy. (2020). List of marine mammal species and subspecies. Society for Marine Mammalogy. Available at: www.marinemammalscience.org [Accessed August 2020]

Constantine, R., Iwata, T., Nieukirk, S.L. & Penry, G.S. (2018). Future directions in research on Bryde's whales. *Frontiers in Marine Science*, 5, 333. https://doi.org/10.3389/fmars.2018.00333

Constantine, R., Johnson, M., Riekkola, L., Jervis, S., Kozmian-Ledward, L., Dennis, T. et al. (2015). Mitigation of vessel-strike mortality of endangered Bryde's whales in the Hauraki Gulf, New Zealand. *Biology Conservation*, 186(1), 49–157. https://doi.org/10.1016/j.biocon.2015.03.008

Cooke, J.G. & Brownell Jr., R.L. (2018). *Balaenoptera edeni*. The IUCN Red List of Threatened Species. e.T2476A50349178. https://doi.org/10.2305/IUCN.UK.2018-1.RLTS.T2476A50349178.en. Downloaded on 23 November 2020.

Corkeron, P.J. & Connor, R.C. (1999). Why do baleen whales migrate? *Marine Mammal Science*, 15(4), 1228–1245. https://doi.org/10.1111/j.1748-7692.1999.tb00887.x

Corkeron, P.J., Minton, G., Collins, T., Findlay, K., Willson, A. & Baldwin, R. (2011). Spatial models of sparse data to inform cetacean conservation planning: An example from Oman. *Endangered Species Research*, 15(1), 39–52. https://doi.org/10.3354/esr00367

Correia, A.M., Gil, A., Valente, R.F., Rosso, M., Sousa-Pinto, I. & Pierce, G.J. (2020). Distribution of cetacean species at a large scale—Connecting continents with the Macaronesian archipelagos in the eastern North Atlantic. *Diversity and Distributions*, 26(10), 1234–1247. https://doi.org/10.1111/ddi.13127

Cunha, I., Freitas, L., Alves, F., Dinis, A., Ribeiro, C., Nicolau, C. et al. (2017). Marine traffic and potential impacts towards cetaceans within the Madeira EEZ. *Journal of Cetacean Research and Management*, 16, 17–28.

De Boer, M.N. (2010). Cetacean distribution and relative abundance in offshore Gabonese waters. *Journal of the Marine Biological Association of the United Kingdom*, 90(8), 1613–1621. https://doi.org/10.1017/S0025315410001165

Dinis, A., Alves, F., Nicolau, C., Ribeiro, C., Kaufmann, M., Cañadas, A. et al. (2016). Bottlenose dolphin *Tursiops truncatus* group dynamics, site fidelity, residency and movement patterns in the Madeira Archipelago (North-East Atlantic). *African Journal of Marine Science*, 38(2), 151–160. https://doi.org/10.2989/1814232X.2016.1167780

Dinis, A., Alves, F., Nicolau, C., Ribeiro, C., Kaufmann, M., Cañadas, A. et al. (2017). Social structure of a population of bottlenose dolphins (*Tursiops truncatus*) in the oceanic archipelago of Madeira, Portugal. *Journal of the Marine Biological Association of the United Kingdom*, 98(5), 1141–1149. https://doi.org/10.1017/S0025315417000650

Dinis, A., Molina, C., Tobeña, M., Sambolino, A., Hartman, K., Fernandez, M. et al. (2021). Large-scale movements of common bottlenose dolphins in the Atlantic: Dolphins with an international courtyard. *PeerJ*, 9, e11069. https://doi.org/10.7717/peerj.11069

Dolman, S.J. & Brakes, P. (2018). Sustainable fisheries management and the welfare of bycaught and entangled cetaceans. *Frontiers in Veterinary Science*, 5, 287. https://doi.org/10.3389/fvets.2018.00287

Dulau-Drouot, V., Fayan, J., Mouysser, L. & Boucaud, V. (2012). Occurrence and residency patterns of humpback whales off Réunion Island during 2004–10. *Journal of Cetacean Research and Management*, 12(2), 255–263.

Dunn, D.C., Harrison, A.L., Curtice, C., DeLand, S., Donnelly, B., Fujioka, E. et al. (2019). The importance of migratory connectivity for global ocean policy. *Proceedings of the Royal Society Series B*, 286(1911), 20191472. https://doi.org/10.1098/rspb.2019.1472

Evans, P.G. & Hammond, P.S. (2004). Monitoring cetaceans in European waters. *Mammal Review*, 34(1–2), 131–156. https://doi.org/10.1046/j.0305-1838.2003.00027.x

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. https://doi.org/10.1371/journal.pone.0150660

Fernandez, M., Alves, F., Ferreira, R., Fischer, J.C., Thake, P., Nunes, N. et al. (2021). Modeling Fine-Scale Cetaceans' Distributions in Oceanic Islands: Madeira Archipelago as a Case Study. *Frontiers in Marine Science*, 8, 688248. https://doi.org/10.3389/fmars.2021.688248

Figueiredo, L.D., Tardin, R.H., Lodi, L., Maciel, I.S., Alves, M.A.S. & Simão, S.M. (2014). Site fidelity of Bryde's whales (*Balaenoptera edeni*) in Cabo Frio Region, Southeastern Brazil, through photoidentification technique. *Brazilian Journal of Aquatic Sciences and Technology*, 18(2), 59–64. https://doi.org/10.14210/bjast.v18n2.p59-6

Fossi, M.C., Panti, C., Baini, M. & Lavers, J.L. (2018). A review of plastic-associated pressures: Cetaceans of the Mediterranean Sea and eastern Australian shearwaters as case studies. *Frontiers in Marine Science*, 5, 173. https://doi.org/10.3389/fmars.2018.00173

Freitas, L., Dinis, A., Nicolau, C., Ribeiro, C. & Alves, F. (2012). New records of cetacean species for Madeira Archipelago with an updated checklist. *Boletim Do Museu Municipal do Funchal*, 62, 25–43.

Freitas, R., Romeiras, M., Silva, L., Cordeiro, R., Madeira, P., González, J.A. et al. (2019). Restructuring of the “Macaronesia” biogeographic unit: A marine multi-taxon biogeographical approach. *Scientific Reports*, 9, 15792. https://doi.org/10.1038/s41598-019-51786-6

Geijer, C.K.A., Notarbartolo di Sciara, G. & Panigada, S. (2016). Mysticete migration revisited: Are Mediterranean fin whales an anomaly? *Mammal Review*, 46(4), 284–296. https://doi.org/10.1111/mam.12069

Geldmacher, J., Van Den Bogaard, P., Hoernle, K. & Schmincke, H.U. (2000). The 40Ar/39Ar age dating of the Madeira Archipelago and hotspot track (eastern North Atlantic). *Geochemistry, Geophysics, Geosystems*, 1(2), 1999GC000018. https://doi.org/10.1029/1999GC000018

Gowans, S., Whitehead, H., Arch, J.K. & Hooker, S.K. (2000). Population size and residency patterns of northern bottlenose whales (*Hyperoodon ampullatus*) using the Gully, Nova Scotia. *Journal of Cetacean Research and Management*, 2(3), 201–210.

Hauser, D.D.W., VanBlaricom, G.R., Holmes, E.E. & Osborne, R.W. (2006). Evaluating the use of whale watching data in determining killer whale (Orcinus orca) distribution patterns. *Journal of Cetacean Research and Management*, 8(3), 273–281.

Hays, G.C., Ferreira, L.C., Sequeira, A.M.M., Meekan, M.G., Duarte, C.M., Bailey, H. et al. (2016). Key questions in marine megafauna movement ecology. *Trends in Ecology & Evolution*, 31(6), 463–475. https://doi.org/10.1016/j.tree.2016.02.015

Hazevoet, C.J. & Wenzel, F.W. (2000). Whales and dolphins (Mammalia, Cetacea) of the Cape Verde Islands, with special reference to the humpback whale Megaptera novaeangliae (Borowski, 1781). *Contributions to Zoology*, 69(3), 197–211. https://doi.org/10.1163/18759866-06903004

Horton, T.W., Hauser, N., Zerbini, A.N., Francis, M.P., Domeier, M.L., Andriolo, A. et al. (2017). Route fidelity during marine megafauna migration. *Frontiers in Marine Science*, 4, 422. https://doi.org/10.3389/fmars.2017.00422

Hoyt, E. (2005). *Marine protected areas for whales, dolphins and porpoises: a world handbook for cetacean habitat conservation*. London, UK: Earthscan.

Hupman, K., Visser, I.N., Martinez, E. & Stockin, K.A. (2014). Using platforms of opportunity to determine the occurrence and group characteristics of orca (*Orcinus orca*) in the Hauraki Gulf, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 49(1), 132–149. https://doi.org/10.1080/00288330.2014.980278

Kaschner, K., Quick, N.J., Jewell, R., Williams, R. & Harris, C.M. (2012). Global coverage of cetacean line-transects surveys: Status quo, data gaps and future challenges. *PLoS ONE*, 7(9), e44075. 10.1371/journal.pone.0044075

Kato, H. & Perrin, W. (2018). Bryde's whale *Balaenoptera edeni*. In: B. Würsig, J.G.M. Thewissen, K.M. Kovacs (Eds.) *Encyclopedia of marine mammals*, 3rd edition. London, UK: Academic Press, pp. 143–145.

Katona, S., Baxter, B., Brazier, O., Kraus, S., Perkins, J. & Whitehead, H. (1979). Identification of humpback whales by fluke photographs. In: H.E. Winn, B.L. Olla (Eds.) *Behavior of marine animals*. Boston, MA: Springer. https://doi.org/10.1007/978-1-4684-2985-5_2

Kershaw, F., Leslie, M.S., Collins, T., Rubaiyat, M.M., Smith, B.D., Minton, G. et al. (2013). Population differentiation of 2 forms of Bryde's whales in the Indian and Pacific Oceans. *Journal of Heredity*, 104(6), 755–764. https://doi.org/10.1093/jhered/est057

Kim, S.C., McGowen, M.R., Lubinsky, P., Barber, J.C., Mort, M.E. & Santos-Guerra, A. (2008). Timing and tempo of early and successive adaptive radiations in Macaronesia. *PLoS ONE*, 3(5), e2139. https://doi.org/10.1371/journal.pone.0002139

Lindsey, P.A., Chapron, G., Petracca, L.S., Burnham, D., Hayward, M.W., Henschel, P. et al. (2017). Relative efforts of countries to conserve world's megafauna. *Global Ecology and Conservation*, 10, 243–252. https://doi.org/10.1016/j.gecco.2017.03.003

Lockyer, C.H. & Brown, S.G. (1981). The migration of whales. In: D.J. Aidley (Ed.) *Animal migration*. Cambridge: Cambridge University Press, pp. 105–138.

Lodi, L., Tardin, R.H., Hetzel, B., Maciel, I.S., Figueiredo, L.D. & Simão, S.M. (2015). Bryde's whale (Cetartiodactyla: Balaenopteridae) occurrence and movements in coastal areas of southeastern Brazil. *Zoologia*, 32(2), 171–175. https://doi.org/10.1590/S1984-46702015000200009

Mann, J. (1999). Behavioral sampling methods for cetaceans: A review and critique. *Marine Mammal Science*, 15(1), 102–122.

Miralles, L., Oremus, M., Silva, M.A., Planes, S. & Garcia-Vazquez, E. (2016). Interspecific hybridization in pilot whales and asymmetric genetic introgression in northern *Globicephala melas* under the scenario of global warming. PLoS ONE, 11(8), e0160080. https://doi.org/10.1371/journal.pone.0160080

Moura, A., Sillero, N. & Rodrigues, A. (2012). Common dolphin (*Delphinus delphis*) habitat preferences using data from two platforms of opportunity. *Acta Oecologica*, 38, 24–32. https://doi.org/10.1016/j.actao.2011.08.006

New, L.F., Hall, A.J., Harcourt, R., Kaufman, G., Parsons, E.C.M., Pearson, H.C. et al. (2015). The modelling and assessment of whale-watching impacts. *Ocean and Coastal Management*, 115, 10–16. https://doi.org/10.1016/j.ocecoaman.2015.04.006

Notarbartolo di Sciara, G., Politi, E., Bayed, A., Beaubrun, P.C. & Knowlton, A. (1998). A winter cetacean survey off southern Morocco, with a special emphasis on right whales. *Reports of the International Whaling Commission*, 48, 547–550.

Parsons, E.C.M. (2012). The negative impacts of whale-watching. *Journal of Marine Science*, 807294, 9. https://doi.org/10.1155/2012/807294

Pastene, L.A., Acevedo, J., Siciliano, S., Sholl, T.G.C., Moura, J.F., Ott, P.H. et al. (2015). Population genetic structure of the South American Bryde's whale. *Revista de Biología Marina Y Oceanografía*, 50(3), 453–464. https://doi.org/10.4067/S0718-19572015000400005

Pérez-Jorge, S., Tobeña, M., Prieto, R., Vandeperre, F., Calmettes, B., Lehodey, P. et al. (2020). Environmental drivers of large-scale movements of baleen whales in the mid-North Atlantic Ocean. *Diversity and Distributions*, 26(6), 1683–1698. https://doi.org/10.1111/ddi.13038

Pérez-Valazza, C., Álvarez-Vásquez, R., Cardona, L., Pintado, C. & Hernández-Brito, J. (2008). Cetacean diversity at the west coast of La Palma Island (Canary Islands). *Journal of the Marine Biological Association of the United Kingdom*, 88(6), 1289–1296. https://doi.org/10.1017/S0025315408001239

Prieto, R., Silva, M.A., Waring, G.T. & Gonçalves, J.M.A. (2014). Sei whale movements and behavior in the North Atlantic inferred from satellite telemetry. Endangered Species Research, 26(2), 103–113. https://doi.org/10.3354/esr00630

Quérouil, S., Freitas, L., Cascão, I., Alves, F., Dinis, A., Almeida, J.R. et al. (2010). Molecular insight into the population structure of common and spotted dolphins inhabiting the pelagic waters of the Northeast Atlantic. *Marine Biology*, 157(11), 2567–2580. https://doi.org/10.1007/s00227-010-1519-0

Quérouil, S., Silva, M.A., Freitas, L., Prieto, R., Magalhães, S., Dinis, A. et al. (2007). High gene flow in oceanic bottlenose dolphins (*Tursiops truncatus*) of the North Atlantic. *Conservation Genetics*, 8(6), 1405–1419. https://doi.org/10.1007/s10592-007-9291-5

Redfern, J.V., Ferguson, M.C., Becker, E.A., Hyrenbach, K.D., Good, C., Barlow, J. et al. (2006). Techniques for cetacean-habitat modeling. *Marine Ecology Progress Series*, 310, 271–295. https://doi.org/10.3354/meps310271

Reiner, F., dos Santos, M.E. & Wenzel, F.W. (1996). Cetaceans of the Cape Verde archipelago. Marine Mammal Science, 12(3), 434–443. https://doi.org/10.1111/j.1748-7692.1996.tb00595.x

Ritter, F. & Neumann, K. (2006). The year of the whale: extraordinary occurrence of Bryde's whales off La Gomera (Canary Islands) in 2005. Poster presented at the Annual Conference of the European Cetacean Society, Gdynia, Poland, April 2006.

Robbins, J., Rosa, L.D., Allen, J.M., Mattila, D.K., Secchi, E.R., Friedlaender, A.S. et al. (2011). Return movement of a humpback whale between the Antarctic Peninsula and American Samoa:

A seasonal migration record. *Endangered Species Research*, 13(2), 117–121. https://doi.org/10.3354/esr00328

Rosel, P.E. & Wilcox, L.A. (2014). Genetic evidence reveals a unique lineage of Bryde's whales in the northern Gulf of Mexico. *Endangered Species Research*, 25, 19–34. https://doi.org/10.3354/esr00606

Rosel, P.E., Wilcox, L.A., Yamada, T.K. & Mullin, K.D. (2021). A new species of baleen whale (Balaenoptera) from the Gulf of Mexico, with a review of its geographic distribution. *Marine Mammal Science*, 126(5), 644–645. https://doi.org/10.1111/mms.12776

Sequeira, A.M.M., Rodríguez, J.P., Eguíluz, V.M., Harcourt, R., Hindelle, M., Sims, D.W. et al. (2018). Convergence of marine megafauna movement patterns in coastal and open oceans. *Proceedings of the National Academy of Sciences of the United States of America*, 115(12), 3072–3077. https://doi.org/10.1073/pnas.1716137115

Silva, M., Prieto, R., Cascão, I., Seabra, M.I., Machete, M., Baumgartner, M.F. et al. (2014). Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. *Marine Biology Research*, 10(2), 123–137. https://doi.org/10.1080/17451000.2013.793814

Silva, M.A., Prieto, R., Magalhães, S., Seabra, M.I., Santos, R.S. & Hammond, P.S. (2008). Ranging patterns of bottlenose dolphins living in oceanic waters: Implications for population structure. *Marine Biology*, 156, 179–192. https://doi.org/10.1007/s00227-008-1075-z

Širović, A., Basset, H.R., Johnson, S.C., Wiggins, S.M. & Hildebrand, J.A. (2013). Bryde's whale calls recorded in the Gulf of Mexico. *Marine Mammal Science*, 30(1), 399–409. https://doi.org/10.1111/mms.12036

Sousa, A., Alves, F., Dinis, A., Bentz, J., Cruz, M.J. & Nunes, J.P. (2019). How vulnerable are cetaceans to climate change? Developing and testing a new index. *Ecological Indicators*, 98, 9–18. https://doi.org/10.1016/j.ecolind.2018.10.046

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M. et al. (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *Bioscience*, 57(7), 573–583. https://doi.org/10.1641/B570707

Steiner, L., Pérez, M., van der Linde, M., Freitas, L., dos Santos, R.P., Martin, V. et al. (2015). Long distance movements of female/immature sperm whales in the North Atlantic. Poster presented at the Biennial Society for Marine Mammalogy Conference, San Francisco, USA, December 2015.

Steiner, L., Silva, M.A., Zereba, J. & Leal, M.J. (2008). Bryde's whales, *Balaenoptera edeni*, observed in the Azores: A new species record for the region. *Marine Biodiversity Records*, 1, e66, 1–6. https://doi.org/10.1017/S1755267207007282

Stevick, P.T., Allen, J., Clapham, P.J., Katona, S.K., Larsen, F., Lien, J. et al. (2006). Population spatial structuring on the feedings grounds in North Atlantic humpback whales (*Megaptera novaeangliae*). *Journal of Zoology*, 270(2), 244–255. https://doi.org/10.1111/j.1469-7998.2006.00128.x

Stevick, P.T., Neves, M.C., Johansen, F., Engel, M.H., Allen, J., Marcondes, M.C.C. et al. (2011). A quarter of a world away: Female humpback whale moves 10 000 km between breeding areas. *Biology Letters*, 7(2), 299–302. https://doi.org/10.1098/rsbl.2010.0717

Tardin, R.H., Chun, Y., Simão, S.M. & Alves, M.A.S. (2017). Modeling habitat use by Bryde's whale *Balaenoptera edeni* off southeastern Brazil. *Marine Ecology Progress Series*, 576, 89–103. https://doi.org/10.3354/meps12228

Tershy, B.R. (1992). Body size, diet, habitat use, and social behavior of Balaenoptera whales in the Gulf of California. *Journal of Mammalogy*, 73(3), 477–486. https://doi.org/10.2307/1382013

Tezanos-Pinto, G., Hupman, K., Wiseman, N., Dwyer, S.L., Baker, C.S., Brooks, L. et al. (2017). Local abundance, apparent survival and site fidelity of Bryde's whales in the Hauraki Gulf (New Zealand) inferred from long-term photo-identification. *Endangered Species Research*, 34, 61–73. https://doi.org/10.3354/esr00839

Thums, M., Fernández-Gracia, J., Sequeira, A.M.M., Eguíluz, V.M., Duarte, C.M. & Meekan, M.G. (2018). How big data fast tracked human mobility research and the lessons for animal movement ecology. *Frontiers in Marine Science*, 5, 21. https://doi.org/10.3389/fmars.2018.00021

Valenzuela, L.O., Sironi, M., Rowntree, V.J. & Seger, J. (2009). Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). *Molecular Ecology*, 18(5), 782–791. https://doi.org/10.1111/j.1365-294X.2008.04069.x

Vinding, K., Bester, M., Kirkman, S.P., Chivell, W. & Elwen, S.H. (2015). The use of data from a platform of opportunity (whale watching) to study coastal cetaceans on the southwest coast of South Africa. *Tourism in Marine Environments*, 11(1), 33–54. https://doi.org/10.3727/154427315X14398263718439

Weir, C. (2010). A review of cetacean occurrence in West African waters from the Gulf of Guinea to Angola. *Mammal Review*, 40(1), 2–39. https://doi.org/10.1111/j.1365-2907.2009.00153.x

Weir, C.R., MacLeod, C.D. & Pierce, G.J. (2012). Habitat preferences and evidence for niche partitioning amongst cetaceans in the waters between Gabon and Angola, eastern tropical Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 92(8), 1735–1749. https://doi.org/10.1017/s0025315412000148

Whitehead, H. (2001). Analysis of animal movement using opportunistic individual identifications: Application to sperm whales. *Ecology*, 82(5), 1417–1432. https://doi.org/10.2307/2679999

Whitehead, H. (2007). Selection of models of lagged identification rates and lagged association rates using AIC and QAIC. *Communications in Statistics: Simulation and Computation*, 36(6), 1233–1246. https://doi.org/10.1080/03610910701569531

Whitehead, H. (2009). SOCPROG programs: Analyzing animal social structures. *Behavioral Ecology and Sociobiology*, 63(5), 765–778. https://doi.org/10.1007/s00265-008-0697-y

Wright, A.J., Aguilar Soto, N. & Baldwin, A.L. (2007). Do marine mammals experience stress related to anthropogenic noise? *International Journal of Comparative Psychology*, 20(2–3), 274–316. https://doi.org/10. 5070/P4202009994

Würsig, B. & Jefferson, T.A. (1990). Methods of photo-identification for small cetaceans. *Report of the International Whaling Commission (Special Issue)*, 12, 42–43.

Zhang, Y., Chen, M., Han, Y., Hao, Y., Wang, K., Mei, Z. & Wang, D. (2021). Community-based population monitoring for large baleen whales: The case study of Bryde's whale in Beibu Gulf of China. *Integrative Zoology*. https://doi.org/10.1111/1749-4877.12525

CHAPTER III - Unraveling Site Fidelity and Residency Patterns of Sperm Whales in the Insular Oceanic Waters of Macaronesia

This chapter is published as:

Ferreira, Rita, Lisa Steiner, Vidal Martín, Francesca Fusar Poli, Ana Dinis, Manfred Kaufmann, Marc Fernandez, and Filipe Alves. 2022. “Unraveling site fidelity and residency patterns of sperm whales in the insular oceanic waters of Macaronesia”. *Frontiers in Marine Science*, 9, 1021635. https://doi.org/10.3389/fmars.2022.1021635

CHAPTER III – Unraveling Site Fidelity and Residency Patterns of Sperm Whales in the Insular Oceanic Waters of Macaronesia

Abstract

Knowledge of the distribution and residency of pelagic marine megafauna, particularly deep-diving species, is scarce due to their high mobility over difficult-to-access oceanic areas and long periods underwater. However, the threatened status of many of these species, such as the sperm whale Physeter macrocephalus, increases the need to obtain quantitative data to support conservation measures. In the warm temperate waters of Macaronesia (Eastern North Atlantic), sperm whales occur year-round in a set of island systems (the Azores, Madeira, and the Canaries), mainly in social groups of females and juveniles with the occasional visits of mature males. Although it is known that they perform inter-archipelago movements, information on site fidelity and residency times is still scarce. Here, based on photographic identification data, site fidelity and residency times of sperm whales were estimated for subareas of the Azores and the Madeira archipelagos, with a preliminary assessment for a subarea of the Canaries. The Azores and Madeira subareas presented similar proportions of individuals with recaptures (≈25%), mainly inter-annual, while in the subarea of the Canaries, only <10% of the individuals were recaptured. Standardized Site Fidelity Indexes showed very low values (<0.01) for both the Azores and Madeira subareas. Lagged identification rates based on models including emigration and reimmigration estimated that an average of 44.8 individuals (SE=4.9) spent 12.9 days (SE=1.5) in the Azores before leaving for 99.1 days (SE=12.5), while 8.4 individuals (SE=16.1) spent 0.8 day (SE=6.6) in Madeira before leaving for 8.6 days (SE=6.9), with a very low mortality rate. This study i) indicates a degree of residency of about ¼ of the identified individuals for the Azores and Madeira subareas and ii) supports that these oceanic archipelagos constitute an important habitat for a Vulnerable species in the Atlantic. Moreover, it also highlights the importance of combining data from opportunistic and dedicated surveys and joint national and international efforts toward the conservation of marine megafauna.

KEYWORDS: marine megafauna, philopatry, transnational conservation, Atlantic, photographic identification, capture-recapture, habitat use

Introduction

Research and conservation of top oceanic predators present unique challenges due to their high mobility over difficult-to-access areas, with costly and logistically complex data collection. Most pelagic marine megafauna is not easily seen and has large ranges extending to offshore areas (Tittensor et al., 2010; Kaschner et al., 2011). In the case of deep-diving species, there are increased difficulties associated with their long submersion periods (Aoki et al., 2012; Li & Rosso, 2021; Badenas et al., 2022). Moreover, many of these species are of significant conservation concern and represent an ecologically and functionally important part of marine biodiversity (Katona & Whitehead, 1988; Schipper et al., 2008; Pimiento et al., 2020; Alves et al., 2022; Braun et al., 2022). Thus, information on the distribution and movements of these species is valuable for planning practical conservation efforts.

The sperm whale *Physeter macrocephalus*, the largest deep-diver and toothed animal, is distributed worldwide. It ranges from the ice edge in both hemispheres to tropical waters (Whitehead, 2018). Its distribution is highly connected to social structure and sex, with social groups of females and immatures inhabiting low and mid-latitudes. On the other hand, males leave their maternal groups and aggregate in bachelors' groups for a few years before living mainly solitary in high latitudes, returning to tropical and subtropical waters to mate (Cantor et al., 2019).

Sperm whales are globally classified as Vulnerable by the International Union for Conservation of Nature, with an unknown worldwide population trend (Taylor et al., 2019), with recent studies indicating a global population of 844 761 individuals (Whitehead & Shin, 2022). This species was extensively hunted worldwide since the 18th century, growing from a shore-based enterprise to industrial whaling that only ceased in the 1980s. This caused a decrease of 68% in the global population, with males being more heavily targeted (Whitehead, 2002; Whitehead, 2018). Due to the low reproduction rates of these long-lived mammals, the populations of sperm whales are still recovering. However, presently, they still face several threats, such as entanglement in fishing gear, ingestion of plastics, chemical pollution, or ship strikes (Schipper et al., 2008; Savery et al., 2013; Notarbartolo-Di-Sciara, 2014; Fais et al., 2016; Whitehead, 2018; Arregui et al., 2019).

The Macaronesian archipelagos of the Azores, Madeira, and Canaries (Eastern North Atlantic) are some of the most isolated oceanic habitats of the North Atlantic, surrounded by steep submarine canyons and deep waters due to their volcanic origin and lack of continental shelf (Carracedo & Troll, 2021), which offer easy access to study deep-divers and oceanic species. Here, social groups of females and immature sperm whales are present year-round, with the occasional presence of visiting males (André, 1997; Silva et al., 2014; Fernandez et al., 2021). This biogeographic region is known to be used by sperm whales for reproduction, besides feeding and calving (Clarke, 1956; André, 1997; Steiner et al., 2012; Correia-Fagundes & Romano, 2013; Silva et al., 2014; Alves et al., 2018; Mullin et al., 2022). The sperm whale was the target species of a whaling activity that killed around 26 000 individuals in the Azores and Madeira, while in the Canaries it was a residual activity. This resulted in a reduction of 55% of the population in this region (Cabral et al., 2005; Brito, 2008; Perez, 2011). Currently, these three archipelagos are important destinations for whale-watching, with as many as 30 cetacean species identified so far, where the sperm whale is one of the target species in the Azores and, to a lesser extent, in Madeira (Freitas et al., 2012; Silva et al., 2014; Ferreira et al., 2017; Alves et al., 2018; Cartagena-Matos et al., 2021; Herrera et al., 2021; McIvor et al., 2022). In Macaronesia, and specifically in the Canaries, collision with ships is nowadays a relevant threat to the population of sperm whales, presenting one of the world's highest rates of ship strikes, with an annual average of two stranded whales from ship-strikes (Fais et al., 2016). Due to the oceanic habits of sperm whales, many more events may go unreported in offshore waters, creating a high level of conservation concern. Therefore, the sperm whale is still vulnerable to human-induced disturbances in these remote archipelagos.

To understand population movement patterns and life history, it is essential to evaluate site fidelity and residency (Baird et al., 2008; Tschopp et al., 2018). Site fidelity, defined as the tendency of an animal to return to a previously occupied place, is a well-documented behavior in many taxonomic groups (e.g., birds, Hoover, 2003; Iverson & Esler, 2006; seals, Lunn & Boyd, 1991; Pomeroy et al., 2001; insects, Switzer, 1997). It is known to provide evolutionary benefits and may increase survival (Greenwood, 1980; Switzer, 1993; Bose et al., 2017). Sperm whales, like other mammalian species (e.g., deers, Bose et al., 2017; elephants, Archie et al., 2006), demonstrate female philopatry and male dispersal due to the higher dependency of females on local resources (Greenwood, 1980). Male sperm whales show limited site fidelity to their feeding grounds, with few possible resident individuals (Jaquet et al., 2000; Lettevall et al., 2002; Rødland & Bjørge, 2015; Somerford et al., 2021). On the other hand, females exhibit site fidelity across years in several locations (e.g., Caribbean, Gero et al., 2014; Mediterranean Sea, Drouot-Dulau & Gannier, 2007), which may lead to genetic differentiation of specific populations (Engelhaupt et al., 2009).

Studies exploring site fidelity and residency of sperm whales in the oceanic environment of the Eastern North Atlantic are limited to the archipelago of the Azores, where both photographic-identification and genetic studies indicate some degree of site fidelity in females, although there are no permanent resident individuals (Matthews et al., 2001; Silva et al., 2006; Pinela et al., 2009; van der Linde & Eriksson, 2020). The more than 40 individual photographic-identification matches within the Macaronesian archipelagos of the Azores, Madeira, and Canaries (Steiner et al., 2015; Steiner, 2022) indicate that these animals carry out inter-archipelago movements and support the existence of a single population in this region of the Atlantic. Nevertheless, quantitative information on site fidelity and residency times is limited (to one archipelago) or unavailable for Macaronesia.

Here, photographic data of sperm whales from three subareas of Macaronesian archipelagos were used to investigate and quantify this species' habitat use, with a main focus on Azores and Madeira. More specifically, composite indexes and likelihood techniques were applied to i) calculate the site fidelity of sperm whales in subareas of the Azores and Madeira, and ii) estimate residency times to inform on the movements in and out of these areas. Filling these knowledge gaps regarding population habitat use will provide novel insights into future coordinated efforts between the countries involved (i.e., Portugal and Spain) to establish transborder conservation measures.

Material and Methods

Study area

This study was conducted in subareas of three oceanic archipelagos of Macaronesia: around Pico and Faial islands in the Azores (approximately 3 500 km^2), south and southeast of Madeira island (approximately 800 km^2), and along the eastern coast of Lanzarote and Fuerteventura in the Canaries (approximately 6 500 km^2) (Figure III.1). The biogeographical unit of Macaronesia, by definition, also includes Cabo Verde islands; however, recent studies support the exclusion of the latter due to considerable differences, specifically regarding marine biodiversity, and aggregates the three remaining archipelagos in one province within the Lusitanian ecoregion (Spalding et al., 2007; Freitas et al., 2019). These warm-temperate archipelagos are located in the Eastern North Atlantic Ocean, between latitudes 28 and 39°N, and share natural, geological, oceanographic, and biogeographical features (Freitas et al., 2019). The Azores archipelago is located approximately 1 800 km west of Lisbon (Portugal), around the Mid-Atlantic Ridge, and is surrounded by very narrow shelves and steep slopes, with the frequent presence of seamounts, and a mean depth of about 3 000 m (Morato et al., 2008). The Madeira archipelago is located approximately 1 000 km off the European continent and 500 km off the African coast, being also surrounded by steep submarine canyons and deep waters (approximately 1 500 m in depth) very close to the coast, due to the lack of a continental shelf (Geldmacher et al., 2000). The Canaries archipelago is located 100 km off the African coastline and is formed by seven main islands, that extend over 500 km. The average depth increases towards the west, from depths of 1 200 m in Lanzarote and Fuerteventura (the most eastern islands) to 4 000 m in La Palma and Hierro (the most western islands) (Valdés & Déniz-González, 2015).

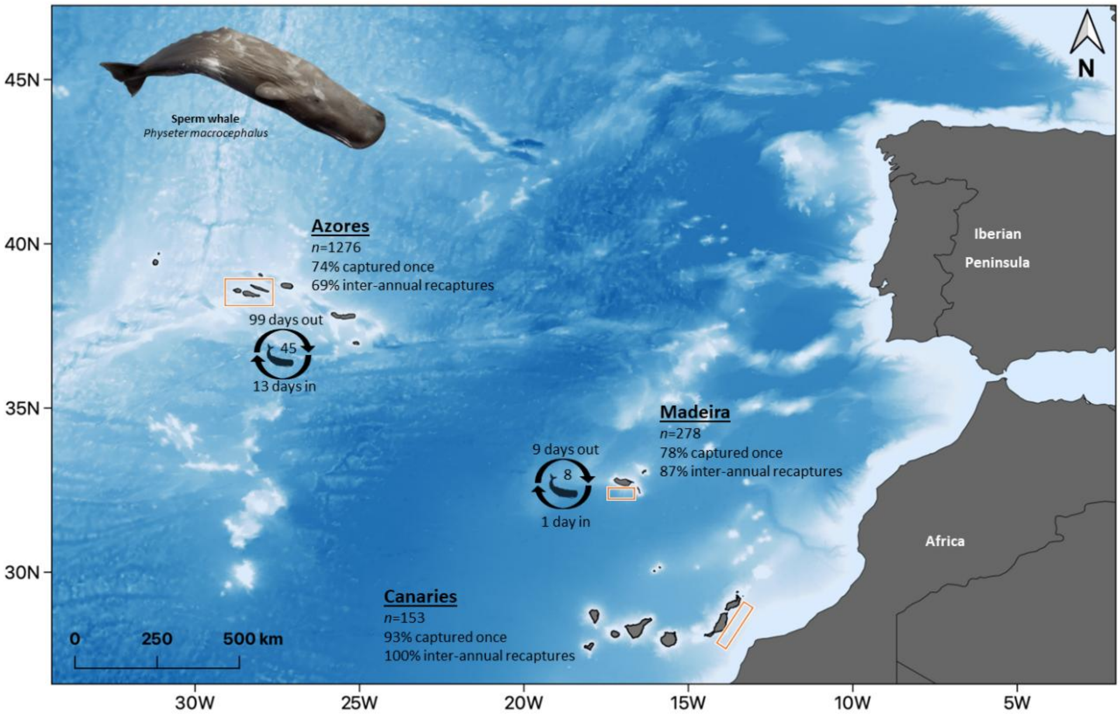

Figure III.1 Location of the study area in the Eastern North Atlantic, Macaronesia, formed by the archipelagos of the Azores, Madeira, and the Canaries. Bathymetry ranging from approximately 1 000 to 4000 m, from white to blue, respectively. n indicates the number of identified individuals in each archipelago. Percentages refer to the proportion of individuals captured once and of individuals recaptured inter-annually. Number of individuals and time spent in and out of the area refer to the estimates of the best model of lagged identification rates (Table III.2). Illustration by E. Berninsone © ARDITI.

Data collection and photographic analysis

Photographic-identification (hereafter, photo-id) data from sperm whales were collected in the three subareas. In the Azores, data was collected from April to October, from 2014 to 2019, during dedicated research and opportunistic surveys (whale-watching trips). In Madeira, data was collected year-round from 2007 to 2019 during dedicated research and opportunistic surveys (whale-watching trips). In the Canaries, data was collected year-round in 2009, 2011 and 2012 during dedicated research surveys.

In each subarea, photographs were collected and classified into a catalogue following standard photo-id procedures (Arnbom, 1987; Würsig & Jefferson, 1990). Sperm whale individuals were identified using photographs of the ventral or dorsal side of the fluke based on natural or acquired markings on the trailing edge. Scars and pigmentation patterns on the fluke and peduncle were used to confirm matches. Each photograph was graded for quality (from 1=poor to 4=excellent) and distinctiveness (from 1=non-distinctive to 4=very distinctive) (Alves et al., 2013). To maximize the reliability of each of the three catalogues (one per subarea), the analysis was limited to photographic quality and distinctiveness ratings from 2 to 4. Each catalogue was compiled visually by a single researcher and verified whenever needed by experienced secondary researchers.

For the three subareas, catalogues were analyzed to determine the number of individuals captured only once and of individuals that presented recaptures. Recaptured individuals were then classified taking into consideration if the recaptures were intra-annual (i.e. all the recaptures of the individual occurred within the same year) or inter-annual (i.e. at least one of the recaptures occurred in a different year). Percentages of the individuals captured once and with intra and inter-annual recaptures were then calculated, and the capture frequency histograms were plotted. Discovery curves were created by plotting the cumulative number of identifications against the number of identified individuals throughout the study period. When the population is fully identified, the curve reaches a plateau; but if the curve is continuously growing and no stabilization occurs, it means that there are still new individuals being added to the catalogue. This analysis was performed with Socprog 2.9 (Whitehead, 2009).

Site fidelity and residency analysis

Evaluation of site fidelity and residency were only conducted for the Azores and Madeira datasets, since the dataset from the Canaries presented very few recaptures, which did not allow further analysis. A truncated dataset was used for Madeira to homogenize the effort, restricting to the years with the highest effort, i.e. from 2014 to 2019.

Site fidelity of sperm whales was assessed using the Standardized Site Fidelity Index (SSFI), a composite site fidelity index developed by Tschopp et al. (2018). Definition and quantification of site fidelity varies greatly among research studies and is largely dependent on species behaviour, life cycle and research objectives, among others (Tschopp et al., 2018). Also, is usually done at an individual level. Therefore, the development of a standardized index that provided information of site fidelity at a populational level and allowed for comparison between studies was needed. SSFI was the index that had the best performance in all of the evaluated scenarios (both theoretical and with real data) and was calculated based on the indicators of permanence and periodicity.

Permanence (IT) is the proportion of time in the study area given by the time between the capture and last recapture (Fi), over the sampling period (F):

$$IT_i = \frac{F_i}{F}$$

Periodicity (It) is the recurrence of an individual, determined by the inverse of the average time between successive recaptures:

$$IT_i = \frac{F_i}{F}$$

where cij indicates a capture (one) or an absence to capture (zero) of an individual i on the sampling occasion j, and T is the number of sampling occasions.

SSFI is therefore defined as:

$$IT_i = \frac{F_i}{F}$$

SSFI quantifies site fidelity at a populational level using capture-recapture data and varies between zero (population without site fidelity) and one (resident population).

This index works when effort is not constant and when the detection of the subject presents difficulties. This is the case with cetaceans in general and sperm whales in particular, due to their long diving periods associated with feeding (Cantor et al., 2019).

Likelihood techniques were used to estimate parameters of residency models (Whitehead, 2001). These techniques use datasets where animals are identified individually, but the identifications are distributed neither randomly nor systematically in space or time, and where the identifications themselves are used as a measure of effort. To estimate residency times, we applied the models developed by Whitehead (2001), that evaluate the estimated population size in the study area, the amount of time an individual spends within an area and the movements into and out of that area. Lagged identification rates (LIR) were calculated, which estimate the probability that an individual identified in the study area at any given time will be identified again in the study area some time lag after (Whitehead, 2001). Due to overdispersion (when the variance inflation factor >3, which may represent fundamental problems with the data; Lebreton et al., 1992), data from the Azores was limited to the months with the most homogeneous number of identifications (June to September). Since overdispersion for the Madeira dataset <3, the entire year was used in the analysis. The sampling period was defined as day for both archipelagos. Estimated LIRs were compared to expected LIRs from exponential mathematical models of residency established by Whitehead (2001) and fitted using maximum-likelihood methods. The model with the lowest quasi-Akaike information criterion (QAIC) was selected as providing the best fit to the data (Whitehead, 2009). Precision (SE) was estimated using a bootstrap method. The analysis was performed with Socprog 2.9 (Whitehead, 2009).

Results

Photographic analysis

Information on the photographic analysis for the three archipelagos is presented in Table III.1.

Table III.1 Total number and percentages of catalogued individuals for the three archipelagos. Individuals were classified into animals presenting one capture and more than one recapture, whether the recaptures were within the same year (intra-annual) or in different years (inter-annual).

Area		Total number of catalogued individuals	Individuals captured once	Individuals with recaptures		
				Total	Intra-annual	Inter-annual
Azores						
	Number	1276	948	328	102	226
	%		*74.3*	*25.7*	*31.1*	*68.9*
Madeira						
	Number	278	216	*62*	8	54
	%		77.7	*22.3*	*12.9*	*87.1*
Canaries						
	Number	153	142	11	0	11
	%		*92.8*	*7.2*	*0*	*100*

The number of individuals identified in the Azores is higher than in Madeira and the Canaries. However, Azores and Madeira showed similarities in the percentages of individuals captured only once (74.3 and 77.7%, respectively) and, consequently, of individuals with recaptures (25.7 and 22.3%, respectively). These two archipelagos also presented a higher prevalence of individuals recaptured in more than one year (68.9% for the Azores and 87.1% for Madeira). In the Canaries, only 11 individuals presented recaptures (maximum two recaptures), all captured on the same two dates in 2009 and 2011. In Madeira, there was a maximum of 14 inter-annual recaptures, while in the Azores, the maximum was 27 (Figure III.2A). The discovery curves indicated that, for all archipelagos, the number of individuals identified has not stabilized, and therefore the whole population is yet to be sampled (Figure III.2B). Nevertheless, the curves for the Azores and Madeira were very similar in shape, despite the differences in the number of identified individuals, and presented an initial tendency for stabilization. The Canaries curve was still in linear growth with no signs of stabilization.

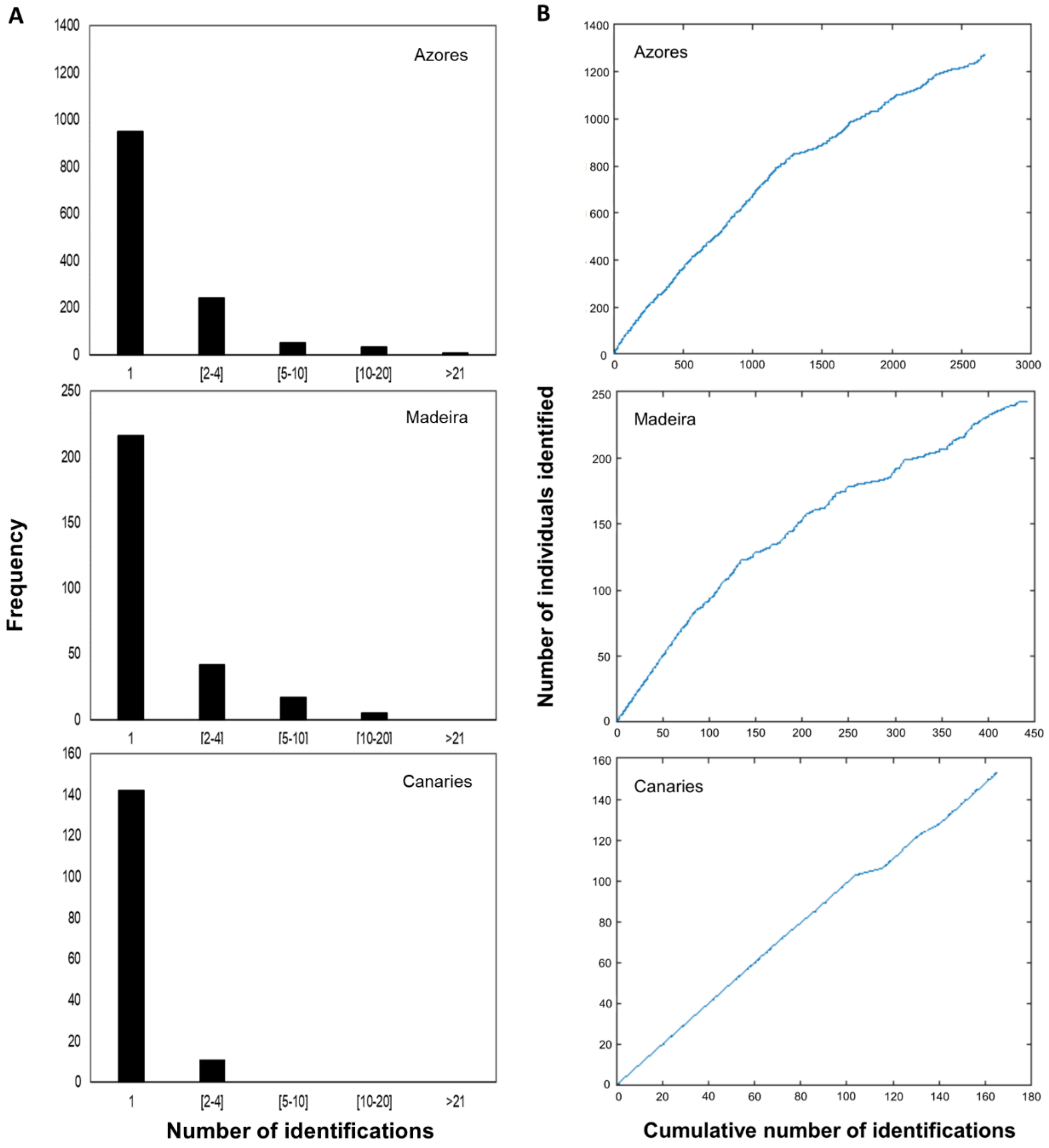

Figure III.2 (A) Capture frequency histograms for individual sperm whales for the three subareas of the Azores, Madeira and the Canaries. Most of the individuals of the three subareas were captured only once. Captures were aggregated in categories to facilitate visualization. **(B)** Discovery curves for individual sperm whales in the three subareas, based on the cumulative number of identifications concerning the number of identified individuals throughout the study period.

Site fidelity and residency analysis

For the subarea of the Azores, the SSFI showed a median of 0.0067 (SD=0.0093, range 0.0056-0.0078; IT median=0.3207, SD=0.2818; It median = 0.0045, SD=0.1946). For the subarea of Madeira, SSFI presented a median of 0.0094 (SD=0.0069, range 0.0076-0.0112; IT median=0.3713, SD=0.2388; It median=0.0056; SD=0.1928) (Figure III.3).

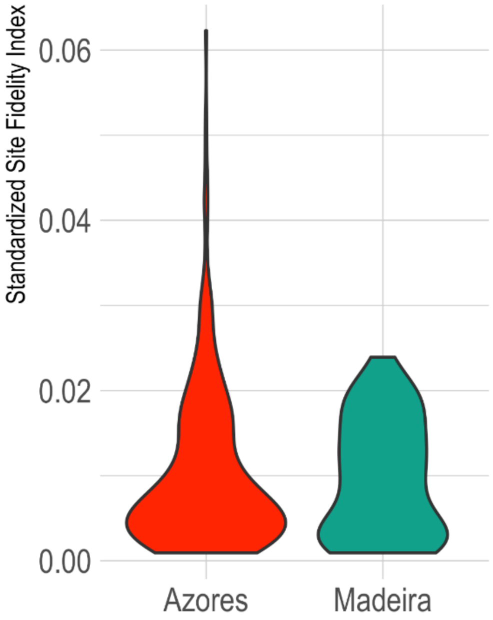

Figure III.3 Violin chart for the Standardized Site Fidelity Index (SSFI) for the archipelagos of Azores and Madeira. SSFI varies between 0 and 1, with zero being a population without site fidelity and one for a resident population

Four residency models were fitted to the lagged identification rate: “closed” (no changes in the individuals present in the area), “emigration/mortality” (individuals leave the area and never return), “emigration + reimmigration” (individuals leave the area and may return), and “emigration + reimmigration + mortality” (individuals leave the area and may or not return due to emigration or mortality) (Table III.2). The model that best fitted the LIR for the Azores subarea was Emigration + reimmigration and for Madeira subarea was Emigration + reimmigration + mortality (Table III.2, Figure III.4). For the Azores subarea, from June to September, there was an average of 44.8 individuals (SE = 4.9) at any given time and individuals resided in the area for 12.9 days (SE = 1.5), before leaving for 99.1 days (SE = 12.5); goodness of fit x2 = 1643.563, df = 455, P = 0. For the Madeira subarea, there was an average of 8.4 individuals (SE = 16.1) at any given time and individuals resided in the area for 0.8 days (SE = 6.6) before leaving for 8.6 days (SE = 6.9), with a very low mortality rate of 0.0008 (SE = 0.0002); goodness of fit x2 = 91.534, df = 58, P = 0.0033.

Table III.2 Models fitted to lagged identification rates (LIRs) for sperm whales in the archipelagos of the Azores and Madeira from 2014 to 2019.

Area			
Model	No. of parameters	QAIC	Summed log likelihood
Azores			
Emigration + reimmigration	3	**20244.6**	-37804.1
Emigration + reimmigration + mortality	4	20281.9	-37869.9
Emigration/mortality	2	20646.0	-38557.4
Closed	1	20763.7	-38781.1
Madeira			
Emigration + reimmigration + mortality	4	**5080.9**	-4004.5
Emigration/mortality	2	5085.8	-4011.6
Emigration + reimmigration	3	5127.3	-4042.7
Closed	1	5141.8	-4057.3

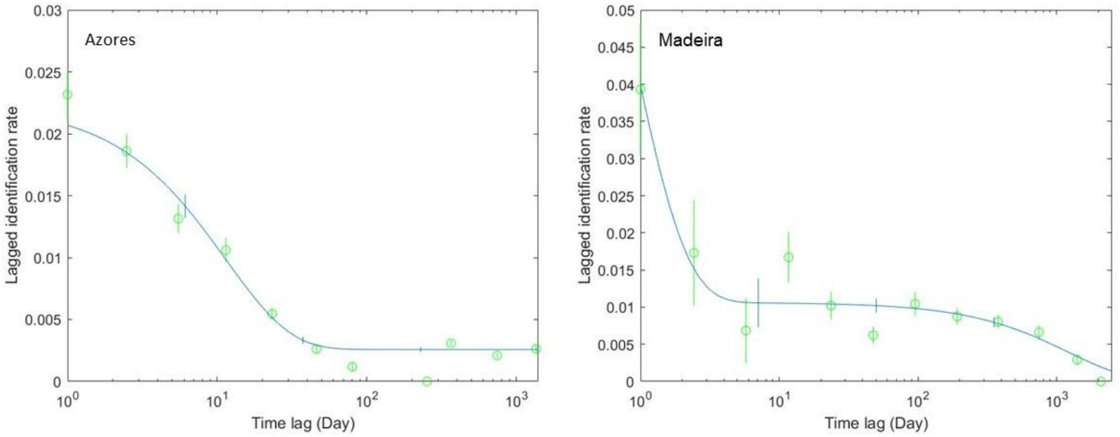

Figure III.4 Lagged identification rates (LIRs) for sperm whales in the archipelagos the Azores (Silva et al., 2013; Prieto et al., 2014; González-Garcia et al., 2022) and Madeira from 2014 to 2019. For the Azores, analysis was restricted to the peak season, from June to September, while for Madeira was year-round. The figures show the probability that an individual identified in the study area at any time will be identified again in the study area some time lag after. The line represents the best-fitting model according to Table III.2, and the vertical bars indicate standard errors calculated using the bootstrap method.

Discussion

This study provides the first assessment of site fidelity and residency of sperm whales in a remote oceanic environment in the Eastern North Atlantic. It brings forth valuable insights for a threatened species population whose offshore habitat and deep-diving behavior impair data collection. Through the collaborative effort from national and international teams, it was possible to identify areas in Macaronesia as important habitats for a portion of the population of sperm whales inhabiting the North Atlantic. Moreover, it is shown that individuals used this region intra- and inter-annually. Although this study brings forth important scientific knowledge, it is nonetheless a preliminary approach due to, among other factors, its geographic limitation that impairs the extrapolation of these conclusions to the whole Macaronesia. This first characterization allows to identify existing data gaps in Macaronesia and highlights the increasing need to obtain reliable quantitative data from more extended areas to obtain a solid assessment of sperm whales in this area of the Eastern North Atlantic. For the Canaries, the dataset did not allow for more than preliminary results, and therefore the main core of this study was conducted in subareas of the Azores and Madeira archipelagos. This study also highlighted the importance of using both opportunistic and dedicated effort when working with species displaying pelagic habits, such as the sperm whale. This contributed to a more profound knowledge that will allow implementing appropriate conservation measures.

The findings of this study are inferred from a combination of different analyses that support three broad main results. First, there is heterogeneity in capture probability, given that approximately ¼ of the identified individuals of the Azores and the Madeira subareas (25.7% and 22.3%, respectively) were captured more than once, with most of these (68.9% for the Azores and 87.1% for Madeira) presenting inter-annual recaptures. This result strongly indicates the importance of these subareas for a portion (¼) of the population that uses it on a regular basis, supporting previous studies (Silva et al., 2006; Boys et al., 2019; van der Linde & Eriksson, 2020). The Canaries dataset presents individuals captured mainly once (92.8%), which, together with the linear growth demonstrated by the discovery curve, indicates that the entire population is still far from being captured. This is most likely due to two reasons: i) low sampling effort, with the dataset covering only three years with homogenous effort and with a relative low number of identified individuals, and ii) geographic limitation (already a limitation for this study in general), with previous studies reporting a higher presence of sperm whales in other areas of the Canaries archipelago unsampled in this study (André, 1997; Fais et al., 2016; Correia et al., 2020; Herrera et al., 2021). Broader and more systematic research on sperm whales is needed for the Canaries, especially considering that this area could work as a sink habitat due to the high mortality associated with ship strikes (Fais et al., 2016). Taking into consideration the existing connection between Macaronesian archipelagos already demonstrated by photo-id and genetics (Pinela et al., 2009; Steiner et al., 2015; Steiner, 2022), this could be causing a decrease in the Macaronesian population (as demonstrated with the stranding in the Canaries in 2019 of an individual already sighted in the Azores, with signs of ship strike; Vidal Martín and Lisa Steiner own data). This impact could include the whole North Atlantic population if we consider the movement of males between Macaronesia, Norway, and the Bahamas (Steiner et al., 2012; Mullin et al., 2022).

Second, the site fidelity index values for the Azores and Madeira subareas are similarly low (0.0067 ± 0.0093 and 0.0094 ± 0.0069, respectively; SSFI varies between 0 and 1). This follows the results of the photo-id analysis and supports that only a minor part of the population presents site fidelity to these subareas, while the majority uses them as passage. Studies focusing on site fidelity of sperm whales in this area of the Atlantic are limited to the Azores archipelago and indicate a lack of geographical and genetic structure, providing indirect evidence of site fidelity over short periods as well as between years from part of a larger oceanic population (Matthews et al., 2001; Pinela et al., 2009). Sperm whales are known as ocean nomads, with both solitary males and social groups of females and juveniles traveling thousands of kilometers regularly (Cantor et al., 2019), although recent studies have identified populations with solid site fidelity (e.g., Gero et al., 2014; Vachon et al., 2022). The complex social structure and the large spatial and temporal scales in which sperm whales occur are challenging for understanding their populations and ecology (Kaschner et al., 2012). Differences arise not only between populations but also between oceans, with the North Atlantic populations of sperm whales being more geographically and genetically structured than the Pacific, demonstrating shorter range movements and smaller group sizes, together with a higher number of calves (Whitehead et al., 2012). Therefore, extrapolating results across geographical areas without corroborating them with regional observations could provide incorrect conclusions (Kaschner et al., 2011; Vachon et al., 2022).

Third, the LIR estimates for the Azores and Madeira subareas support the previous results, with individuals spending more extended periods out of the sampled areas than within. For each area, the best model presented differences in QAIC that vastly surpassed the minimum value of two required for the model choice, reinforcing the selection of the best-fitting model as the most appropriate one (Burnham & Anderson, 2002). This is also in agreement with the model selected from an ecological viewpoint, given the high levels of emigration and reimmigration expected from highly mobile species inhabiting vast oceanic areas, as also shown by other cetaceans in the region (Silva et al., 2013; Prieto et al., 2014; Dinis et al., 2016; Alves et al., 2019; Ferreira et al., 2021; Badenas et al., 2022; González-Garcia et al., 2022). Moreover, previous studies on the target species for the Azores Archipelago support these results (Silva et al., 2006; Boys et al., 2019; van der Linde & Eriksson, 2020), while for Madeira, this is the first study to conduct such analysis.

This study presents inevitable limitations associated with data collection, by joining information from multiple platforms across several areas, that covered only a small part of each archipelago. This invalidates the comparison between archipelagos, providing instead a characterization for each of the surveyed subareas: Pico and Faial islands in the Azores, south and southeast of Madeira island, and the eastern coast of Lanzarote and Fuerteventura in the Canaries. Also, while in Madeira and the Canaries the surveys took place year-round, in the Azores the weather conditions in the Winter invalidated such temporal scale, and data does not cover the entire year. However, the extended data collection period, together with the use of only good quality pictures and distinctive individuals, helped minimizing biases. In the Canaries, the smaller dataset hindered part of the analysis, and therefore more effort is needed for conclusions to be made regarding this area. This is already taking place with an ongoing project dedicated to the sperm whales in the Canaries. Opportunistic data is increasingly being used in cetacean research (e.g., Moura et al., 2012; Hupman et al., 2015; Alves et al., 2018; Fernandez et al., 2021). Although it presents limitations, those can be surpassed with adequate data analysis. The chosen index for this study, SSFI (Tschopp et al., 2018), is appropriate for situations where detection is not perfect, and the effort is heterogeneous, as in our study, thus providing robust quantifications of site fidelity at a populational level. This index accounts for the behavioral aspects of the target species and the characteristics of the sampling effort, which significantly improved the reliability of these results. Moreover, the use of likelihood techniques for residency parameters takes into consideration heterogeneous effort (Whitehead, 2001; Vachon et al., 2022).

Knowledge of biogeographical movement patterns is still limited for most pelagic species. Nevertheless, it is pivotal since many animals may encompass large geographical ranges within and beyond national waters (Dunn et al., 2019). The sperm whale is a cosmopolitan species with a complex differentiated behavior between sexes and populations. Yet, although having been the target of several studies worldwide (e.g., Drouot-Dulau & Gannier, 2007; Engelhaupt et al., 2009; Whitehead et al., 2012; Boys et al., 2019; Cantor et al., 2019), information on movements at the individual level is scarce for many populations. Its global threatened statuses require dedicated effort to establish conservation measures; however, its oceanic habitat hinders data collection and the coordination between stakeholders and governments. Conservation measures should include not only the core-used areas where social groups spend most of their time, exhibiting higher degrees of philopatry, but also the corridors used by males during their migrations between feeding and breeding grounds (Gero et al., 2014; Sahri et al., 2022). Remote islands such as the ones in Macaronesia provide an excellent location for studying this marine predator and/or the effects of anthropogenic threats, but surveillance of the open ocean is paramount since only a small part of the population approaches the islands regularly. For example, recent assessments of the cetaceans' vulnerability to climate change in the biogeographic region of Macaronesia showed that the sperm whale presented a moderate to high vulnerability score (Sousa et al., 2019; Sousa et al., 2021). All combined, identifying the critical habitats for sperm whales, both offshore and closer to islands, as well as quantifying parameters of fidelity and residency at the individual level, is a crucial issue in the conservation of populations that may show considerable variability in their habitat use (Vachon et al., 2022).

Funding

This study had the support of FCT through the strategic project UIDB/04292/2020 awarded to MARE and through the project LA/P/0069/2020 granted to the Associate Laboratory ARNET. It was also supported through the strategic project M1420-01-0142-FEDER-000001 for the Oceanic Observatory of Madeira and from Oceanário de Lisboa and Oceano Azul Foundation through Whale Tales Project (ODL/2019/003). RF was supported by the FCT grant SFRH/BD/147225/2019, MF by the MAC2/1.1a/385 in the framework of INTERTAGUA (MAC INTERREG 2014-2020), AD by ARDITI throughout the project M1420-09-5369-FSE-000002 and FA by the FCT project UIDP/04292/2020 granted to MARE.

Acknowledgments

We thank all researchers, volunteers, whale-watching operators and lookouts, and photographers who contributed with data. Thanks to Biosphere Expeditions for supporting research in the Spring in the Azores. In the Canary Islands, this research has been carried out with the scientific permission of the Ministerio de Transición Ecológica of the Government of Spain.

References

Alves F., Alessandrini A., Servidio A., Mendonça A. S., Hartman K. L., Prieto R., et al. (2019). Complex biogeographical patterns support an ecological connectivity network of a large marine predator in the northeast Atlantic. *Divers. Distrib*. 25 (2), 269–284. doi: 10.1111/ddi.12848

Alves F., Ferreira R., Fernandes M., Halicka Z., Dias L., Dinis A. (2018). Analysis of occurrence patterns and biological factors of cetaceans based on long-term and fine-scale data from platforms of opportunity: Madeira island as a case study. *Mar. Ecol*. 39 (2), e12499. doi: 10.1111/maec.12499

Alves F., Quérouil S., Dinis A., Nicolau C., Ribeiro C., Freitas L., et al. (2013). Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: Implications for conservation. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 23 (5), 758–776. doi: 10.1002/aqc.2332

Alves F., Rosso M., Li S., Nowacek D. P. (2022). A sea of possibilities for marine megafauna. *Science* 375 (6579), 391–392. doi: 10.1126/science.abn6022

André M. (1997). *Distribución y conservación del cachalote (Physeter macrocephalus) en las Islas Canarias*. PhD thesis (Gran Canaria, Canaries, Spain: University of Las Palmas de Gran Canaria).

Aoki K., Amano M., Mori K., Kourogi A., Kubodera T., Miyazaki N. (2012). Active hunting by deep-diving sperm whales: 3D dive profiles and maneuvers during bursts of speed. *Mar. Ecol. Prog. Ser.* 444, 289–301. doi: 10.3354/meps09371

Archie E. A., Moss C., Alberts S. C. (2006). The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proc. R. Soc B* 273, 513e522. doi: 10.1098/rspb.2005.3361

Arnbom T. (1987). Individual identification of sperm whales. *Rep. Int. Whal. Comm* 37 (SC/38/Sp4), 201–204.

Arregui M., Quirós Y., Saavedra P., Sierra E., Suárez-Santana C., Arbelo M., et al. (2019). Fat embolism and sperm whale ship strikes. *Front. Mar. Sci*. 6. doi: 10.3389/fmars.2019.00379

Badenas A., Dinis A., Ferreira R., Sambolino A., Hamard E., Berninsone L., et al. (2022). Behavioural ecology traits of elusive deep-diver whales unravel a complex social structure influenced by female philopatry and defence polygyny. *Front. Mar. Sci*. 9. doi: 10.3389/fmars.2022.809902

Baird R., Webster D., Mahaffy S., McSweeney D., Schorr G., Ligon A. (2008). Site fidelity and association patterns in a deep-water dolphin: Rough-toothed dolphins (*Steno bredanensis*) in the Hawaiian archipelago. *Mar. Mamm. Sci.* 24 (3), 535–553. doi: 10.1111/j.1748-7692.2008.00201.x

Bose S., Forrester T., Brazeal J., Sacks B., Casady D., Wittmer H. (2017). Implications of fidelity and philopatry for the population structure of female black-tailed deer. *Behav. Ecol*. 28 (4), 983–990. doi: 10.1093/beheco/arx047

Boys R., Oliveira C., Pérez-Jorge S., Prieto R., Steiner L., Silva M. (2019). Multi-state open robust design applied to opportunistic data reveals dynamics of wide-ranging taxa: The sperm whale case. *Ecosphere* 10 (3), e02610. doi: 10.1002/ecs2.2610

Braun C., Arostegui M., Thorrold S., Papastamatiou Y., Gaube P., Fontes J., et al. (2022). The functional and ecological significance of deep diving by large marine predators. *Ann. Rev. Mar. Sci.* 14 (1), 129–159. doi: 10.1146/annurev-marine-032521-103517

Brito C. (2008). Assessment of catch statistics during the land-based whaling in Portugal. *Mar. Biodiver. Rec*. 1, e92. doi: 10.1017/S175526720700930X

Burnham K. P., Anderson D. R. (2002*). Model selection and multimodel inference: a practical information theoretic approach* (New York: Springer Verlag).

Cabral M. J., Almeida J., Almeida P. R., Dellinger T., Almeida N. F., Oliveira M. E., et al. (2005). *Livro vermelho dos vertebrados de Portugal* (Lisboa: Instituto de Conservação da Natureza).

Cantor M., Gero S., Whitehead H., Rendell L. (2019). "Sperm Whale: The Largest Toothed Creature on Earth", in Ethology and Behavioral Ecology of Odontocetes. Eds. Würsig B.. *Ethology and behavioral ecology of odontocetes* (Springer, Cham). doi: 10.1007/978-3-030-16663-2_12

Carracedo J., Troll V. (2021). North-East Atlantic islands: The macaronesian archipelagos, in *Encyclopedia of geology*, 2nd Edition. Eds. Alderton D., Elias S. A. (Academic Press), 674–699. doi: 10.1016/B978-0-08-102908-4.00027-8

Cartagena-Matos B., Lugué K., Fonseca P., Marques T., Prieto R., Alves F. (2021). Trends in cetacean research in the Eastern north Atlantic. *Mamm. Rev*. 51 (3), 436–453. doi: 10.1111/mam.12238

Clarke R. (1956). Sperm whales of the Azores. *Discovery Rep*. 28, 237–298.

Correia-Fagundes C., Romano H. (2013). Observation of a birth of a sperm whale *Physeter macrocephalus* at Madeira (NE Atlantic). *Bocagiana* 236, 1–3.

Correia M., Gil A., Valente R., Rosso M., Sousa-Pinto I., Pierce G. (2020). Distribution of cetacean species at a large scale - connecting continents with the macaronesian archipelagos in the Eastern north Atlantic. *Divers. Distrib*. 26 (10), 1234–1247. doi: 10.1111/ddi.13127

Dinis A., Alves F., Nicolau C., Ribeiro C., Kaufmann M., Cañadas A., et al. (2016). Bottlenose dolphins *Tursiops truncatus* group dynamics, site fidelity, residency and movement patterns in the Madeira archipelago (North-East Atlantic*). Afr. J. Mar. Sci*. 38 (2), 151–160. doi: 10.2989/1814232X.2016.1167780

Drouot-Dulau V., Gannier A. (2007). Movements of sperm whale in the Western Mediterranean Sea: Preliminary photo-identification results. *J. Mar. Biolog. Assoc. U.K.* 87 (1), 195–200. doi: 10.1017/S0025315407054860

Dunn D., Harrison A., Curtice C., DeLand S., Donnelly B., Fujioka E., et al. (2019). The importance of migratory connectivity for global ocean policy. *Proc. R. Soc B* 286 (1911), 20191472. doi: 10.1098/rspb.2019.1472

Engelhaupt D., Hoelzel A., Nicholson C., Frantzis A., Mesnick S., Gero S., et al. (2009). Female philopatry in coastal basins and male dispersion across the north Atlantic in a highly mobile marine species, the sperm whale (*Physeter macrocephalus*): Sperm whale female philopatry and male dispersal. *Mol. Ecol.* 18 (20), 4193–4205. doi: 10.1111/j.1365-294X.2009.04355.x

Fais A., Lewis T., Zitterbart D., Álvarez O., Tejedor A., Soto N. A. (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. doi: 10.1371/journal.pone.0150660

Fernandez M., Alves F., Ferreira R., Fischer J. C., Thake P., Nunes N., et al. (2021). Modeling fine-scale cetaceans' distributions in oceanic islands: Madeira archipelago as a case study. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.688248

Ferreira R., Alves F., Gomes C., Jardim D., Kok J., Dinis A. (2017). First confirmed record of northern bottlenose whale (*Hyperoodon ampullatus*) in Madeira archipelago, northeast Atlantic. *Aquat. Mamm.* 43 (5), 474–478. doi: 10.1578/AM.43.5.2017.474

Ferreira R., Dinis A., Badenas A., Sambolino A., Marrero-Pérez J., Crespo A., et al. (2021). Bryde's whales in the north-East Atlantic: New insights on site fidelity and connectivity between oceanic archipelagos. *Aquat. Conserv: Mar. Freshw. Ecosyst*. 31 (10), 2938–2950. doi: 10.1002/aqc.3665

Freitas L., Dinis A., Nicolau C., Ribeiro C., Alves F. (2012). New records of cetacean species for Madeira archipelago with an updated checklist. *Bol. Mus. Mun. Funchal* 62, 25–43.

Freitas R., Romeiras M., Silva L., Cordeiro R., Madeira P., González J., et al. (2019). Restructuring of the 'Macaronesia' biogeographic unit: a marine multi-taxon biogeographical approach. *Sci. Rep.* 9 (1), 15792. doi: 10.1038/s41598-019-51786-6

Geldmacher J., Van Den Bogaard P., Hoernle K., Schmincke H. U. (2020). The 40Ar/39Ar age dating of the Madeira Archipelago and hotspot track (eastern North Atlantic). *Geochemistry, Geophysics, Geosystems* 1 (2), 1999GC000018. doi: 10.1029/1999GC000018

Gero S., Milligan M., Rinaldi C., Francis P., Gordon J., Carlson C., et al. (2014). Behavior and social structure of the sperm whales of Dominica, West indies. *Mar. Mamm. Sci.* 30 (3), 905–922. doi: 10.1111/mms.12086

González Garcia L., Pierce G. J., Autret, Palenzuela J. M. T. (2022). Alongside but separate: Sympatric baleen whales choose different habitat conditions in São Miguel, Azores. *Deep Sea Res.* 184, 103766. doi: 10.1016/j.dsr.2022.103766

Greenwood P. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28, 1140–1162. doi: 10.1016/S0003-3472(80)80103-5

Herrera I., Carrillo M., Esteban M. C., Haroun R. (2021). Distribution of cetaceans in the Canary Islands (Northeast Atlantic Ocean): implications for the Natura 2000 network and future conservation measures. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.669790

Hoover J. (2003). Decision rules for site fidelity in a migratory bird, the prohonotary warbler. *Ecology* 84 (3), 416–430. doi: 10.1890/0012-9658(2003)084[0416:DRFSFI]2.0.CO;2

Hupman K., Visser F., Martinez E., Stockin K. (2015). Using platforms of opportunity to determine the occurrence and group characteristics of orca (*Orcinus orca*) in the Hauraki Gulf, New Zealand. *N. Z. J. Mar. Freshw. Res.* 49 (1), 132–149. doi: 10.1080/00288330.2014.980278

Iverson S., Esler D. (2006). Site fidelity and the demographic implications of winter movements by a migratory bird, the harlequin duck *Histrionicus histrionicus*. *J. Avian Biol.* 37 (3), 219–228. doi: 10.1111/j.2006.0908-8857.03616.x

Jaquet N., Dawson S., Slooten E. (2000). Seasonal distribution and diving behaviour of male sperm whales off Kaikoura: foraging implications. *Can. J. Zool*. 78 (3), 407–419. doi: 10.1139/z99-208

Kaschner K., Quick N., Jewell R., Williams R., Harris C. (2012). Global coverage of cetacean line-transect surveys: status quo, data gaps and future challenges. *PLos One* 7 (9), e44075. doi: 10.1371/journal.pone.0044075

Kaschner K., Tittensor D., Ready J., Gerrodette T., Worm B. (2011). Current and future patterns of global marine mammal biodiversity. *PLos One* 6 (5), e19653. doi: 10.1371/journal.pone.0019653

Katona S., Whitehead H. (1988). Are cetacea ecologically important? *Oceanogr. Mar. Biol.* 26, 553–568.

Lebreton J. D., Burnham K. P., Clobert J., Anderson D. R. (1992). Modelling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecol. Monog.* 62, 67–118. doi: 10.2307/2937171

Lettevall E., Richter C., Jaquet N., Slooten E., Dawson S., Whitehead H., et al. (2002). Social structure and residency in aggregations of male sperm whales. *Can. J. Zool.* 80 (7), 1189–1196. doi: 10.1139/z02-102

Li S., Rosso M. (2021). Lack of knowledge threatens beaked whales. *Science* 371 (6531), 791. doi: 10.1126/science.abg892

Lunn N., Boyd I. (1991). Pupping-site fidelity of Antarctic fur seals at bird island, south Georgia. *J. Mammal*. 72 (1), 202–206. doi: 10.2307/1381999

Matthews J. N., Steiner L., Gordon J. (2001). Mark-recapture analysis of sperm whale (*Physeter macrocephalus*) photo-id data from the Azores, (1987–1995). *J. Cetacean Res. Manage.* 3 (3), 219–226.

McIvor A., Williams C., Alves F., Dinis A., Pais M., Canning-Clode J. (2022). The status of marine megafauna research in Macaronesia: a systematic review. *Front. Mar. Sci*. 9. doi: 10.3389/fmars.2022.819581

Morato T., Machete M., Kitchingman A., Tempera F., Lai S., Menezes G., et al. (2008). Abundance and distribution of seamounts in the Azores. *Mar. Ecol. Prog. Ser.* 357, 17–21. doi: 10.3354/meps07268

Moura A., Sillero N., Rodrigues A. (2012). Common dolphin (*Delphinus delphis*) habitat preferences using data from two platforms of opportunity. *Acta Oecol.* 38, 24–32. doi: 10.1016/j.actao.2011.08.006

Mullin K., Steiner L., Dunn C., Claridge D., González L., Gordon J., et al. (2022). Long-range longitudinal movements of sperm whales (*Physeter macrocephalus*) in the north Atlantic Ocean revealed by photo-identification. *Aquat. Mamm*. 48 (1), 3–8. doi: 10.1578/AM.48.1.2022.3

Notarbartolo-Di-Sciara G. (2014). Sperm whales, *Physeter macrocephalus*, in the Mediterranean Sea: a summary of status, threats, and conservation recommendations. *Aquat. Conserv: Mar. Freshw. Ecosyst*. 24 (S1), 4–10. doi: 10.1002/aqc.2409

Perez J. (2011). The cetacean fishing in the Canary Islands. *Anuario Estudos Atlânticos* 57, 277–300.

Pimiento C., Leprieur F., Silvestro D., Lefcheck J. S., Albouy C., Rasher D. B., et al. (2020). Functional diversity of marine megafauna in the Anthropocene. *Sci. Adv.* 6 (16), eaay7650. doi: 10.1126/sciadv.aay7650

Pinela A., Quérouil S., Magalhães S., Silva M., Prieto R., Matos J. A., et al. (2009). Population genetics and social organization of the sperm whale (*Physeter macrocephalus*) in the Azores inferred by microsatellite analyses. *Can. J. Zool*. 87 (9), 802–813. doi: 10.1139/Z09-066

Pomeroy P., Twiss S., Redman P. (2001). Philopatry, site fidelity and local kin associations within grey seals breeding colonies. *Ethology* 106 (10), 899–919. doi: 10.1046/j.1439-0310.2000.00610.x

Prieto R., Silva M. A., Waring G. T., Gonçalves J. M. A. (2014). Sei whale movements and behaviour in the North Atlantic inferred from satellite telemetry. *Endang. Species Res*. 26, 103–113. doi: 10.3354/esr00630

Rødland E., Bjørge A. (2015). Residency and abundance of sperm whales (*Physeter macrocephalus*) in the Bleik Canyon, Norway. *Mar. Biol. Res*. 11 (9), 974–982. doi: 10.1080/17451000.2015.1031800

Sahri A., Jak C., Putra M., Murk A., Andrews-Goff V., Double M., et al. (2022). Telemetry-based home range and habitat modelling reveals that the majority of areas important for pygmy blue whales are currently unprotected. *Biol. Conserv*. 272, 109594. doi: 10.1016/j.biocon.2022.109594

Savery L., Evers D., Wise S., Falank C., Wise J., Gianios C., et al. (2013). Global mercury and selenium concentrations in skin from free-ranging sperm whales (*Physeter macrocephalus*). *Sci. Total Environ*. 450–451, 59–71. doi: 10.1016/j.scitotenv.2013.01.070

Schipper J., Chanson J., Chiozza F., Cox N., Hoffmann M., Katariya V., et al. (2008). The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* 322 (5899), 225–230. doi: 10.1126/science.1165115

Silva M., Magalhães S., Prieto R., Quérouil S., Pinela A., Seabra M. I., et al. (2006). Ecologia e estrutura populacional dos roazes e cachalotes nos açores: relação com as características do habitat. *Arquivos Do DOP Série Estudos* 4, 1–30.

Silva M., 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), e76507. doi: 10.1371/journal.pone.0076507

Silva M., Prieto R., Cascão I., Seabra M., Machete M., Baumgartner M., et al. (2014). Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. *Mar. Biol. Res*. 10 (2), 123–137. doi: 10.1080/17451000.2013.793814

Somerford T., Dawson S., Slooten E., Guerra M., Childerhouse S., Richter C., et al. (2021). Long-term decline in abundance of male sperm whales visiting Kaikōura, New Zealand. *Mar. Mamm. Sci*. 38 (2), 606–625. doi: 10.1111/mms.12886

Sousa A., Alves F., Arranz P., Dinis A., Fernandez M., Gonzalez L., et al. (2021). Climate change vulnerability of cetaceans in Macaronesia: insights from a trait-based assessment. *Sci. Total Environ*. 795, 148652. doi: 10.1016/j.scitotenv.2021.148652

Sousa A., Alves F., Dinis A., Bentz J., Cruz M. J., Nunes J. P. (2019). How vulnerable are cetaceans to climate change? developing and testing a new index. *Ecol. Indic*. 98, 9–18. doi: 10.1016/j.ecolind.2018.10.046

Spalding M., Fox H., Allen G., Davidson N., Ferdaña Z., Finlayson M., et al. (2007). Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience* 57 (7), 573–583. doi: 10.1641/B570707

Steiner L. (2022). "Sperm whale movements around the north Atlantic and a glimpse at the new fluke matching algorithm," in *Cachalote Consortium Workshop*, *24th Biennial Conference on the Biology of Marine Mammals*, Palm Beach, USA, 1-5 August.

Steiner L., Lamoni L., Plata M., Jensen S., Lettevall E., Gordon J. (2012). A link between male sperm whales, *Physeter macrocephalus*, of the Azores and Norway. *J. Mar. Biolog. Assoc. U.K.* 92 (8), 1751–1756. doi: 10.1017/S0025315412000793

Steiner L., Pérez M., van der Linde M., Freitas L., Santos R. P., Martin V., et al. (2015). "*Long distance movements of female/immature sperm whales in the North Atlantic* [Poster]," in *21st Biennial Conference of Society of Marine Mammalogy*, San Francisco, USA, 13-18 December.

Switzer P. V. (1993). Site fidelity in predictable and unpredictable habitats. *Evol. Ecol*. 7, 533–555. doi: 10.1007/BF01237820

Switzer P. (1997). Factors affecting site fidelity in a territorial animal, *Perithemis tenera*. *Anim. Behav*. 53 (4), 865–877. doi: 10.1006/anbe.1996.0352

Taylor B. L., Baird R., Barlow J., Dawson S. M., Ford J., Mead J. G., et al (2019). *Physeter macrocephalus* (amended version of 2008 assessment). The IUCN Red List of Threatened Species. 2019, e.T41755A160983555. doi: 10.2305/IUCN.UK.2008.RLTS.T41755A160983555.en. Accessed on 28 November 2022.

Tittensor D. P., Mora C., Jetz W., Lotze H., Ricard D., Berghe E., et al. (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature* 466 (7310), 1098–1101. doi: 10.1038/nature09329

Tschopp A., Ferrari M., Crespo E., Coscarella M. (2018). Development of a site fidelity index based on population capture-recapture data. *PeerJ* 6, e4782. doi: 10.7717/peerj.4782

Vachon F., Hersh T., Rendell L., Gero S., Whitehead H. (2022). Ocean nomads or island specialists? culturally driven habitat partitioning contrasts in scale between geographically isolated sperm whale populations. *R. Soc Open Sci.* 9 (5), 211737. doi: 10.1098/rsos.211737

Valdés L., Déniz-González I. (Eds.) (2015). *Oceanographic and biological features in the canary current Large marine ecosystem* (Paris: IOC-UNESCO), 383.

van der Linde M., Eriksson I. (2020). An assessment of sperm whale occurrence and social structure off são Miguel island, Azores using fluke and dorsal identification photographs. *Mar. Mamm. Sci*. 36 (1), 47–65. doi: 10.1111/mms.12617

Whitehead H. (2001). Analysis of animal movement using opportunistic individual identifications: application to sperm whales. *Ecology* 82 (5), 1417–1432. doi: 10.2307/2679999

Whitehead H. (2002). Current global population size, post-whaling trend and historical trajectory of sperm whales. *Sci. Rep*. 12: 19468. doi: 10.1038/s41598-022-24107-7

Whitehead H. (2009). SOCPROG programs: analysing animal social structures. *Behav. Ecol. Sociobiol*. 63 (5), 765–778. doi: 10.1007/s00265-008-0697-y

Whitehead H. (2018). “Sperm whale,” in *Encyclopedia of marine mammals, 3rd Editions*. Eds. Würsig B., Thewissen J. G. M., Kovacs K. M. (London, UK: Academic Press), 919–924.

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? *Int. J. Primatol*. 33 (5), 1142–1164. doi: 10.1007/s10764-012-9598-z

Whitehead H., Shin M. (2022). Current global population size, post-whaling trend and historical trajectory of sperm whales. *Sci. Rep.* 12, 19468. doi: 10.1038/s41598-022-24107-7

Würsig B., Jefferson T. A. (1990). Methods of photo-identification for small cetaceans. *Rep. Internat. Whal. Commun. Special issue* 12, 43–52.

CHAPTER IV - Behavioural Ecology Traits of Elusive Deep-Diver Whales Unravel a Complex Social Structure Influenced by Female Philopatry and Defence Polygyny

This chapter is published as:

Badenas, Anja, Ana Dinis, Rita Ferreira, Annalisa Sambolino, Eliette Hamard, Leonardo G. Berninsone, Marc Fernandez, and Filipe Alves. 2022. "Behavioural ecology traits of elusive deep-diver whales unravel a complex social structure influenced by female philopatry and defence polygyny". *Frontiers in Marine Science*, 9, 809902. https://doi.org/10.3389/fmars.2022.809902

CHAPTER IV - Behavioural Ecology Traits of Elusive Deep-Diver Whales Unravel a Complex Social Structure Influenced by Female Philopatry and Defence Polygyny

Abstract

Knowledge of the role of individual associations has provided an insightful understanding of the structures of animal societies, especially in highly social mammals such as primates. Yet, this is unbalanced towards marine mammals, particularly to beaked whales, due to their elusive nature. In addition, information on the fundamental drivers of the social structure of these deep-diving animals is still scarce. Here, the hypothesis of female defence polygyny was tested in Blainville's beaked whales (*Mesoplodon densirostris*) and discussed within the context of marine and terrestrial organisms displaying similar patterns, by (i) estimating residency times to obtain information on the movements into and out of the area, (ii) analysing social networks to assess individual association metrics, (iii) measuring the strength of the associations to assess the existence of preferred or avoided relationships among individuals, and (iv) modelling different social structures to address temporal patterns in social relationships. Using a 9-year photographic dataset derived from the pelagic habitat, individual associations were inferred based on likelihood techniques. This approach allowed to infer on the species' social structure in relation to age class, sex, residency status, and spatio-temporal patterns, which can be a good practice to be applied for other taxa. Heterogeneity in capture probability and residency times was observed between age-sex classes, with adult females exhibiting long-term site fidelity. This suggests different habitat roles and spatial structuring within this social organisation. Strong and long dyadic associations occurred between adult females and immatures, contrarily to between males, and the best-fitting models of the temporal patterns suggested long-lasting and temporary associations. The present findings unravel a complex social structure stratified by age-sex class and influenced by female philopatry and defence polygyny, like an unimale group mating system, which varies from other beaked whales but is similar to some birds, pinnipeds, or non-human primates.

KEYWORDS: age/sex-specific, beaked whales, individual temporal associations, island systems, megafauna, movement and residency patterns, pelagic habitat, social network

Introduction

Movement patterns and habitat composition are known to influence complex animal social structures (He et al., 2019). Animal movements are generally driven by resource availability, mating accessibility, predator avoidance and habitat complexity (e.g., Bailey and Thompson, 2006; Duijns et al., 2019), which in turn modulate social behaviour, group composition and population dynamics at a broader scale (Morales et al., 2010). The resulting social structure plays a pivotal role in the population's ecology since it influences the spread of diseases and genetic flow (Sutherland, 1998). Therefore, social structure is considered a determining factor in conservation management plans (Wilson, 1975).

To study a population's social structure, data on interactions between known individuals through time are needed (Hinde, 1976; Whitehead, 2008), which can sometimes be challenging to witness. Once associations are established, various tools exist to describe and model social structure (reviewed in Farine and Whitehead, 2015), which has provided a profound understanding of animal associations and their socio-ecological processes in highly social terrestrial mammals (e.g., Schreier and Swedell, 2009; Foerster et al., 2015; Berger et al., 2021). However, little attention had been given to the societies of species whose meaningful relationships are difficult to assess, such as cetaceans (whales and dolphins) (Lusseau et al., 2006; Rendell et al., 2019). Cetaceans associate with conspecifics (and occasionally interspecifically) when survival, access to resources and reproductive success are increased by group formation (Gowans et al., 2007). Nonetheless, the longevity and strength of those associations, and hence social structures, are modulated by the individuals' residency patterns and habitat selection, which differ among and within species. As a result, cetacean's social structures range from highly fluid, so-called fission-fusion societies, where individuals associate in groups that change in composition and size daily (e.g., bottlenose dolphin *Tursiops truncatus*, Connor et al., 2000), to permanent associated matrilineal groups (e.g., killer whales *Orcinus orca*, Baird and Whitehead, 2000).

Nevertheless, most information on cetacean social systems is from common and accessible species (i.e., abundant, inhabiting coastal waters, or easily approachable), thus exists a gap in the knowledge of the societal patterns of lesser studied Families such as beaked whales (Li and Rosso, 2021; Weiss et al., 2021). This is mainly because beaked whales inhabit pelagic and difficult-to-access environments and because of their short surfacing periods and cryptic behaviour (Tyack et al., 2006). Although research on beaked whales has increased in the last two decades (reviewed in Hooker et al., 2019) due to their high vulnerability to anthropogenic noise and specifically to navy sonar (Tyack et al., 2011), studies on these animals' social structures cover only four species (out of at least 24 extant species, Carroll et al., 2021) and are still on their early stages (Baird, 2019; Weiss et al., 2021). In Blainville's beaked whales (*Mesoplodon densirostris*), resident populations of this medium-sized (4–5 m long) deep-diver have only been described in a few remote archipelagos (Hooker et al., 2019) and only one peer-reviewed study, wherever known, has provided insights on its social structure (McSweeney et al., 2007). That study suggested ephemeral relationships and female defence polygyny (characterised when males control females directly by defending them against conspecifics males; Shuster and Wade, 2003), yet it was based on descriptive analyses.

Here, photographic data of Blainville's beaked whales from an oceanic pelagic habitat was used to analyse individual associations and consequently to serve as a model system to infer the social structure in relation to age class, sex, residency status, and spatio-temporal patterns. To better understand the species' socio-behavioural traits and test the hypothesis of female defence polygyny, likelihood techniques were used to (i) estimate residency times, thus providing information on the movements into and out of the area, (ii) analyse the social network to assess individual association metrics, (iii) measure the strength of the associations to assess the existence of preferred or avoided relationships among individuals, and (iv) model different social structures to address temporal patterns in social relationships. Such an integrative approach is expected to contribute to a more comprehensive view of the species' social structure and enlighten the mysterious life habits of elusive and lesser-known animals. Finally, it is expected to advance the theoretical understanding of a specific social strategy related to philopatry, mating, and parental care in free-ranging animals, given that cetaceans provide a powerful outgroup for inferring the evolution of the social structure of other highly related mammals (Pearson, 2011).

Material and Methods

Study Area and Data Collection

Photographic data of Blainville's beaked whales were collected in the southern waters of Madeira Island (Portugal, 32°N 017°W), in a core area covering about 1,000 km2 up to 15 km off the coast (see Fernandez et al., 2021). The study area is surrounded by warm-temperate Atlantic waters and is characterised by a narrow continental shelf and steep submarine canyons (Geldmacher et al., 2000; Martins et al., 2007). These characteristics offer a privileged access to the pelagic environment where the target species commonly occurs throughout the year (Alves et al., 2018; Fernandez et al., 2021) and where some individuals are likely island-associated (Dinis et al., 2017). The data were collected year-round through whale-watching platforms (see Acknowledgments; procedures detailed in Alves et al., 2018) and in research trips, between 2011 and 2019 (Table IV.1 and Supplementary Table 1). On each occasion with Blainville's beaked whales, animals were approached and photographed using digital reflex cameras with zoom lenses, independently of age class, sex, and distinctiveness.

Table IV.1 Summary of the photographic data used in the analysis, i.e., truncated to distinctive animals and good quality pictures.

Year	No. of photographic occasions	No. of captures	No. of newly identified individuals
2011	13	30	13
2012	6	9	4
2013	7	13	3
2014	9	14	4
2015	20	47	18
2016	17	41	12
2017	29	52	8
2018	23	52	9
2019	30	67	8
Total	154	325	79

Photographic Analysis and Site Fidelity

A previous photographic-identification (hereafter “photo-id”) catalogue and dataset of all animals’ capture histories from 2011 to 2016 (Dinis et al., 2017) was updated with the newly collected data following standardised procedures (Würsig and Jefferson, 1990). Individuals were identified using unique scarring patterns on the body as well as nicks on dorsal fins (McSweeney et al., 2007; Dinis et al., 2017). The distinctiveness of each whale was rated from 1 (poorly distinctive) to 4 (very distinctive) following McSweeney et al. (2007), and the photographs were assigned a quality grade ranging from 1 to 4 (low- to high-quality) based on Alves et al. (2013). Only good quality pictures (grade 3 or 4) and individuals with distinctiveness 2–4 (slightly to very distinctive) were used in the analyses to enhance the reliability of the data. A capture was defined as an individual identification from a photographic occasion (Würsig and Jefferson, 1990).

Three catalogues were compiled: one for females, one for males, and one for immature whales of unknown sex. Sex and age class (immature, subadult male, adult male, or adult female) was determined based on body size and colour, body scarring, association with calves, and the presence or absence of erupted teeth in the lower jaws (Claridge, 2006; McSweeney et al., 2007; Dinis et al., 2017). Photographic comparisons were performed visually (Robbins et al., 2011; Alves et al., 2019), and at least two co-authors confirmed individual matches, sex, and age class.

Additionally, a residency pattern was attributed to each individual. Three residency patterns were established based on the capture histories. Individuals that exhibited multi-year and year-round site fidelity (captured in at least 4 years and three seasons, i.e., January–March, April–June, July–September, October-December) were termed residents; individuals captured only once or a few times within a week and never captured again were termed transients; and individuals that fell between these two categories were considered emigrants/immigrants or regular visitors and were consequently termed visitors (adapted from Alves et al., 2013). Two exceptions were made for whales Md99 and Md119 that were only seen during 3 (consecutive) years but during the four seasons and always with resident whales, and therefore were termed residents.

A discovery curve was plotted using the capture histories, and the recapture rates (RRs) per age class were calculated to assess site fidelity. The discovery curve was created by plotting the cumulative number of identified individuals against the cumulative number of captures. The RRs were calculated by dividing the number of individuals with ≥2 captures by the total number of individuals. Recaptures within the same day were excluded.

Movement Analysis

The amount of time animals spent within the study area was examined using Lagged Identification Rates (LIR). The LIR is the probability that an individual observed in the area at a given time will still be present τ time-lags later (Whitehead, 2001). Given the difference between the capture histories of the age classes and the fact that immatures were almost always seen with an adult female, two different LIR were performed: one for all males and one for females and immatures. All individuals captured between 2015 and 2019 (years with the higher number of captures, Table 1), independently of the number of captures, were included in the analysis. Four models were fitted to each dataset using maximum likelihood, binomial loss, and bootstrapped standard error (SE), following Whitehead (2009). The model with the lowest Quasi Akaike Information Criteria (QAIC) was selected as the best-fitting model (Whitehead, 2008, 2009). The sampling period was defined as day, and associations were defined as individuals grouped within an occasion. LIR was conducted using SOCPROG version 2.9 (Whitehead, 2009).

Social Analyses

Network Analyses

A social network diagram was created using NetDraw 2.158 (Borgatti, 2002) to illustrate the species social structure (Kappeler, 2019). All occasions between 2011 and 2019 were considered, excluding only those resulting in single captures as they did not provide any linking information (and such cases likely represented incomplete sampling effort in photographing the entire group instead of solitary animals, given these were never recorded during the research trips). Residency pattern and age-sex class were included as individual attributes. Nodes correspond to individuals, while lines between nodes represent the strength of association among dyads, with thicker lines indicating stronger associations.

Two network metrics (strength and clustering coefficient) were obtained using SOCPROG's network statistics (Whitehead, 2009). The strength is the sum of the weights of all links of a given node, and can be used as a measure of individual social centrality (Barrat et al., 2004). The clustering coefficient measures whether the associates of an individual are themselves associated (Barrat et al., 2004; Lusseau, 2007). Significant differences in the network measures among attributes of age/sex and residency patterns were tested with a double permutation test (Farine and Carter, 2022) using the aspine R package (Farine, 2013).

Preferred Associations

To reduce the chance of including spurious associations, only whales with ≥3 captures from occasions with medium- (where at least half of the group was photographed) and high-coverage (where essentially all individuals were photographed) between 2011 and 2019 were included in this analysis. Because of the opportunistic nature of data, the photographic coverage of individuals during sightings was unknown. To overcome this issue, 50 high-quality photographs, including at least three whales in the frame, were selected to calculate the percentage of marked individuals in a group and infer photographic coverage. The rate of distinctive individuals was obtained by dividing the number of marked individuals by the total individuals captured in the frame for each photograph and calculating an overall mean for all pictures. This resulted in 71% (±19%) of the individuals in a group being marked. Based on this and on the Blainville's beaked whales mean group size of 3.7 (SD = 1.7) individuals in the study area (Alves et al., 2018; which is similar to other regions, see Ritter and Brederlau, 1999; Claridge, 2006; McSweeney et al., 2007), sightings with ≥2 captures were considered to be of medium- and high-coverage, and were therefore used in the subsequent analyses.

The half-weight association index (HWI) (Cairns and Schwager, 1987) was used to represent the strength of the association between beaked whale dyads (following Whitehead, 2008; Hoppitt and Farine, 2018), where "0" indicated that individuals were never captured together and "1" that individuals were always together. The mean and the maximum of associations were also calculated.

Permutation tests were used to assess whether preferred or avoided relationships among individuals and among age classes existed (Bejder et al., 1998; Whitehead, 1999). The null hypothesis was that individuals were associated with the same probability with other individuals. Observed coefficients of variation (CV) of the pairwise association indices significantly higher than those from permuted datasets were taken as evidence that individuals had preferred companions (Whitehead, 1999; Whitehead et al., 2005). The number of permutations generated was increased until the p-values stabilised (Bejder et al., 1998; Whitehead, 1999), at 1,000 trial flips per permutation. Based on the LIR results, three different sampling periods were used to assess associations between individuals and among age classes (adapted from Gero et al., 2015): (1) "hour," hourly sampling period to test for short-term associations, (2) "month," a monthly sampling period to test for medium-term associations, and (3) "year," yearly sampling period to test for long-term associations. This procedure removes any existing autocorrelation between groups that have been sighted together for short periods (hours or days) (personal communication, H. Whitehead, 2020). The association was defined as individuals grouped within an occasion for all three sampling periods, and associations were permuted between sampling periods.

Temporal Patterns

Standardised lagged association rates (SLAR) were used to address temporal patterns in social relationships (Whitehead, 1995). SLAR assessed the probability that two associated individuals at a given time would still be associated at a certain time-lag in the future. To aid in the interpretation of SLAR, the null association rate was also considered (Whitehead, 2009). The moving average was chosen to adjust best between precision and smoothing, and SE was estimated using the temporal jackknife method on each sampling period (Whitehead, 2009). Four exponential models that represented simulated social structures were fitted to the SLAR: the first model had no decay and suggests permanent associations; the second model had a decay down to zero and suggests that associations decrease until complete disassociation; the third model had a decay that levelled off and suggests long-lasting and temporary associations; and the fourth model had two decays and suggests two levels of disassociation, one at shorter and one at longer time lags (Whitehead, 2008). The best fitting model was chosen through the lowest QAIC (Whitehead, 2008, 2009). Since the patterning of all associations is important, data from 2011 to 2019 including all individuals, independently of the number of times captured, during medium- and high-coverage events were used for two SLARs: one for all individuals and other for adult female associations. The sampling period was defined as day, and associations were defined as individuals grouped within an occasion. Preferred association and temporal pattern analyses were performed using SOCPROG 2.9 (Whitehead, 2009).

Results

A total of 325 captures based on good quality pictures were obtained from 154 photographic occasions, allowing the identification of 79 distinctive animals (Table IV.1). There was a mean of 2.1 captures (SD = 1.1, range 1–5) per occasion, and of the total catalogued whales, 29 were adult females, 19 were adult males, 12 were subadult males, and 19 were immature (Table IV.2).

Table IV.2 Frequency table of age-sex class per residency patterns of Blainville's beaked whales in Madeira.

	Adult females	Adult males	Subadult males	Immature	Total
Residents	7	2	0	2	11
Visitors	15	6	3	7	31
Transients	7	11	9	10	37
Total	29	19	12	19	79

Sixty-six percent of the animals (n = 52) were captured on multiple occasions (mean = 4 captures, range 2–31). Fifty-seven percent of the animals (n = 45) were captured intra-annually and the remaining were captured inter-annually [of which 53% (n = 18) were adult females, 21% (n = 7) adult males, 9% (n = 3) subadult males, and 18% (n = 6) immatures]. Inter-annual recaptures ranged from 2 to 8 years, but only adult females were recaptured in >5 years (Supplementary Table IV.1 and Supplementary Figure IV.1).

Residents comprised 14% of the animals (n = 11), visitors 39% (n = 31), and transients 47% (n = 37). Adult females were the dominant age-sex class of residents (64%, 7/11) and visitors (48%, 15/31), whereas adult and subadult males and immatures were mainly transients (Table IV.2).

The overall RR was 0.66. Adult females presented the highest value (RR = 0.86), followed by immature individuals (RR = 0.63) and adult males (RR = 0.58), while subadult males had the lowest (RR = 0.42). The discovery curve showed a slight decrease between 200 and 300 cumulative captures, and thereafter the curve begins to stabilise (Figure IV.1).

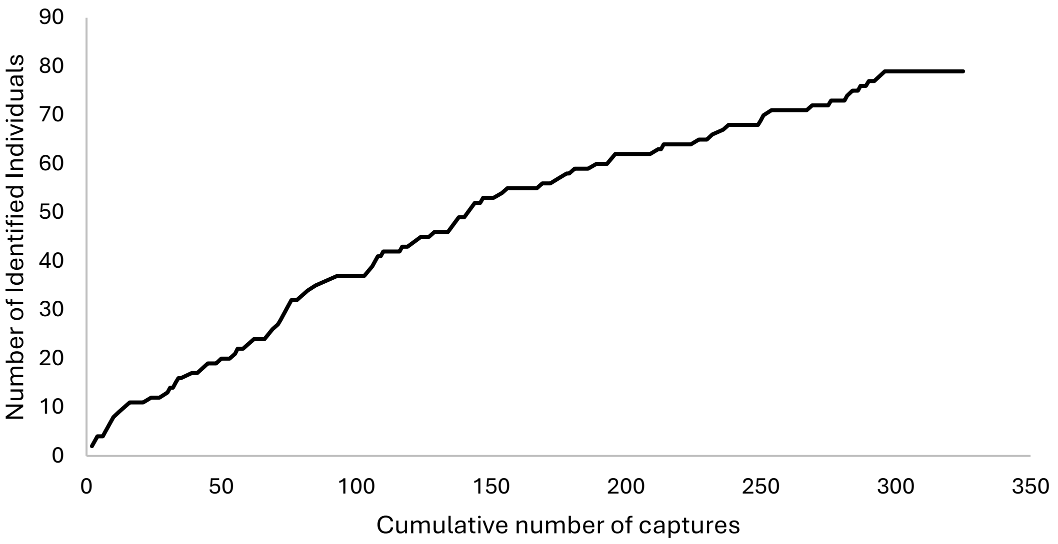

Figure IV.1 Discovery curve for distinctive whales based on good quality images.

Movement Analysis

The best-fitting LIR model for the adult females and immatures, and for the adult and subadult males, was the “Emigration + Reimmigration + Mortality” (Table IV.3).

Table IV.3 Models fitted to Lagged Identification Rates (LIR) for adult females and immatures, and for adult and subadult males of Blainville’s beaked whales captured between 2015 and 2019.

Age-sex class	Model	a1	a2	a3	a4	QAIC
Adult female + immature (n=48)	Closed	22.10 (2.43)	-	-	-	4899.37
	Emigration/mortality	14.97 (2.79)	1424.11 (1574.56)	-	-	4848.00
	Emigration + reimmigration	12.40 (2.48)	503.82 (430.32)	800.99 (*)	-	4843.14
	Emigration + reimmigration + mortality	**10.89 (2.29)**	**214.44(99.68)**	**158.43 (448.63)**	**0.0004 (0.0004)**	**4842.27**
Adult + subadult males (n=31)	Closed	17.43 (4.49)	-	-	-	813.78
	Emigration/mortality	9.80 (4.25)	862.12 (16186.45)	-	-	794.42
	Emigration + reimmigration	2.91 (1.99)	10.61 (184.84)	58.92 (*)		802.39
	Emigration + reimmigration + mortality	**0.94 (2.13)**	**1.38 (21.16)**	**14.36 (44.48)**	**0.001 (0.0006)**	**791.08**

τ is time lag in days. The lowest QAIC (in bold) indicates the best-fitting model. Estimated residency parameters and standard errors (SE) for the best-fitting model for adult females and immatures are: population size in the study area at a given time = 10.89 (2.29); residence time in the study area = 214.44 (99.68) days; residence time out of the study area = 158.43 (448.63) days; and mortality = 0.0004 (0.0004). Estimated parameters for the best-fitting model for adult and subadult males are: population size in the study area at a given time = 0.94 (2.13); residence time in the study area = 1.38 (21.16) days; residence time out of the study area = 14.36 (44.48) days; and mortality = 0.001 (0.0006). *very large SE

The model indicates that 11 adult females and immatures (SE = 2) spent an average of 214 days (SE = 99) in the area before leaving to return after 158 days (SE = 448) with a mortality rate of < 0.001 (Figure IV.2A). It also estimated that 1 male (SE = 0.94) spends an average of 1 day (SE = 21) before leaving to return to the study area 14 days later (SE = 44) with a mortality rate of <0.001 (Figure IV.2B).

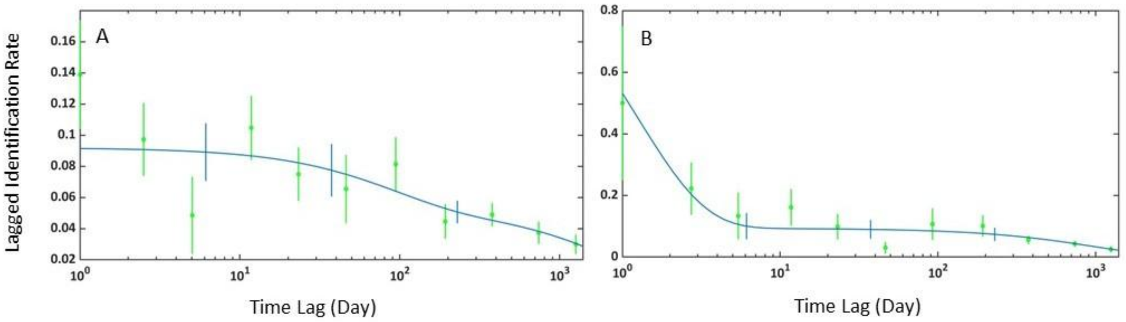

Figure IV.2 Lagged Identification Rates (LIR) for (A) adult females and immatures and (B) adult and subadult males in Madeira between 2015 and 2019. The graph shows the probability that an individual Blainville's beaked whale captured at an initial time "0" will be captured again at x time later in the study area. Blue lines represent the best-fitting model according to Table IV.3, green circles represent the data, and vertical bars indicate SE calculated using a bootstrap method on each sampling period.

Social Analyses

Network Analyses

The social network analyses comprised 70 individuals from 97 photographic occasions with a total of 267 captures, of which 28 were adult females, 18 adult males, 9 subadult males, and 15 immature individuals. The network diagram shows that most individuals (92%; n = 64) are linked by association in the main social core, while the remaining six individuals (8%) form satellite dyads (Figure IV.3). The main cluster includes all the resident individuals, 29 visitors (93%) and 24 transients (86%). In contrast, the remaining three satellite clusters only include transients and visitors (two visitor-transient dyads and one transient-transient dyad).

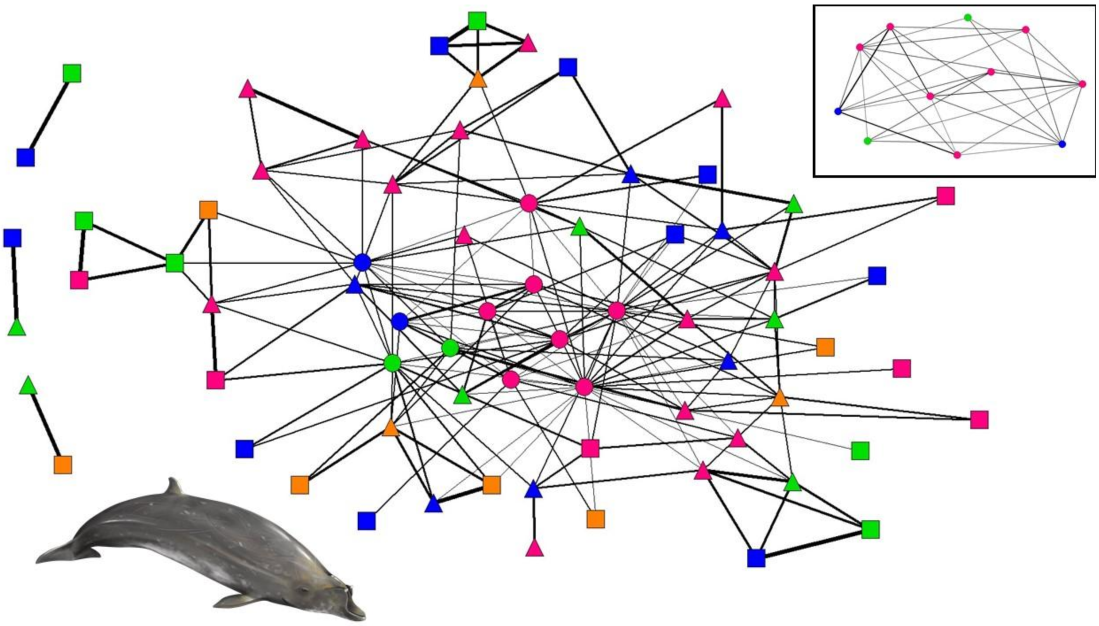

Figure IV.3 Network diagram of Blainville's beaked whales. Nodes represent individuals and are coloured and shaped for age-sex class and residency attributes: pink- adult female, blue- adult male, orange- subadult male, green- immature; circle- resident, triangle- visitor, and square- transient. The thickness of the lines between nodes represents the strength of association among dyads, where thicker lines correspond to stronger associations. The embedded network at the top right is the network of the resident whales only. Illustration E. Berninsone © ARDITI.

Network measures varied greatly between residency patterns but were similar between age classes and sexes (Figure IV.4 and Supplementary Table IV.2). The double permutation test showed no significant differences in the strength and clustering coefficient when testing the influence of age-sex classes and residency patterns.

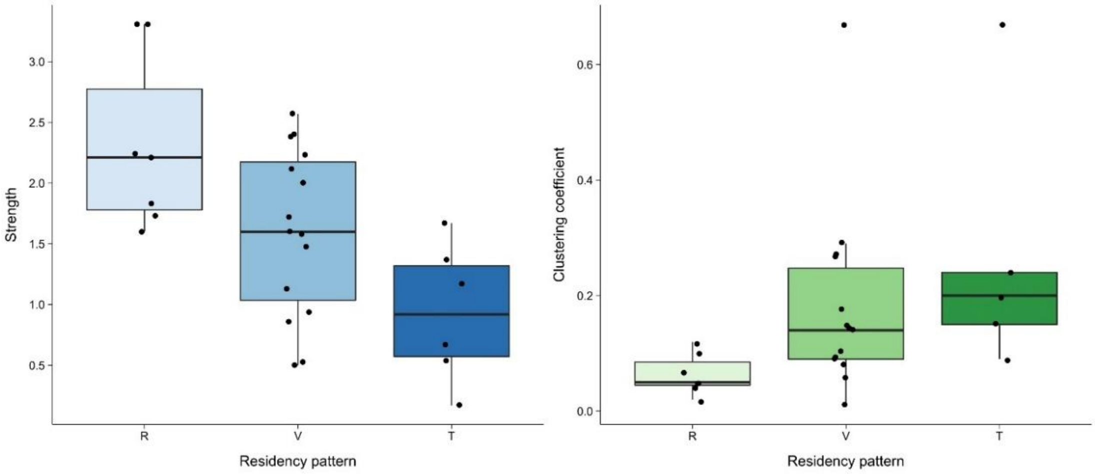

Figure IV.4 Boxplot for strength and clustering coefficient for each residency pattern (R–resident, V–visitor, T–transient) in adult females (the most representative group). The horizontal line in the box represents the median, the bottom and top of the boxes represent the first and third quartiles and whiskers show values within 1.5 times of the interquartile range from the boxes. Raw data are plotted as single points. A double permutation test showed no significant differences on the influence of residency patterns in the social network structure.

Preferred Associations

The mean association indices were low (HWI = 0.04 ± 0.02), but the maximums were high (Supplementary Figure IV.2). The highest maximum association indices were found between immature whales and adult females (0.51 ± 0.13), followed by adult males with adult females (0.34 ± 0.12), and within adult females (0.25 ± 0.13). The lowest mean and maximum association indices were found for all combinations of subadult males and adult males' dyads (HWI = 0 for subadult-subadult and male-male dyads, HWI = 0.01 ± 0.01 for subadult male—adult male dyads). The sum of association indices indicated that the associates per individual ranged from 1.3 to 4 whales (mean = 2.48 ± 0.59, Supplementary Figure IV.3).

Permutation tests within and between adult males, subadult males, and immature whales, could not be permuted, for which the null hypothesis that individuals associate randomly could not be rejected. However, preferred associations within adult females and between adult females and the other age-sex classes varied for short-, medium-, and long-term sampling periods (Table IV.4). The observed CV was significantly higher than the random CV for the dataset, including all the individuals for short-, medium-, and long-term periods. Adult females had short- and medium-term preferred associations within their category and between all age-sex classes ($p < 0.05$) except for subadult males with whom they associated randomly. The significant monthly associations between adult females and adult males revealed that Md119 (adult resident male) had strong associations with Md55 and Md99 (adult resident females, HWI = 0.45 and 0.48 respectively, $p < 0.05$). Long-term preferred associations occurred within adult females, and between adult females and immatures ($p < 0.05$), and long-term random associations occurred between adult females and all males independently of age class.

Table IV.4 Permutation tests for preferred associations within and between age classes and sexes for individuals captured on ≥ 3 occasions for short-, medium-, and long-term between 2011 and 2019.

	CV of observed HWI mean	CV of random HWI mean	*p*-value
	Short-term (sampling period hours)		
All individuals (n = 36)	2.31	2.00	0.001
Adult female - Adult female (n = 19)	2.17	1.99	0.02
Adult female- Adult male (n=26)	1.74	1.61	0.02
Adult female - Subadult male (n=21)	2.34	2.29	0.25
Adult female - Immature (n=26)	2.40	2.04	0.002
	Medium-term (sampling period months)		
All individuals	2.26	2.09	0.001
Adult female - Adult female	2.30	2.03	0.003
Adult female- Adult male	1.75	1.63	0.03
Adult female - Subadult male	could not be permuted		
Adult female - Immature	2.25	1.97	0.00
	Long-term (sampling period years)		
All individuals	2.26	2.09	0.001
Adult female – Adult female	2.30	2.10	0.01
Adult female – Adult male	1.75	1.68	0.16
Adult female – Subadult male	2.34	2.24	0.13
Adult female – Immature	2.26	2.05	0.01

Temporal Patterns

The third model was the best-fitting model for all individuals and for adult females (Table IV.5). For all individuals, SLAR was highest for short time lags and started decreasing fast after 100 days, reaching the null association rate in about 1 year (Figure IV.5A). Adult females showed a similar pattern, except that SLAR constantly declined from the short time lags and that the null association rate was reached later (Figure IV.5B).

Table IV.5 Models fitted to the standardised lagged association rate (SLAR) for all individuals and for adult females.

Age-sex class	Model	Number of parameters	QAIC
All individuals	PC	1	677.69
	CA	2	596.57
	PC+CA	**3**	**569.24**
	Two levels of CA	4	571.12
Adult females	PC	1	153.99
	CA	2	129.93
	PC+CA	**3**	**123.87**
	Two Levels of CA	4	164.17

The lowest QAIC (in bold) indicates the best-fitting model. The first model (with one parameter) suggests permanent associations, the second model (with two parameters) suggests that association decreases until complete disassociation, the third model (with three parameters) suggests long-lasting and temporary associations, and the fourth model (with four parameters) suggests two levels of disassociation (detailed in section Materials and Methods). τ is time lag in days.

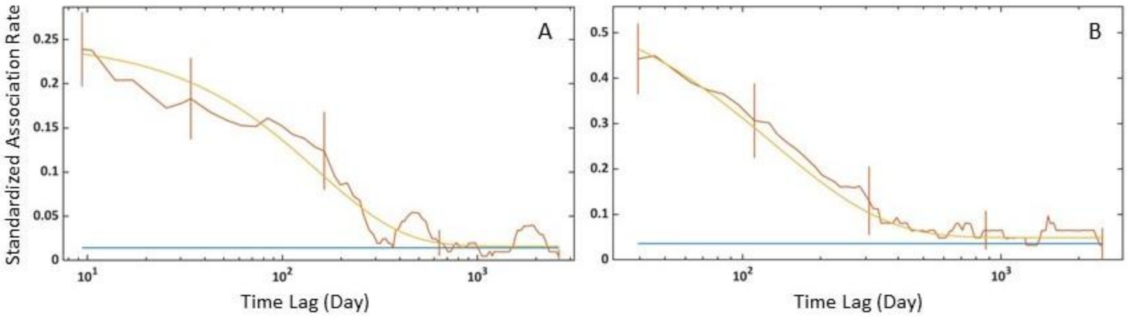

Figure IV.5 Standardised lagged association rate (SLAR) for **(A)** all individuals and **(B)** adult females captured between 2011 and 2019. Vertical bars indicate SE calculated using the temporal jackknife method. The brown line is the observed data, the yellow line is the best-fitting model according to Table IV.5, and the blue line is the standardised null association rate (i.e., if individuals associated randomly).

Discussion

This study provides an analysis of the social structure of Blainville’s beaked whales in insular oceanic ecosystems, which are characterised by specific topographic and oceanographic variables that are known to influence predators’ habits, such as cetaceans (Abecassis et al., 2015; Fernandez et al., 2021). The analysis of a longitudinal dataset on individual associations in relationship to age class, sex, residency status, and spatio-temporal patterns showed a social structure modulated by adult females. This agrees with analyses of mammalians’ social complexity where a female-based sociality prevails (Lukas and Clutton-Brock, 2018), in which cetaceans, and especially toothed whales, are no exception (Rendell et al., 2019). The present findings support the hypothesis of female defence polygyny suggested by McSweeney et al. (2007) for a population in Hawaii’, as well as reported in the Bahamas and Canary Islands (Claridge, 2006; Suárez, 2018). In addition, the present findings support information on female philopatry based on higher residency levels by adult females and provide a discussion on this social strategy.

The findings obtained in this study are inferred from a good agreement of the combination of movement and social analyses, from which five broad main results have emerged. First, there was heterogeneity in capture probability, given that 60% of the animals were captured on multiple occasions and most of the inter-annual recaptures (and the longer ones; >5 years) were from adult females. Island-associated animals (i.e., residents and visitors) were also mainly adult females, which presented the highest RR (0.86). The asymptotic discovery curve, observed from approximately > 300 cumulative captures, reveals that the studied island-associated population seems relatively small (likely < 50 animals). This also shows that recruits are less common throughout the years and some adult females exhibit high site fidelity, supporting Dinis et al. (2017).

Second, the best-fitting models from the LIR analysis included emigration and reimmigration with (residual rates of) mortality, which suggests temporary migration into and out of the area and transiency, with mortality within expected values given the duration of the study and the long-living nature of this mammal species. Additionally, it shows heterogeneity in residency times between age-sex classes. A higher number of adult females and immatures spent more time in the area than adult and subadult males, but also left for more extended periods. This reinforces the more constant presence of adult females and immatures in Madeira. The differentiated habitat use by Blainville's beaked whales of different age classes, sexes and residency patterns has also been described in the Hawaii', Bahamas and Canaries from photo-id analysis (Claridge, 2006; McSweeney et al., 2007; Suárez, 2018). Moreover, the heterogeneity in residency times between age-sex classes suggests different habitat roles, supporting spatial structuring within the species social organisation, with an indication of female philopatry.

Third, the social network analyses shows that the main cluster includes all the resident individuals and 93% of the visitors, supporting an island-associated population in the study area. This agrees with the previous points and with Dinis et al. (2017). Central individuals can be information carriers in dolphin societies (Lusseau and Newman, 2004), yet there was no significant influence of the age-sex classes and residency patterns in the network measures. This could be related to the sampling area that likely represents a portion of the home range of these animals, especially of the transients, making it difficult to confirm the role that different residency patterns might play in the social network analyses of Blainville's beaked whales.

Fourth, the tests for preferred associations show strong dyadic associations between adult females and immatures, contrarily to between males, as expected for a long-lived mammal species (Lukas and Clutton-Brock, 2018). This is based on the highest maximum association indices between adult females and immatures and the lowest mean and maximum association indices among all combinations of subadult males and adult males' dyads. The sum of association indices indicated that the typical number of associates per individual ranged from 1.3 to 4, indicating small group sizes similar to other areas (reviewed in Baird, 2019). Adult females exhibited short- and medium-term preferred associations between all age-sex classes, except for subadult males with whom they associated randomly. The significant monthly associations between adult females and adult males were likely influenced by pairs of dyads composed by a particular adult resident male (Md119) with two adult resident females (Md55 and Md99; based on their capture histories, Supplementary Table 1). In the long-term, preferred associations occurred only within adult females, and between adult females and immatures, supporting the hypothesis of female defence polygyny in this species.

Fifth, the best-fitting models from the analysis of the temporal pattern included a decay that levelled off and suggested long-lasting and temporary associations. The fast decrease of SLAR after 100 days for all individuals, indicated that many associations between individuals did not last longer than 3 months. The null association rate was reached in about 1 year, meaning that individuals associated randomly more often than expected for about a year. The peaks formed at 400 and ≈1,500 days are, most probably, a sampling by-product. For adult females, the null association rate was reached later (approximately 3.5 years). Therefore, adult females associated more often than expected if they associated randomly for periods of at least 3.5 years, although the SLAR stays above the null association rate for more extended periods. Such period could be related to time invested in nursing and/or alloparental care, which is a socioecological strategy commonly displayed by mammals (Greenwood, 1980; Berger et al., 2021), and particularly by deep-diving cetaceans like pilot (Globicephala spp.) or sperm whales (Physeter macrocephalus) (Whitehead, 1996; Augusto et al., 2017). While the obtained SLAR slope for adult females declines faster, their association rates are higher than those from all individuals, indicating that other age-sex classes, such as adult males, subadult males, and immatures, have more ephemeral associations between individuals and hence decreased the values of the association rates. The jackknife precision estimates indicate that associations between adult females last longer than all age classes combined.

As an overview, there were intra- and inter-annual preferred associations between females, but preferred associations with males occurred only intra-annually. In addition, adult females and immatures stayed extended periods in the area when compared to adult and subadult males. It is suggested that Blainville's beaked whales exhibit a general pattern of one adult male leading a small group of females during a short- to mid-period of time (hours to months) and that females are the ones "controlling" the area (i.e., higher site fidelity) and displaying longer-term associations; thus having a social structure driven by female philopatry and defence polygyny. This agrees with the unimale group mating system described in Clutton-Brock (1989) where the cost-effectiveness of territoriality declines and males are more likely to defend groups of females or to search receptive females, as observed in several terrestrial mammals (Clutton-Brock, 1989) and similar to sperm whales (Rendell et al., 2019). It can therefore be inferred that Blainville's beaked whales have a social structure stratified by age-sex class, and that they can combine a mix of the sociality found in smaller delphinids where ephemeral relationships usually take place (Gowans et al., 2007) and in mid- to large-sized toothed whales where "matrifocal" or matrilineal systems occur (Rendell et al., 2019). Different or mixed social structures are not uncommon among mammals, such as, for example, the stratified community and the multi-male mating system of Risso's dolphins (Grampus griseus) (Hartman et al., 2008, 2015), which differs from the fission-fusion and matrilineal society models.

The findings presented here shed light on a single species of the second-most speciose family (Ziphiidae) of cetaceans. Studies on the social structure of beaked whales exist only for four species (17% of all known beaked whale's species; Carroll et al., 2021), derived from restricted areas (reviewed in Weiss et al., 2021). While for Cuvier's beaked whales (*Ziphius cavirostris*), sperm competition seems to play a role in the mating system (Baird, 2019), in northern bottlenose whales (Hyperoodon ampullatus), there are strong associations between males (Gowans et al., 2001), whereas, in Baird's beaked whales (*Berardius bairdii*), there are stable associations among more scarred (old and/or male) individuals (Fedutin et al., 2015). Thus, beaked whales' social structures should not be generalised, given that association patterns, mating structures and societies vary between species (Hooker et al., 2019).

This study also increases our knowledge of the social strategy related to female philopatry and female defence polygyny. Here, both are present, but one does not necessarily imply the other. One and/or the other has been described for birds, pinnipeds, deers, or non-human primates (Greenwood, 1980; Le Boeuf, 1991; Koening et al., 2013; Bose et al., 2017), thus suggesting interspecific flexibility of mating systems and social structure, which could arise from several factors such as more cooperative male resource defence (Koening et al., 2013). The formation of stable associations can be correlated with biological and ecological factors (Morales et al., 2010), with long-term bonds being recorded within age-sex classes and with female-biased kinship organisation being found among larger species (Weiss et al., 2021). Such stable relationships provide certain advantages over sporadic bonds, like allomaternal care in deep-diving species (Rendell et al., 2019) or increased male mating success and herding of females during breeding seasons (Clutton-Brock, 1989; Connor et al., 1992), which could partially explain the described social system of the Blainville's beaked whales.

Potential biases in the present study, especially those related to heterogeneity in capturability and residency, could be related to using data from platforms of opportunity. Nevertheless, likelihood techniques were used to estimate parameters of movement models (Whitehead, 2001), which allowed dealing with the effort associated with collecting the individual identifications that had been neither randomly nor systematically distributed in space-time. In addition, the fact that the data were collected year-round over a relatively long period, and that it was restricted to good quality pictures and distinctive individuals, helped minimising biases. Moreover, the HWI was selected to represent the strength of the behavioural relationships between dyads since it is potentially less biased and recommended to be used when not all individuals have been identified in a sampling period (Whitehead, 2008), as in this case. Although other indices such as the Simple Ratio (Ginsberg and Young, 1992) could also be a good candidate (following Hoppitt and Farine, 2018), the inferences drawn from that index (not shown) were similar to the HWI and therefore the latter was preferred based on Whitehead (2008), even being aware that it does not fully correct biases. Another issue is that, when there is a difference in QAIC by less than two, the second best-fitting model should not be disregarded since it still offers substantial support (Burnham and Anderson, 2002). In this study, there was one case in the LIR and another in the SLAR analyses. In the former case, the only difference with the best model was that the second-best did not include mortality. Given that it makes sense to consider mortality in a real-life scenario, the model with the lowest QAIC was in accordance with being the best one. In the latter case, the third model was the best-fitting and the fourth model was the second best. Again, the best-fitting suggests being the most logical because permanent association (or preferred companions) occurred to some extent (i.e., long-term associations among adult females) in the targeted population. Finally, analyses on the social structure of animals that spend most of its time submerged, such as beaked whales (Tyack et al., 2006), should be inferred with caution. However, we believe that the findings obtained from surface data should reflect, in a general way, the species social system.

To further assess the socioecology of deep-diving species within an evolutionary approach, future studies should combine photo-id analyses with genomics and/or biotelemetry (e.g., Aguilar de Soto et al., 2012; Abecassis et al., 2015; Visser et al., 2021). Although challenging, targeting several individuals of the same group would help clarify these elusive species' matrilineal kinship. Comprehensive studies, such as the present one, allow incrementing our knowledge on the social behaviour of beaked whales and identifying resident populations. This information is necessary to better understand, manage and protect such cryptic species from increasing anthropogenic disturbances for which they are vulnerable.

Funding

The Oceanic Observatory of Madeira and the Portuguese Foundation for Science and Technology (FCT) throughout the strategic projects M1420-01-0142-FEDER-000001 and

UIDB/04292/2020, respectively. AB was supported by a MARE grant throughout the project UIDB/04292/2020, AD by ARDITI throughout the project M1420-09-5369-FSE-000002, RF by the FCT grant SFRH/BD/147225/2019, AS by the FCT grant SFRH/BD/141609/2018, MF by the MAC2/1.1a/385 in the framework of INTERTAGUA (MAC INTERREG 2014-2020), and FA by the FCT project UIDP/04292/2020 granted to MARE.

Acknowledgments

We thank all researchers, volunteers, and whale-watching operators who contributed with photographic data, especially to Ventura | nature emotions, H2O-Madeira, VMT Madeira, and Lobosonda. We thank Hal Whitehead for valuable inputs in the social analysis. We also thank Ashlie McIvor and both reviewers for valuable comments.

References

Abecassis, M., Polovina, J., Baird, R. W., Copeland, A., Drazen, J. C., Domokos, R., et al. (2015). Characterising a foraging hotspot for short-finned pilot whales and Blainville's beaked whales located off the west side of Hawaiʻi Island by using tagging and oceanographic data. *PLoS One* 10:e0142628. doi: 10.1371/journal.pone.0142628

Aguilar de Soto, N., Madsen, P. T., Tyack, P., Arranz, P., Marrero, J., et al. (2012). No shallow talk: Cryptic strategy in the vocal communication of Blainville's beaked whales. *Mar. Mamm. Sci*. 28, E75–E92. doi: 10.1111/j.1748-7692.2011.00495.x

Alves, F., Alessandrini, A., Servidio, A., Mendonça, A. S., Hartman, K. L., Prieto, R., et al. (2019). Complex biogeographical patterns support an ecological connectivity network of a large marine predator in the north-east Atlantic. *Divers. Distrib*. 25, 269–284. doi: 10.1111/ddi.12848

Alves, F., Ferreira, R., Fernandes, M., Halicka, Z., Dias, L., and Dinis, A. (2018). Analysis of occurrence patterns and biological factors of cetaceans based on long-term and fine-scale data from platforms of opportunity: Madeira Island as a case study. *Mar. Ecol*. 39:e12499. doi: 10.1111/maec.12499

Alves, F., Quérouil, S., Dinis, A., Nicolau, C., Ribeiro, C., Freitas, L., et al. (2013). Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: Implications for conservation. *Aquat. Conserv.: Mar. Freshw. Ecosyst*. 23, 758–776. doi: 10.1002/aqc.2332

Augusto, J. F., Frasier, T. R., and Whitehead, H. (2017). Characterizing alloparental care in the pilot whale (Globicephala melas) population that summers off Cape Breton, Nova Scotia, Canada. *Mar. Mamm. Sci*. 33, 440–456. doi: 10.1111/mms.12377

Bailey, H., and Thompson, P. (2006). Quantitative analysis of bottlenose dolphin movement patterns and their relationship with foraging: Movement patterns and foraging. *J. Anim. Ecol*. 75, 456–465. doi: 10.1111/j.1365-2656.2006.01066.x

Baird, R. W. (2019). "Behavior and ecology of not-so-social odontocetes: Cuvier's and Blainville's beaked whales," in *Ethology and Behavioral Ecology of Odontocetes*, ed. B. Würsig (Cham: Springer International Publishing), 305–329. doi: 10.1007/978-3-030-16663-2_14

Baird, R. W., and Whitehead, H. (2000). Social organisation of mammal-eating killer whales: group stability and dispersal patterns. *Can. J. Zool*. 78, 2096–2105. doi: 10.1139/z00-155

Barrat, A., Barthelemy, M., Pastor-Satorras, R., and Vespignani, A. (2004). The architecture of complex weighted networks. *Proc. Natl. Acad. Sci.* 101, 3747–3752. doi: 10.1073/pnas.0400087101

Bejder, L., Fletcher, D., and Bräger, S. (1998). A method for testing association patterns of social animals. *Anim. Behav*. 56, 719–725. doi: 10.1006/anbe.1998.0802

Berger, V., Reichert, S., Lahdenperä, M., Jackson, J., Htut, W., and Lummaa, V. (2021). The elephant in the family: costs and benefits of elder siblings on younger offspring life-history trajectory in a matrilineal mammal. *J. Anim. Ecol*. 2021:13573. doi: 10.1111/1365-2656.13573

Borgatti, S. P. (2002). *NetDraw: Graph Visualization Software*. Harvard: Analytic Technologies.

Bose, S., Forrester, T. D., Brazeal, J. L., Sacks, B. N., Casady, D. S., and Wittmer, H. U. (2017). Implications of fidelity and philopatry for the population structure of female black-tailed deer. *Behav. Ecol*. 28, 983–990. doi: 10.1093/beheco/arx047

Burnham, K. P., and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York, NY: Springe-Verlag.

Cairns, S. J., and Schwager, S. J. (1987). A comparison of association indices. *Anim. Behav*. 35, 1454–1469. doi: 10.1016/S0003-3472(87)80018-0

Carroll, E. L., McGowen, M. R., McCarthy, M. L., Marx, F. G., Aguilar, N., Dalebout, M. L., et al. (2021). Speciation in the deep: genomics and morphology reveal a new species of beaked whale *Mesoplodon eueu*. *Proc. R. Soc. B* 288:20211213. doi: 10.1098/rspb.2021.1213

Claridge, D. E. (2006). *Fine-scale distribution and habitat selection of beaked whales*. M.Sc. thesis. Aberdeen: University of Aberdeen.

Clutton-Brock, T. H. (1989). Mammalian mating systems. *Proc. Royal Soc. Lond. B* 236, 339–372. doi: 10.1098/rspb.1989.0027)

Connor, R. C., Smolker, R. A., and Richards, A. F. (1992). Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proc. Natl. Acad. Sci*. 89, 987–990. doi: 10.1073/pnas.89.3.987

Connor, R. C., Wells, R. S., Mann, J., and Read, A. J. (2000). “The bottlenose dolphin: social relationships in a fission-fusion society,” in *Cetacean Societies*, eds J. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead (London: University of Chicago Press).

Dinis, A., Marques, R., Dias, L., Sousa, D., Gomes, C., Abreu, N., et al. (2017). Site Fidelity of Blainville’s Beaked Whale (*Mesoplodon densirostris*) off Madeira Island (Northeast Atlantic). *Aquat. Mamm*. 43, 387–390. doi: 10.1578/AM.43.4.2017.387

Duijns, S., Anderson, A. M., Aubry, Y., Dey, A., Flemming, S. A., Francis, C. M., et al. (2019). Long-distance migratory shorebirds travel faster towards their breeding grounds, but fly faster post-breeding. *Sci. Rep*. 9:9420. doi: 10.1038/s41598-019-45862-0

Farine, D. R. (2013). Animal social network inference and permutations for ecologists in R using asnipe. *Methods Ecol. Evol*. 4, 1187–1194. doi: 10.1111/2041-210X.12121

Farine, D. R., and Carter, G. G. (2022). Permutation tests for hypothesis testing with animal social network data: Problems and potential solutions. *Methods Ecol. Evol*. 13, 144–156. doi: 10.1111/2041-210X.13741

Farine, D. R., and Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *J. Anim. Ecol*. 84, 1144–1163. doi: 10.1111/1365-2656.12418

Fedutin, I. D., Filatova, O. A., Mamaev, E. G., Burdin, A. M., and Hoyt, E. (2015). Occurrence and social structure of Baird’s beaked whales, *Berardius bairdii*, in the Commander Islands, Russia. *Mar. Mamm. Sci*. 31, 853–865. doi: 10.1111/mms.12204

Fernandez, M., Alves, F., Ferreira, R., Fischer, J.-C., Thake, P., Nunes, N., et al. (2021). Modeling fine-scale cetaceans’ distributions in oceanic islands: Madeira Archipelago as a case study. *Front. Mar. Sci*. 8:688248. doi: 10.3389/fmars.2021.688248

Foerster, S., McLellan, K., Schroepfer-Walker, K., Murray, C. M., Krupenye, C., Gilby, I. C., et al. (2015). Social bonds in the dispersing sex: partner preferences among adult female chimpanzees. *Anim. Behav*. 105, 139–152. doi: 10.1016/j.anbehav.2015.04.012

Geldmacher, J., van den Bogaard, P., Hoernle, K., and Schmincke, H.-U. (2000). The 40Ar/39Ar age dating of the Madeira Archipelago and hotspot track (eastern North Atlantic). *Geochem. Geophys. Geosystems* 1:1008. doi: 10.1029/1999GC000018

Gero, S., Gordon, J., and Whitehead, H. (2015). Individualised social preferences and long-term social fidelity between social units of sperm whales. *Anim. Behav*. 102, 15–23. doi: 10.1016/j.anbehav.2015.01.008

Ginsberg, J. R., and Young, T. P. (1992). Measuring association between individuals or groups in behavioural studies. *Anim. Behav*. 44, 377–379. doi: 10.1016/0003-3472(92)90042-8

Gowans, S., Whitehead, H., and Hooker, S. K. (2001). Social organisation in northern bottlenose whales (*Hyperoodon ampullatus*): not driven by deep-water foraging. *Anim. Behav*. 62, 369–377. doi: 10.1006/anbe.2001.1756

Gowans, S., Würsig, B., and Karczmarski, L. (2007). The Social Structure and Strategies of Delphinids: Predictions Based on an Ecological Framework. *Adv. Mar. Biol*. 53, 195–294. doi: 10.1016/S0065-2881(07)53003-8

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav*. 28, 1140–1162. doi: 10.1016/S0003-3472(80)80103-5

Hartman, K. L., Fernandez, M., Wittich, A., and Azevedo, J. M. N. (2015). Sex differences in residency patterns of Risso's dolphins (*Grampus griseus*) in the Azores: causes and management implications. *Mar. Mamm. Sci.* 31, 1153–1167. doi: 10.1111/mms.12209

Hartman, K. L., Visser, F., and Hendriks, A. J. E. (2008). Social structure of Risso's dolphins (*Grampus griseus*) at the Azores: A stratified community based on highly associated social units. *Can. J. Zool*. 86, 294–306. doi: 10.1139/Z07-138

He, P., Maldonado-Chaparro, A. A., and Farine, D. R. (2019). The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. *Behav. Ecol. Sociobiol*. 73:9. doi: 10.1007/s00265-018-2602-7

Hinde, R. A. (1976). Interactions, Relationships and Social Structure. *Man* 11, 1–17. doi: 10.2307/2800384

Hooker, S. K., de Soto, N. A., Baird, R. W., Carroll, E. L., Claridge, D., Feyrer, L., et al. (2019). Future directions in research on beaked whales. *Front. Mar. Sci*. 5:514. doi: 10.3389/fmars.2018.00514

Hoppitt, W. J. E., and Farine, D. R. (2018). Association indices for quantifying social relationships: how to deal with missing observations of individuals or groups. *Anim. Behav.* 136, 227–238. doi: 10.1016/j.anbehav.2017.08.029

Kappeler, P. M. (2019). A framework for studying social complexity. *Behav. Ecol. Sociobiol*. 73:13. doi: 10.1007/s00265-018-2601-8

Koening, A., Scarry, C. J., Wheeler, B. C., and Borries, C. (2013). Variation in grouping patterns, mating systems and social structure: what socio-ecological models attempt to explain. *Philos. Trans. R. Soc. B* 368:20120348. doi: 10.1098/rstb.2012.0348

Le Boeuf, B. J. (1991). "Pinniped mating systems on land, ice and in the water: Emphasis on the Phocidae," in *The Behaviour of Pinnipeds*, ed. D. Renouf (Dordrecht: Springer), doi: 10.1007/978-94-011-3100-1_2

Li, S., and Rosso, M. (2021). Lack of knowledge threatens beaked whales. *Science* 371:791. doi: 10.1126/science.abg8922

Lukas, D., and Clutton-Brock, T. (2018). Social complexity and kinship in animal societies. *Ecol. Lett*. 21, 1129–1134. doi: 10.1111/ele.13079

Lusseau, D. (2007). Why are male social relationships complex in the doubtful sound bottlenose dolphin population? *PLoS One* 2:e348. doi: 10.1371/journal.pone.0000348

Lusseau, D., and Newman, M. E. J. (2004). Identifying the role that animals play in their social networks. *Proc. R. Soc. Lond. B* 271, S477–S481. doi: 10.1098/rsbl.2004.0225

Lusseau, D., Wilson, B., Hammond, P. S., Grellier, K., Durban, J. W., Parsons, K. M., et al. (2006). Quantifying the influence of sociality on population structure in bottlenose dolphins. *J. Anim. Ecol*. 75, 14–24. doi: 10.1111/j.1365-2656.2005.01013.x

Martins, A. M., Amorim, A. S. B., Figueiredo, M. P., Souza, R. J., Mendonça, A. P., Bashmachnikov, I. L., et al. (2007). *Sea surface temperature (AVHRR, MODIS) and ocean colour (MODIS) seasonal and interannual variability in the Macaronesian islands of Azores, Madeira, and Canaries*. Florence: SPIE Remote Sensing. doi: 10.1117/12.738373

McSweeney, D. J., Baird, R. W., and Mahaffy, S. D. (2007). Site Fidelity, Associations, and Movements of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) Beaked Whales Off the Island of Hawai'i. Mar. Mamm. Sci. 23, 666–687. doi: 10.1111/j.1748-7692.2007.00135.x

Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., et al. (2010). Building the bridge between animal movement and population dynamics. *Philos. Trans. R. Soc. B* 365, 2289–2301. doi: 10.1098/rstb.2010.0082

Pearson, H. C. (2011). Sociability of female bottlenose dolphins (*Tursiops* spp.) and chimpanzees (*Pan troglodytes*): Understanding evolutionary pathways toward social convergence. *Evol. Anthropol*. 20, 85–95. doi: 10.1002/evan.20296

Rendell, L., Cantor, M., Gero, S., Whitehead, H., and Mann, J. (2019). Causes and consequences of female centrality in cetacean societies. *Philos. Trans. R. Soc. B* 374:20180066. doi: 10.1098/rstb.2018.0066

Ritter, F., and Brederlau, B. (1999). Behavioural observations of dense beaked whales (*Mesoplodon densirostris*) off La Gomera, Canary Islands (1995-1997). *Aquat. Mamm*. 25, 55–61.

Robbins, J., Rosa, L. D., Allen, J. M., Mattila, D. K., Secchi, E. R., Friedlaender, A. S., et al. (2011). Return movement of a humpback whale between the Antarctic Peninsula and American Samoa: A seasonal migration record. *Endanger. Species Res.* 13, 117–121. doi: 10.3354/esr00328

Schreier, A. L., and Swedell, L. (2009). The fourth level of social structure in a multi-level society: ecological and social functions of clans in hamadryas baboons. *Am. J. Primatol*. 71, 948–955. doi: 10.1002/ajp.20736

Shuster, S. M., and Wade, M. J. (2003). *Mating systems and strategies*. Princeton: Princeton University Press.

Suárez, C.R. (2018). *Abundance estimate, survival and site fidelity patterns of Blainville's (Mesoplodon densirostris) and Cuvier's (Ziphius cavirostris) beaked whales off El Hierro (Canary Islands).* M.Sc. thesis. Scotland: University of Saint Andrews.

Sutherland, W. J. (1998). The importance of behavioural studies in conservation biology. *Anim. Behav*. 56, 801–809. doi: 10.1006/anbe.1998.0896

Tyack, P. L., Johnson, M., Aguilar Soto, N., Sturlese, A., and Madsen, P. T. (2006). Extreme diving of beaked whales. *J. Exp. Biol*. 209, 4238–4253. doi: 10.1242/jeb.02505

Tyack, P. L., Zimmer, W. M. X., Moretti, D., Southall, B. L., Claridge, D. E., Durban, J. W., et al. (2011). Beaked whales respond to simulated and actual navy sonar. *PLoS One* 6:e17009. doi: 10.1371/journal.pone.0017009

Visser, F., Merten, V. J., Bayer, T., Oudejans, M. G., de Jonge, D. S. W., Puebla, O., et al. (2021). Deep-sea predator niche segregation revealed by combined cetacean biologging and eDNA analysis of cephalopod prey. *Sci. Adv*. 7:eabf5908. doi: 10.1126/sciadv.abf5908

Weiss, M. N., Ellis, S., and Croft, D. P. (2021). Diversity and consequences of social network structure in toothed whales. *Front. Mar. Sci*. 8:688842. doi: 10.3389/fmars.2021.688842

Whitehead, H. (1995). Investigating structure and temporal scale in social organisations using identified individuals. *Behav. Ecol.* 6, 199–208. doi: 10.1093/beheco/6.2.199

Whitehead, H. (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behav. Ecol. Sociobiol*. 38, 237–244. doi: 10.1007/s002650050238

Whitehead, H. (1999). Testing association patterns of social animals. *Anim. Behav*. 57, F26–F29. doi: 10.1006/anbe.1999.1099

Whitehead, H. (2001). Analysis of animal movement using opportunistic individual identifications: Application to Sperm Whales. *Ecology* 82, 1417–1432. doi: 10.2307/2679999

Whitehead, H. (2008). *Analysing animal societies: quantitative methods for vertebrate social analysis.* Chicago: University of Chicago Press.

Whitehead, H. (2009). SOCPROG programs: analysing animal social structures. *Behav. Ecol. Sociobiol*. 63, 765–778. doi: 10.1007/s00265-008-0697-y

Whitehead, H., Bejder, L., and Ottensmeyer, A. C. (2005). Testing association patterns: issues arising and extensions. *Anim. behav*. 69:e1. doi: 10.1016/j.anbehav.2004.11.004

Wilson, E. O. (1975). *Sociobiology: the new synthesis*. Cambridge, MA: Belknap Press.

Würsig, B., and Jefferson, T. (1990). Methods of photo-identification for small cetaceans. *Rep. Int. Whal. Comm. Sp. Issue* 12, 43–52.

CHAPTER V - Revealing Trophic Interactions Among Sympatric Odontocetes with Oceanic Ecosystem Traits

This chapter is submitted as:

Ferreira, Rita, Ester Dias, Manfred Kaufmann, Marc Fernandez, and Filipe Alves. "Revealing trophic interactions among sympatric odontocetes with oceanic ecosystem traits". Submitted July 2024 to Journal of Zoology.

CHAPTER V - Revealing Trophic Interactions Among Sympatric Odontocetes with Oceanic Ecosystem Traits

Abstract

Odontocetes, comprising toothed whales, dolphins, and porpoises, are pivotal top predators within marine ecosystems. However, our understanding of their habitat utilization and trophic niche still needs to be improved. While traditionally employed, stomach content analysis presents limitations such as prey digestibility, carcass accessibility, and short-term dietary assessments. Conversely, stable isotope analysis presents a non-invasive and temporally integrated approach for research on trophic ecology, particularly beneficial in remote pelagic environments. In this study, trophic ecology of six odontocete species in the Madeira Archipelago was investigated: *Delphinus delphis* (short-beaked common dolphin), *Stenella frontalis* (Atlantic spotted dolphin), *Tursiops truncatus* (common bottlenose dolphin), *Pseudorca crassidens* (false killer whale), *Globicephala macrorhynchus* (short-finned pilot whale), and *Physeter macrocephalus* (sperm whale). Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes in skin samples obtained from free-ranging adults were used to evaluate trophic position, isotopic niche size, foraging habitat, and sex-based differences. Results delineated two distinct groups among the studied species. The first group (*D. delphis*, *S. frontalis*, *T. truncatus*) exhibited relatively low $\delta^{13}C$ and $\delta^{15}N$ values and trophic position. In contrast, the second group (*P. crassidens*, *G. macrorhynchus*, *P. macrocephalus*) displayed higher isotopic values and trophic positions, and smaller trophic niche sizes than the first group. While foraging habitats appeared similar within these two groups, deep-diving species likely consumed unsampled prey in this study. Notably, the highest niche overlaps were observed between *S. frontalis* and *T. truncatus,* as well as *P. crassidens* and *G. macrorhynchus*. No significant sex-based isotopic differences were detected across species for both isotopes. This study examines the trophic ecology of several oceanic apex predators within a pelagic environment, where they serve as keystone species regulating the trophic web. Enhancing our understanding of odontocete trophic ecology contributes to measuring the ecological importance of these megafauna species in connecting isolated ecosystems within the ocean.

KEYWORDS: Stable isotopes; pelagic; cetaceans; SIBER; isotopic niche

Introduction

Marine top predators play a crucial role in the pelagic food webs, exerting top-down and bottom-up influences that contribute to the overall ecosystem dynamics (Ainley et al., 2010; Estes et al., 2011; Gilbert et al., 2023). Odontocetes, a group of cetaceans that includes toothed whales, porpoises and dolphins, is a diversified group that occupies the highest trophic levels, together with other species of marine megafauna (e.g., large teleosts, Frisch et al. 2014; sharks, Rastgoo & Navarro 2016; pinnipeds, Falk-Petersen et al. 2004), with potential interspecific competition and with trophic interactions that can shape trade-offs between management targets (Kadin et al., 2019; Kiszka et al., 2022). Nonetheless, odontocetes' trophic ecology has historically relied on stomach contents analysis of either hunted (e.g. Clarke & MacLeod, 1980), by-caught (e.g., Giménez et al., 2018), or stranded individuals (e.g. Mintzer et al., 2008), since the observation of feeding events is, in many cases, not possible (as in deep-diving species) or challenging (as in oceanic species) (Naito et al., 2013). Although it provides relatively high taxonomic resolution, the analysis of stomach contents is time-consuming, highly invasive, requires a large number of samples (with prey with differential digestibility rates), provides only a snapshot of the recently consumed prey, and sampling of sick or debilitated individuals is common (Dalerum & Angerbjörn, 2005). Furthermore, some sites include physiographical features that make it difficult to access the carcasses (such as a shoreline with inaccessible beaches), thereby rendering it impossible to conduct thorough studies (Palacios et al., 2004).

Stable isotope analysis provides information about trophic ecology by capturing intricate interactions and tracking energy flow through ecological communities (Sanders et al., 2015). The growing use of stable isotopes has provided valuable information on the trophic ecology, dietary preferences, trophic positions, migration patterns, or responses to environmental changes in odontocetes (e.g., Abend & Smith, 1995; Méndes et al., 2007; Knoff et al., 2008; Bode et al., 2022). Nevertheless, several biological tissues can be used for stable isotopes analysis, which enables the sampling of free-ranging individuals, stranded animals, or specimens in scientific collections (Teixeira et al., 2022). Also, different tissues have different turnover rates (i.e., the rate at which stable isotopes are incorporated into an organism's tissues), that can vary from a few days (e.g., liver; Tieszen et al., 1983) to months (e.g., skin and blubber; Abend & Smith, 1995; Giménez et al., 2016), years (e.g., bone collagen; Dalerum & Angerbjörn, 2005) or a lifetime, meaning there is no turnover (e.g., tooth dentin; Koch, 2007) (Teixeira et al., 2022). This variation in isotopic turnover among tissues requires adequate samples to be selected, depending on the research questions.

Carbon and nitrogen stable isotope analysis have been used to investigate trophic interactions within odontocetes communities (e.g., Costa et al., 2020; Kiszka et al., 2022; Vianna-Gatts et al., 2023). Stable isotopes of carbon ($\delta^{13}C$: $^{13}C/^{12}C$) indicate the primary carbon source in the individuals' diet (DeNiro & Epstein, 1978) and inform on their foraging habitat, since its values vary with both distance to shore and depth (Cherel & Hobson, 2007). Stable isotopes of nitrogen ($\delta^{15}N$: $^{15}N/^{14}N$), on the other hand, generally increase with increasing trophic position within a food web (DeNiro & Epstein, 1981), allowing for the assessment of an organism's trophic position (Vander Zanden & Rasmussen, 2001). Thus, $\delta^{13}C$ - $\delta^{15}N$ bi-plots provide a graphical representation of the isotopic niche occupied by each species, informing on niche overlap or resource partitioning in interspecific studies (Layman et al., 2007). However, trophic studies of sympatric odontocetes in oceanic habitats are scarce due to these animals' highly dynamic nature and the associated logistical constraints (Alves et al., 2023a; Palacios & Cantor, 2023).

In the Eastern North Atlantic, the few studies using stable isotopes on odontocetes focused on differences of $\delta^{13}C$ and $\delta^{15}N$ in the same species between archipelagos (Quérouil et al., 2013), on temporal changes in delphinids' trophic position (Bode et al., 2022), or on single species trophic ecology (Dias et al., 2023). The archipelago of Madeira, located in the oceanic biogeographical region of Macaronesia, is an area of high cetacean diversity, with nearly 30 recorded species, the majority of which are odontocetes with distinct habitat uses (Freitas et al., 2012; Alves et al., 2018; Ferreira et al., 2017; Fernandez et al., 2021). Common bottlenose dolphins *Tursiops truncatus*, short-finned pilot whales *Globicephala macrorhynchus,* and sperm whales *Physeter macrocephalus* are common year-round, including island-associated and transient animals (Alves et al., 2013; Dinis et al., 2016; Ferreira et al., 2022). Short-beaked common dolphins *Delphinus delphis* and Atlantic spotted dolphins *Stenella frontalis* are seasonal residents and exhibit temporal segregation, with the former species occurring mainly in Winter/Spring and the latter in Summer/Autumn (Alves et al., 2018; Fernandez et al., 2021). Unlike the previous species, false killer whales, *Pseudorca crassidens* are occasional visitors whose habitat use is little known (Alves et al., 2018). Therefore, this archipelago offers a privileged location to deepen our knowledge of the trophic ecology of multiple species of odontocetes in an oceanic habitat.

In this study, carbon and nitrogen stable isotopes obtained from the skin of free-ranging individuals were used to investigate the trophic position, isotopic niche sizes, foraging habitats, and sex-specific differences of six sympatric species of odontocetes inhabiting an oceanic ecosystem and of which some exhibit temporal segregation.

Materials and Methods

Study area and data collection

All biological samples were collected in the waters of the Madeira Archipelago in the Macaronesia biogeographical region (Eastern North Atlantic). This archipelago presents deep waters, steep submarine canyons, and a limited continental shelf (Gelmacher et al., 2000). It benefits from intricate geophysical wake flows like fronts and eddies, which can increase primary output due to the island mass effect (Caldeira et al., 2002), attracting predators and consumers of all trophic levels (Kaufmann et al., 2015; Friedlander et al., 2017; Alves et al., 2018).

Biopsy samples from six species of odontocetes were collected between 2017 and 2019. Those included short-beaked common dolphins (hereafter, common dolphins), Atlantic spotted dolphins (hereafter, spotted dolphins), common bottlenose dolphins (hereafter, bottlenose dolphins), short-finned pilot whales (hereafter, pilot whales), false killer whales, and sperm whales.

Biopsy sampling of cetaceans is a well-establish technique, used in numerous studies and in more than 40 species worldwide (reviewed in Noren & Mocklin, 2012). This technique shows very low reactions by the individuals and the group, specifically by odontocetes, and the wounds are small and heal quickly, with no adverse health effects. (Noren & Mocklin, 2012; Van Cise et al., 2024). Biopsy samples were acquired under the required legal permits from the local authorities (Institute of Forests and Nature Conservation of Madeira, licenses number 1856/2017, 508/2018, 535/2019), and by researchers with ample training and experience in collecting these samples. Collection took place only when the group and/or individuals showed no signs of stress to the approximation of the boat, and weather conditions were good (Beaufort sea state ≤3) to increase the chances of success. The targeted individuals were adults in apparent healthy conditions (i.e., with no signs of emaciation or debilitation), not accompanied by calves. Biopsies were collected using a 150-lb crossbow, with arrows and darts specially designed for cetaceans (Finn Larsen, Ceta-Dart), and of adequate size for each species (smaller darts for all the species except sperm whales). The individuals were hit just below the dorsal fin when they were close enough, and the distance at which sampling was conducted depended on the size of the species. Samples were collected when the angle of impact was perpendicular to the body (Brown et al., 1991; Barret-Lennard et al., 1996; Gauthier and Sears, 1999) and when animals were moving in a consistent direction and spent time at the surface (Wenzel et al., 2010). Biopsy samples of smaller species were collected at closer distances than of larger species (Weller et al., 1997; Möller and Beheregaray, 2001; Krützen et al., 2002). After collection, biopsies were immediately stored onboard in liquid nitrogen and then preserved at -80℃ until further analysis.

Laboratory analyses

The biopsy samples were divided into skin and blubber, and skin was used for stable isotope analysis (SIA) and molecular sexing.

For SIA, the skin was dried in an oven at 60℃ for 24 hours and ground to a fine powder with a mortar and pestle. Stable isotope ratios were measured using a Thermo Scientific Delta V Advantage IRMS via a Conflo IV interface (Marinnova, University of Porto).

Stable isotope ratios are reported in δ notation and were calculated as follows:

$$\delta X = (R_{sample}/R_{standard} - 1) \times 1000$$

where X is the carbon or nitrogen stable isotope, and R is the ratio of heavy: light stable isotopes. The $\delta^{13}C$ and $\delta^{15}N$ are expressed in units per mill (‰) relative to Vienna Pee Dee Belemnite and air, respectively. The analytical error, the mean SD of replicate reference material, was ±0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$. To control for sample processing quality, samples with an SD between replicates (i.e., two sub-samples of the same sample) > 0.2‰ $\delta^{13}C$ or $\delta^{15}N$ were not included in subsequent data analyses (Dias et al., 2023).

For molecular sexing of cetaceans, genomic DNA was isolated from skin tissue samples through GeneJET genomic DNA purification kit (Thermo Fisher Scientific) following the manufacturer's instructions. The DNA was quantified by the NanoDrop One Spectrophotometer (Thermo Fisher Scientific) and stored at -20°C until further use. A Multiplex PCR reaction simultaneously targeted the SRY and ZFX genes to identify the sex of the specimens. The primers described by Rosel (2003) TtSRYR and PMSRYF produce a fragment of 339 bp in males, and the pair ZFX0582F ZFX0923R produces a fragment of 382 bp both in males and females. PCR reactions were carried out in a total volume of 20 μL containing 30-75 ng of genomic DNA, 1x MyTaq Reaction buffer (Bioline), 0.2 μM primers (ZFX0582F, ZFX0923R, PMSRYF), 0.06 μM TtSRYR and 1U of MyTaq HS DNA polymerase (Bioline). The amplification was performed in an Applied Biosystems 2720 PCR thermal cycler (Thermo Fisher Scientific) as follows: initial denaturation at 95°C for 60 seconds, followed by 35 cycles of 95°C for 15 seconds, 51°C for 5 seconds, 72℃ for 15 seconds and a final extension of 72℃ for 15 seconds. Amplified PCR products were confirmed by electrophoresis on agarose gels (2.5%) stained with ethidium bromide and visualized by a UV transilluminator. Gel images were recorded in the gel documentation system-BL (Axygen®). To confirm that the amplified fragments correspond to SRY and ZFX genes, several amplicons were purified by Extractme DNA gel-ou kit (Blirt, Poland) following the manufacturer's instructions and then sequenced (Sanger sequencing) in both directions at Macrogen Europe (Madrid, Spain). DNA sequences were compared to those deposited at the NCBI database using online BLAST software (www.ncbi.nlm.nih.gov/BLAST) (Altschul et al. 1997).

Stable isotopes analyses

All $\delta^{13}C$ values were corrected for lipid content since lipids are depleted in ^{13}C compared to protein and carbohydrates (DeNiro and Epstein, 1977). In this study, cetacean-specific mathematical normalization formulas were applied. For all species except common dolphins, $\delta^{13}C$ corrected values were calculated as follows:

$$\delta^{13}C_{LEC} = 0.5301486 \times \delta^{13}C - 7.322335$$

where $\delta^{13}C$ is the non-lipid extracted value, and $\delta^{13}C_{LEC}$ is the mathematically corrected value (Peters et al., 2022). For common dolphins, Peters et al. (2020) developed a specific correction formula that performed better for that species:

$$\delta^{13}C_{LEC} = 0.5409 \times \delta^{13}C - 7.4674$$

The correction for the decadal decrease in atmospheric $\delta^{13}C$ (i.e., Suess effect), was not applied prior to statistical analyses. The decrease is ca. -0.022‰ yr-1 in the subtropical Atlantic (Quay et al., 2003) which would result in a maximum difference between the measured and corrected values of 0.044‰ in $\delta^{13}C$. This difference is not ecologically meaningful.

The assumptions of normality and homoscedasticity of both isotopic values were tested using Shapiro-Wilk and Levene's test, respectively. Since both isotopic values failed the normality assumption, a non-parametric Kruskall-Wallis was conducted with a pairwise

Wilcoxon post hoc test with Bonferroni comparison for paired contrasts to test for interspecific differences in stable isotope values. A Wilcoxon rank sum test was used to test for differences between sexes. Standard deviation (SD) was used as a measure of data dispersion when reporting mean values.

To estimate the trophic niche width for each species, stable isotopes values were used to calculate the standard ellipse area (SEA), a bivariate measure of the distribution of individuals in the trophic space. To account for the small sample size, the corrected standard ellipse area (SEA_C; considering 40% of central data points) and the corresponding 95% Bayesian ellipse area (SEA_B) were estimated for each species (Jackson et al., 2011; Jackson et al., 2012). Overlap between isotopic niches was calculated for both the core dietary niches, using the SEA_C, and the 95% SEA_B, calculated as a proportion of the SEA_B of one species over another, for each pair of species, and vice versa (Jackson et al., 2012; Peters et al., 2022). Analyses were conducted using the SIBER (Stable Isotope Bayesian Ellipses) package in R (Jackson & Parnell, 2023).

Trophic position (TP) was calculated following Post (2002):

$$\mathrm{TP} = \frac{(\delta^{15}N_s - \delta^{15}N_p)}{TEF} + \lambda$$

where λ represents the trophic level of the baseline organism, $\delta^{15}N_S$ is the stable isotope value of the consumer, $\delta^{15}N_p$ is the stable isotope value of the baseline organism, and TEF refers to the trophic enrichment factor, i.e., the average increase in $\delta^{15}N$ between consecutive trophic levels. In this study, we used 3.72 ± 0.30 ‰ for $\delta^{15}N_p$ (Table S.V.1), obtained by averaging the values of zooplankton samples collected in the same area during 2018 (Dromby, 2018). For TEF (Δ), we used the estimate of 3.30 ± 0.26‰ from McCutchan et al. (2003), which captures the variability in the quality of the food assimilated across trophic levels in the food web (Bode et al., 2022). Previous studies, using this estimate, reported similar TP values for cetacean species as those derived from diet studies (Bode et al., 2022).

To test for differences between the odontocetes' TP values, a non-parametric Kruskall-Wallis was conducted after testing for the assumptions of normality and homoscedasticity using Shapiro-Wilk and Levene's tests, respectively. The Wilcoxon post hoc test with Bonferroni correction was used for pairwise comparisons.

To investigate the foraging habitat of the six species of odontocetes, their stable isotopes values were compared with those of their potential prey (demersal and pelagic squids, small schooling fish, and tuna; Clarke & Lu, 1995; Clarke, 2006; Hermida & Delgado, 2016; Tejerina et al., 2019) after adjusting for one trophic level ($\Delta\delta^{13}C = 1.01 \pm 0.37‰$, $\Delta\delta^{15}N = 1.57 \pm 0.52‰$; Giménez et al., 2016). Here, a lower $\Delta\delta^{15}N$ value was considered than for computing TP values because it reflects the assimilation of high-quality, protein-rich diets by cetaceans. Prey species were grouped according to their taxonomic group and habitat, following Dias et al. (2023) (Table S.V.1). Epipelagic and benthopelagic small fish were grouped as "small pelagic fish A", except for blue jack mackerel *Trachurus picturatus*, which was separated into "small pelagic fish B" due to its ^{13}C- and ^{15}N-enriched composition. The tuna species were grouped as "large pelagic fish". Squids were divided into demersal and pelagic, the latter being divided into two groups ("pelagic squids A" and "pelagic squids B") due to differences in their mean $\delta^{15}N$ and $\delta^{13}C$ values (Dias et al. 2023 for detailed explanation).

Results

A total of 165 biopsy samples were obtained, ranging from seven (sperm whales) to 47 (common dolphins) (Table V.1).

Table V.1 Cetacean species and number of individuals (*n*) sampled, number of females (F) and males (M) molecularly sexed, mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values (‰) after correction for lipids and mean (± SD) trophic position.

Cetacean species	***n***	**Sex (*n*)**		**$\delta^{13}C$**	**$\delta^{15}N$**	**TP**
		F	M			
Short-beaked common dolphin	47	19	28	-17.99 ± 0.27	9.79 ± 0.77	3.84 ± 0.23
Atlantic spotted dolphin	33	14	19	-17.47 ± 0.23	10.37 ± 0.89	4.02 ± 0.27
Common bottlenose dolphin	38	19	19	-17.05 ± 0.39	10.15 ± 0.70	3.95 ± 0.21
False killer whale	8	4	4	-16.65 ± 0.21	12.07 ± 0.17	4.53 ± 0.05
Short-finned pilot whale	32	20	12	-16.52 ± 0.28	12.40 ± 0.68	4.63 ± 0.20
Sperm whale	7	7	0	-16.90 ± 0.14	12.55 ± 0.42	4.68 ± 0.13

Common dolphins presented the most ^{13}C- and ^{15}N- depleted values ($\delta^{13}C$ = -17.99 ± 0.27‰, $\delta^{15}N$ = 9.79 ± 0.77‰), presenting statistically significant differences in $\delta^{13}C$ values with all other species, and in $\delta^{15}N$ values with all species except bottlenose dolphins (Table S2 and S3). Pilot whales were the most ^{13}C-enriched (-16.52 ± 0.28‰), showing significant differences with all species except sperm whales (Tables V.1 and S.V.2). Sperm whales were the most ^{15}N-enriched (12.55 ± 0.42‰), presenting significant differences with common, spotted, and bottlenose dolphins (Tables V.1 and S.V.3).

Table V.2 Isotopic niche metrics for cetacean species. SEA_C = standard ellipse area corrected for small sample size, SEA_B = Bayesian standard ellipse area (mode ± credibility intervals).

Cetacean species	**SEA_C**	**SEA_B**
Short-beaked common dolphin	0.66	0.64 (0.48 – 0.85)
Atlantic spotted dolphin	0.67	0.65 (0.44 – 0.91)
Common bottlenose dolphin	0.87	0.84 (0.61 – 1.15)
False killer whale	0.12	0.10 (0.05 – 0.22)
Short-finned pilot whale	0.53	0.50 (0.36 – 0.73)
Sperm whale	0.15	0.12 (0.06 – 0.30)

There were no statistically significant differences in the $\delta^{13}C$ and $\delta^{15}N$ values between sexes for the analyzed species (Table S.V.4). No comparison was made for sperm whales since only females were sampled.

Bottlenose dolphins presented the largest trophic niche among the species sampled, followed by spotted and common dolphins (Figure V.1 and V.2). False killer whales and sperm whales, on the other hand, presented the smallest trophic niches (Table V.2).

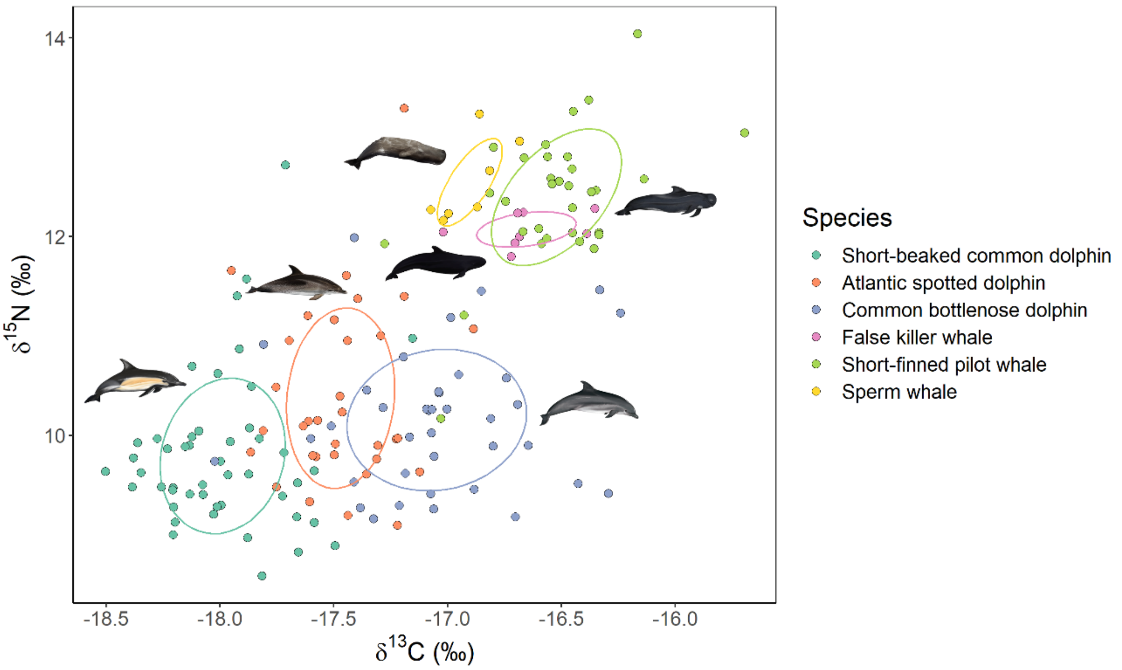

Figure V.1 Standard ellipse areas corrected for small sample size (SEA$_C$) for the six species of cetaceans. Ellipse areas hold 40% of the data. Illustration E. Berninsone © ARDITI.

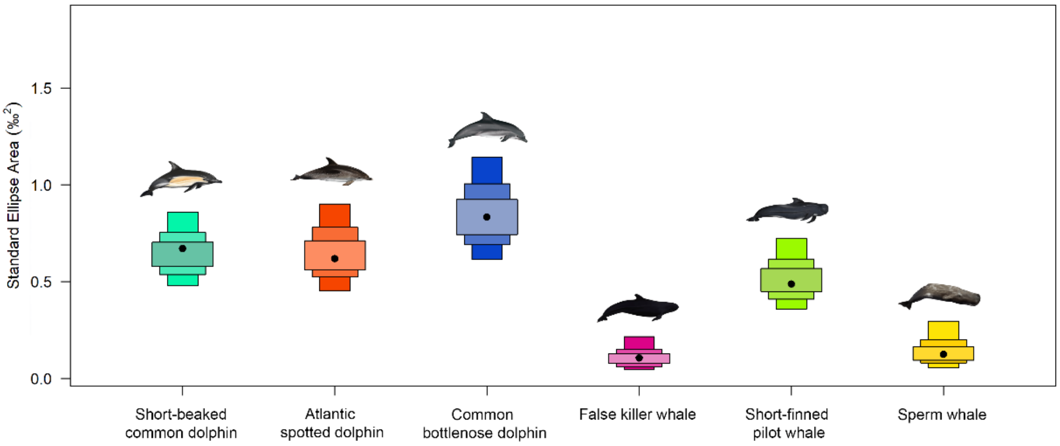

Figure V.2 Density plot showing the 95, 75 and 50% credible intervals of standard ellipses areas using Bayesian techniques (SEA$_B$) for the six species of cetaceans. Black dot represents mode. Illustration E. Berninsone © ARDITI.

Bayesian niche overlaps were calculated between each pair of species (Table V.3). The trophic niche of false killer whales showed the highest overlap with that of pilot whales. Spotted dolphins also presented a high overlap, but with bottlenose dolphins. Sperm whales' trophic niche overlapped only with that of pilot whales, but pilot whales' niche overlapped with all species except common dolphins. There was overlap between all trophic niches of common, spotted, and bottlenose dolphins.

Table V.3 Bayesian niche overlap (95%) for each species (left column) with each other species (top row).

	Short-beaked common dolphin	Atlantic spotted dolphin	Common bottlenose dolphin	False killer whale	Short-finned pilot whale	Sperm whale
Short-beaked common dolphin	NA	0.40117	0.37224	0	0	0
Atlantic spotted dolphin	0.40471	NA	0.69089	0	0.00063	0
Common bottlenose dolphin	0.29345	0.53990	NA	0	0.14898	0
False killer whale	0	0	0	NA	0.69507	0
Short-finned pilot whale	0	0.0008	0.24333	0.14851	NA	0.00064
Sperm whale	0	0	0	0	0.00263	NA

When considering core trophic niches, overlap occurred only between spotted and bottlenose dolphins (area overlap of 14%) and between false killer and pilot whales (area overlap of 11%).

The mean values of TP for the six species of cetaceans ranged from 3.84 ± 0.23 for common dolphins and 4.68 ± 0.13 for sperm whales (Figure V.3). False killer, pilot, and sperm whales presented statistically significant higher TP values than common, spotted, and bottlenose dolphins (Table V.1). Spotted and common dolphins also demonstrated significant differences between their TP values. Results on paired comparisons are available in the supplementary material (Table S.V.5).

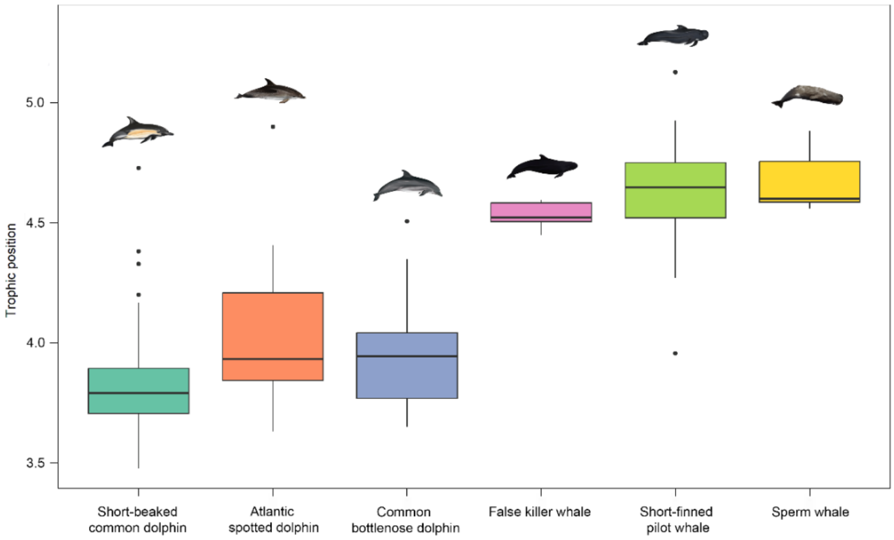

Figure V.3 Boxplots of trophic positions of the six species of cetaceans following Post (2002). Zooplankton was used as the baseline of the trophic web (trophic position 2). Illustration E. Berninsone © ARDITI.

After adjusting for trophic fractionation, the $\delta^{13}C$ and $\delta^{15}N$ values of common dolphins suggest the assimilation of prey from pelagic and demersal habitats (Figure V.4). Spotted and bottlenose dolphins present a similar foraging habitat, and their $\delta^{13}C$ and $\delta^{15}N$ suggest reliance on pelagic fish and squids. False killer, pilot, and sperm whales presented similar isotopic values to that of "large pelagic fish", suggesting the assimilation of these prey or of prey with similar foraging habitats. The ^{13}C- and ^{15}N-enriched values presented by some individuals of pilot whales and the ^{15}N-enriched values presented by some sperm whales and spotted dolphins (i.e. outside the mixing polygon formed by the potential prey groups) suggest the assimilation of prey at higher trophic levels or with origin in other habitats such as coastal or deep habitats, or both. Also, the high dispersion in the $\delta^{13}C$ and $\delta^{15}N$ values in bottlenose dolphins suggest intraspecific variability in their foraging habitats.

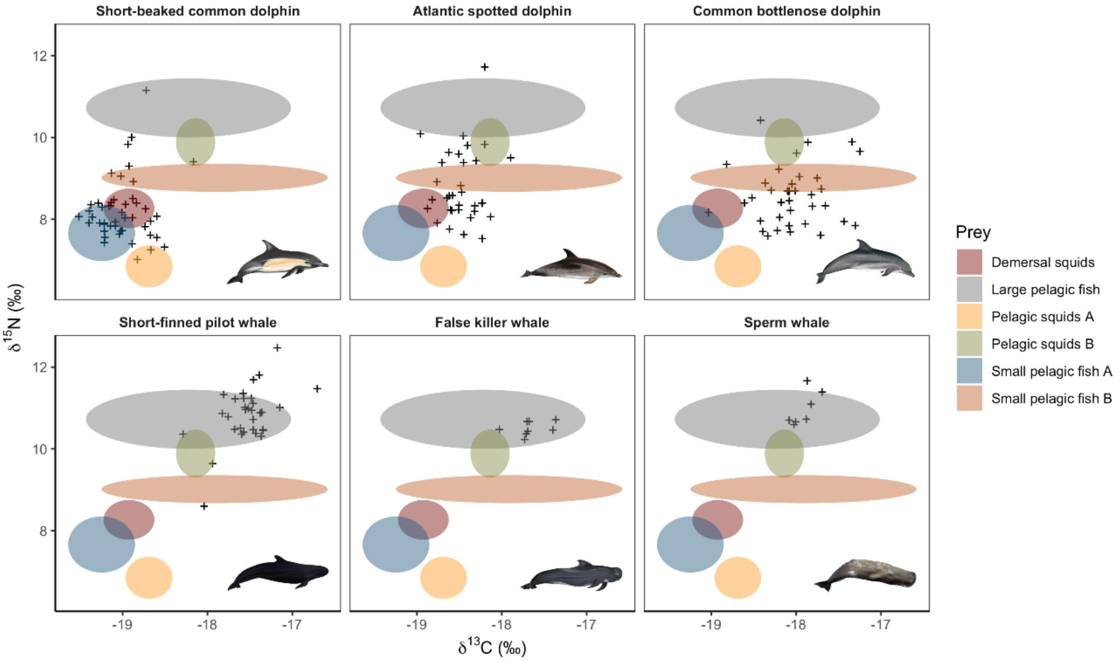

Figure V.4 Biplots with mean $\delta^{13}C$ and $\delta^{15}N$ values (‰) of each cetacean species, adjusted for one trophic level fractionation ($\delta^{13}C = 1.01 \pm 0.37$‰, $\delta^{15}N = 1.57 \pm 0.52$‰, Giménez et al. 2016), and their potential prey, divided by group as explained in 'Material and Methods' section. Ellipses were designed based on mean and standard deviation values. Illustration E. Berninsone © ARDITI.

Discussion

Information on trophic ecology is crucial when characterizing biological communities and understanding ecosystem functioning and dynamics. This study contributes to expanding the knowledge of odontocetes' role in pelagic environments, providing a first glimpse into the trophic ecology of multiple species in the remote archipelago of Madeira, where these top predators have important roles as keystone species and regulators of the food web (Romero et al., 2024). The characterization of the isotopic niches and overlaps offers new perspectives on the local dynamics for a higher number of species than previously targeted in Madeira (Quérouil et al., 2013; Bode et al., 2022; Dias et al., 2023). Moreover, the evaluation of sex-related differences in $\delta^{13}C$ and $\delta^{15}N$ in several species from which the existing knowledge is limited (e.g., false killer whales, Haro et al., 2018; bottlenose dolphins, Dias et al., 2023; common and spotted dolphins, Quérouil et al., 2013) is of relevant importance to better understand these species' foraging ecology. This is mainly due to the fact that the evaluation of sex in cetaceans before sampling is limited to species with sexual dimorphism (e.g., killer whales), and therefore, in the remaining species, there is uncertainty until molecular sexing is conducted. Furthermore, identifying foraging habitats is significant given the variety of feeding habits that these six species display in a pelagic environment.

Based on the stable isotope values, it was clear a distinction between two groups. One group presents overall ^{13}C- and ^{15}N- depleted values and occupy a relatively low trophic position (3.8-4.0), and is formed by common, spotted and bottlenose dolphins. The other group presents higher isotope values and trophic position (4.5-4.7), when compared to the first group, and is formed by false killer whales, pilot whales, and sperm whales. Common dolphins presented the lowest values of $\delta^{13}C$ and $\delta^{15}N$ and were the species with the lowest trophic position (3.84 ± 0.23), followed closely by bottlenose (3.95 ± 0.21) and spotted dolphins (4.02 ± 0.27). These three species are described as generalist predators that feed on prey of low trophic levels (González et al., 1994; Férnandez et al., 2009; Mendez-Fernandez et al., 2012). These species' occurrence in the trophic level four is in accordance with a previous study in Macaronesia, where Bode et al. (2022) presented results on trophic positions of common dolphins of 4.09 (± 0.31), spotted dolphins of 3.92 (± 0.12) and bottlenose dolphins of 4.28 (± 0.26). In the latter species, a study conducted on the Atlantic coast of the Iberian Peninsula identified a higher trophic level of five (Mendéz-Fernandez et al., 2012). This difference is probably related to variability in prey availability between oceanic and coastal habitats. The highest trophic position was found for sperm whales (4.68±0.13), and it was similar to that of pilot whales (4.63±0.20) and false killer whales (4.53±0.05). These results are in line with studies conducted across their distribution range (Kiszka et al., 2010; Bode et al., 2022; Días-Gamboa et al., 2022; Costa et al., 2020; Pinela et al., 2010).

The widest trophic niches were found for common, spotted, and bottlenose dolphins. This is justified by the fact they are generalist predators with high plasticity and dynamism in their feeding habits (Quérouil et al., 2013; Plint et al., 2023). In the Madeira Archipelago, spotted and common dolphins occur mainly in different seasons – the former species is associated with temperate/warm waters with low productivity values during Summer and Autumn (June until November), while the latter is linked to productivity and occurs in Winter and Spring (December to June) (Fernandez et al., 2021). Previous studies, based on stomach contents, found that common dolphins might vary their diet depending on their habitat. In coastal areas, they feed mainly on small epipelagic, shoaling fish and some cephalopods (Silva et al., 1999; Santos et al., 2004). In contrast, in oceanic areas, they mainly feed on species of the deep scattering layer, especially meso- and bathypelagic species, such as myctophids (Brophy et al., 2006; Pusineri et al., 2007). Moreover, Giménez et al. (2018) found that common dolphins in the Mediterranean Sea side of the Strait of Gibraltar feed both on epipelagic and mesopelagic species, suggesting a prey consumption shift between day and night. The higher values of $\delta^{15}N$ found in common dolphins for some individuals indicate that feeding might occur in ^{15}N-enriched prey. However, most individuals seem to forage in the habitat of demersal and pelagic squids (*Loligo vulgaris* and *Ommastrephes caroli*, respectively) and small pelagic fishes. Therefore, findings of this study align with prior research, indicating that common dolphins in Madeira also likely prey on both epipelagic and mesopelagic species. Also, the higher $\delta^{15}N$ values might be related to seasonal differences in the prey preferences. Some common dolphin populations have different foraging behaviors related to seasonal changes in seawater temperature, which can indicate prey-switching behavior during the warmer months (Simonis et al., 2017). This factor was not taken into account in the present study and should be explored in future studies to provide further insights into the trophic ecology of this species.

Regarding spotted dolphins, their foraging habitats incorporate more enriched prey in both isotopes but with a higher dispersion in their stable isotope ranges when compared to common dolphins. This may include other small pelagic fish (*Trachurus picturatus*) and pelagic squids (*Sthenoteuthis pteropus*). In this area of the Atlantic, spotted dolphins prefer deep offshore waters around 1,000 m bathymetry (Fernandez et al., 2018, 2021). Previous studies across their distribution indicate that this species has teuthophagous and ichthyophagous feeding habits (e.g., Herzing, 1996; Melo et al., 2010; Lopes et al., 2012), with some variation in terms of species across their geographic location, and may also incorporate benthic invertebrates (Perrin et al., 1994) and crustaceans (Férnandez et al., 2009).

Bottlenose dolphins presented the largest isotopic niches in this study. This might indicate opportunistic foraging at various trophic levels and in various spatially distinct habitats, preying on a broad spectrum of fish and squid species (Santos et al., 2001, 2007; Plint et al., 2023). Recent studies have shown intra-seasonal variability of stable isotopes in bottlenose dolphins in the Madeira Archipelago, with dolphins feeding during summer and autumn on demersal and pelagic squids, as well as small pelagic fishes, and during winter and spring preying on large pelagic fishes (Dias et al., 2023). In Madeira, bottlenose dolphins of different residency patterns (island-associated and transients; Dinis et al., 2016) co-occur year-round, and differences in foraging habitats have not been explored. Therefore, the large isotopic niche could be associated with one or a combination of these factors. The separation of analyses of different populations of bottlenose dolphins has been taken into consideration in other areas (e.g., Fernández et al., 2011; Plint et al., 2023) and could be an essential future step to better understand the trophic ecology of bottlenose dolphins in Madeira (and Macaronesia), given the co-occurrence of animals with different residency patterns.

The relatively small isotopic niche of pilot whales reflects their tendency towards more specialized feeding behavior while also displaying considerable adaptability to local environmental conditions throughout their geographical range (Thorne et al., 2017; Shearer et al., 2022). This species is mainly teuthophagous but may occasionally prey on fish and octopuses (de Soto & Alves, 2023). Information on its feeding habitats is limited (e.g., Seagars and Henderson, 1985; Mintzer et al., 2008), and only four stomach contents were analyzed in this region of the Atlantic, with remains of mesopelagic squids (in the Canaries; Hernández-García & Martín, 1994; Fernández et al., 2009; Luna et al., 2024). The foraging habitats identified for pilot whales in this study are the ones of tuna fish (classified as "large pelagic fish"). Researchers and fishermen have identified associations between these species (pers. com.), but predation has not been reported in the literature. However, predation on similar-sized species has been identified (e.g., García-Rivas et al., 2013), and therefore, predation on tuna fish by pilot whales cannot be rejected. Pilot whales also show an association with the habitats of mesopelagic squids (*Sthenoteuthis pteropus*, identified as "Pelagic squids B"), which is in accordance with previous findings. However, pilot whales are a deep-diving species, and prey originated from habitats at greater depths than those considered in this study could partially explain the ^{13}C- and ^{15}N- enriched values presented by the individuals of this species in the present study. These habitats should be considered in future studies to investigate in greater detail their trophic ecology.

The smallest trophic niches were those of false killer and sperm whales. This may be related to the small sample size since the sampled number of individuals was below the minimum of 10 samples suggested by Jackson et al. (2011) for the analysis of isotopic niches conducted with SIBER. However, due to the lack of information on these species in this area, the analyses were performed as a preliminary approach, and results should be interpreted with caution.

False killer whales foraging habitats were associated with large pelagic fish, such as tuna fish, in accordance with literature (e.g., Kratofil et al., 2020) and *in situ* observations at Madeira (unpublished data). Cephalopods are also reported as prey (Odell & McClune, 1999), and the isotopic values of some individuals in the present study are close to those of “pelagic squids B” (*Sthenoteuthis pteropus*), after correcting for trophic enrichment. Due to their feeding habits, interaction with fisheries is a concern, specifically with tuna fishing boats, as commonly reported in Hawai'i (Baird, 2018) and where interactions and aggressive attitudes from fishermen have been observed in Madeira (pers. comm). The foraging habitats of sperm whales could not be clearly identified in this study due to preying mainly on deep water cephalopods and demersal and mesopelagic fish (Whitehead, 2018), which were not possible to obtain for this study.

In this study, bottlenose dolphins were the species whose isotopic niche most frequently overlapped with the isotopic niches of other species. Regarding its core niche area, bottlenose dolphins overlapped with spotted dolphins, while in SEA_B, it overlapped with common and spotted dolphins, as well as pilot whales. Bottlenose dolphins are generalist predators (González et al., 1994) and, therefore, demonstrate the largest trophic niche and the largest range of $\delta^{13}C$ values, suggesting a wide variety of foraging habitats. The overlap with the isotopic niche of pilot whales was expected due to the frequent association between these two species (in around 10% of the sightings in the study area; Dinis et al., 2016). In fact, in Madeira, the bottlenose dolphin is the cetacean species most frequently recorded in interspecific associations, including with spotted and common dolphins (Alves et al., 2018). Overlap between the isotopic niches of false killer and pilot whales was also observed. However, it is expected to originate no interspecific competition due to the differences in habitat use by these two species. False killer whales are occasional visitors to this area, while pilot whales have an island-associated population (Alves et al., 2013). However, an extended assessment of foraging ecology between overlapping species, using complementary diet assessment methods, is required to understand the ecological consequences of such trophic niche overlap.

Differences in the stable isotopes between sexes have been demonstrated for some odontocetes (killer whales, Reisinger et al., 2016; false killer whales, Haro et al., 2018; sperm whales, Pirotta et al., 2020) but not for others (e.g., short-finned pilot whales, roughed-toothed dolphins, melon-headed whales, and spinner dolphins, Kiszka et al., 2010; common and spotted dolphins, Quérouil et al., 2013). In this study, no differences were found in the isotopic composition between sexes. For sperm whales, only females were sampled, and comparing stable isotopes between sexes was impossible. In subtropical areas such as the Madeira Archipelago, sperm whale groups are mainly formed by females, calves, and immature individuals (Whitehead, 2018; Ferreira et al., 2022), and since biopsying was restricted to adult individuals, the sampling bias towards females was an expected limitation.

Stable isotope analysis is a powerful tool for studying ecological processes, trophic interactions, and ecosystem dynamics. However, this study presents some limitations that may impair the conclusions obtained. One of the limitations is related to the sampling of free-ranging individuals. Besides sampling individuals of the same sex (as happened with sperm whales), sampling individuals from the same groups may have also occurred. Although biopsying was limited to 10% of the group size to minimize sampling of the same individuals, the same group might have been sampled in different days. Another limitation is related to the presence of individuals of difference residency patterns. In Madeira, individuals of different residency patterns have been identified in short-finned pilot whales (Alves et al., 2013), bottlenose dolphins (Dinis et al., 2016), Bryde's whales (Ferreira et al., 2021), sperm whales (Ferreira et al., 2022) and Blainville's beaked whales (Badenas et al., 2021), therefore future studies on trophic ecology on these species should incorporate this variable in the analysis.

Interpreting stable isotopes data can be complex due to the multiple factors influencing isotopic values. Although the size of the isotopic niches can be associated with the diversity of prey and/or foraging habitats, it should be noted that isotopic variability of the prey items consumed significantly impacts the size of an isotopic niche for a population. As a result, consumers ingesting a variety of prey species with similar isotopic values will produce small isotopic niches (Troina et al., 2020). This problem may extend to the ecological meaning of overlaps between isotopic niches of different species that may not always be related to feeding on the same prey but of prey of similar isotopic composition (Troina et al., 2020). Therefore, interpretation of these results should take this information into account.

In summary, this study provides novel insights into the isotopic niche of six odontocete species and their overlaps for this area of the Atlantic, enhancing the understanding of trophic interactions among species within oceanic ecosystems. The absence of significant differences in isotopic compositions between sexes for five pelagic species is relevant due to the limited information available on these top predators, especially regarding studies incorporating balanced sampling of both sexes. Furthermore, the identification of foraging habitats is of considerable interest, given the challenges associated with accessing stomach contents. Cetacean strandings are rare in small oceanic islands like Madeira Archipelago, and when stomach contents are available, they may not fully capture the feeding ecology of individual specimens.

Future steps in research of trophic ecology of odontocetes in this area should encompass the integration of additional biochemical tracers, such as fatty acids, as well as other stable isotopes (e.g., sulfur, $\delta^{34}S$; Troina et al., 2020), to offer more nuanced insights into resource pathways and habitat use. The long-term assessment of stable isotopes would enable the identification of temporal and spatial trends in resource utilization and allow for the examination of relationships with environmental variability (Bode et al., 2022; Palacios & Cantor, 2023). To enhance prey identification, the application of metabarcoding techniques to analyze prey in stomach contents and fecal samples represents a valuable and non-invasive approach. For direct observation of feeding events, the utilization of biologgers equipped with cameras presents an intriguing avenue (Dias et al., 2023). Incorporating individual-level information, such as residency patterns, is particularly crucial for species with co-occurring populations, such as pilot whales, bottlenose dolphins, and sperm whales. Information on trophic ecology is essential for understanding interactions with fisheries, especially for species that prey on commercially important species, and for identifying potential contaminant exposure. Therefore, expanding knowledge on the trophic ecology of odontocetes will facilitate measuring the ecological significance of these megafauna species in connecting the ocean's isolated ecosystems.

Funding

This study had the support of the following entities: project MARCET (MAC/1.1b/149) supported by MAC 2014–2020 program under the Interreg fund; project MarInfo (NORTE-01-0145-FEDER-000031) supported by NORTE 2020 under the PORTUGAL 2020 Partnership Agreement through the European Regional Development Fund (ERDF); Oceanic Observatory of Madeira throughout the project M1420-01-0145-FEDER-000001-OOM; Portuguese Foundation for Science and Technology (FCT) throughout the strategic projects UIDB/04292/2020 granted to MARE, LA/P/0069/2020 granted to the Associate Laboratory ARNET, and UIDB/04423/2020 and UIDP/04423/2020 granted to CIIMAR. RF was supported by a FCT doctoral grant (SFRH/BD/147225/2019, https://doi.org/10.54499/SFRH/BD/147225/2019). ED was supported by a FCT research contract (DL57/2016/CP1344/CT0021).

References

Abend, A.G., Smith, T.D. (1995). Differences in ratios of stable isotopes of nitrogen in long-finned pilot whales (*Globicephala melas*) in the western and eastern North Atlantic. ICES J. Mar. Sci., 52(5) 837-841. https://doi.org/10.1006/jmsc.1995.0080

Ainley, D., Ballard, G., Blight, L. K., Ackley, S., Emslie, S. D., Lescroël, A., Olmastroni, S., Townsend, S. E., Tynan, C. T., Wilson, P., Woehler, E. (2010). Impacts of cetaceans on the structure of Southern Ocean food webs. Mar. Mamm. Sci., 26(2), 482-498. https://doi.org/10.1111/j.1748-7692.2009.00337.x

Altschul, S. F., Madden, T. L., Schäffer, A. A., Zhang, J., Zhang, Z., Miller, W., Lipman, D. J. (1997). Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. Nucleic Acids. Res. 25, 3389–3402. https://doi.org/10.1093/nar/25.17.3389

Alves, F., Quérouil, S., Dinis, A., Nicolau, C., Ribeiro, C., Freitas, L., Kaufmann, M., Fortuna, C. (2013). Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photoidentification and genetic analyses: Implications for conservation. Aquat. Conserv.: Mar. Freshw. Ecosyst., 23, 758–776. https://doi.org/10.1002/aqc.2332

Alves, F., Ferreira, R., Fernandes, M., Halicka, Z., Dias, L., Dinis, A. (2018). Analysis of occurrence patterns and biological factors of cetaceans based on long-term and fine-scale data from platforms of opportunity: Madeira Island as a case study. Mar. Ecol. 39:e12499. https://doi.org/10.1111/maec.12499

Alves, F., Queiroz, N., Jodice, P. G. (2023). Editorial: Ecological and behavioral traits of apex predators in oceanic insular ecosystems: Advances and challenges in research and conservation. Front. Mar. Sci., 10, 1252360. https://doi.org/10.3389/fmars.2023.1252360

Badenas, A., Dinis, A., Ferreira, R., Sambolino, A., Hamard, E., Berninsone, L. G., Fernandez, M., & Alves, F. (2022). Behavioural ecology traits of elusive deep-diver whales unravel a complex social structure influenced by female philopatry and defence polygyny. Front. Mar. Sci., 9, 809902. https://doi.org/10.3389/fmars.2022.809902

Baird, R.W. (2018). False killer whale. In: Würsig, B., Thewissen, J.G.M., Kovacs, K. (Eds.), Encyclopedia of Marine Mammals, 3rd edition Elsevier Inc.

Bode, A., Saavedra, C., Álvarez-González, M., Arregui, M., Arbelo, M., Fernández, A., Freitas, L., Silva, M., Prieto, R., Azevedo, J.M.N., Giménez, J., Pierce, G.J., Santos, M.B. (2022). Trophic position of dolphins tracks recent changes in the pelagic ecosystem of the Macaronesian region (NE Atlantic). Mar. Ecol. Prog. Ser., 699, 167-180. https://doi.org/10.3354/meps14176

Brophy, J., Murphy, S., Rogan, E. (2006). Records from the Irish Whale and Dolphin Group for 2003. The Irish Naturalists' Journal 28(5), 214–19. http://www.jstor.org/stable/25536715

Caldeira, R. M. A., Groom, S., Miller, P., Pilgrim, D., Nezlin, N. (2002). Sea-surface signatures of the island mass effect phenomena around Madeira Island, Northeast Atlantic. Remote Sens. Environ. 80, 336–360. https://doi.org/10.1016/S0034-4257(01)00316-9

Cherel, Y., Hobson, K. (2007). Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar. Ecol. Prog. Ser. 329, 281–287. https://doi.org/10.3354/meps329281

Clarke, M.R., MacLeod, N. (1980). Cephalopod remains from sperm whales caught off western Canada. Mar. Biol. 59, 241–246. https://doi.org/10.1007/BF00404747

Clarke, M.R., Lu, C.C. (1995). Cephalopoda of Madeiran waters. Bol. Mus. Munic. Funchal 4, 181–200.

Clarke, M. R. (2006). Oceanic cephalopod distribution and species diversity in the eastern north Atlantic. Arquipelago Life and Marine Sciences 23A, 27–46.

Costa, A. F., Botta, S., Siciliano, S., Giarrizzo, T. (2020). Resource partitioning among stranded aquatic mammals from Amazon and Northeastern coast of Brazil revealed through Carbon and Nitrogen Stable Isotopes. Sci. Rep., 10:12897. https://doi.org/10.1038/s41598-020-69516-8

Dalerum, F., Angerbjörn, A. (2005). Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. Oecologia, 144, 647–658. https://doi.org/10.1007/s00442-005-0118-0

DeNiro, M.J., Epstein, S. (1977). Mechanism of carbon isotope fractionation associated with lipid synthesis. Science 197, 261–263. https://doi.org/10.1126/science.327543

DeNiro, M. J., Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. Geochim. Cosmochim. Acta, 42(5), 495-506. https://doi.org/10-1016/0016-7037(78)90199-0

DeNiro, M.J., Epstein, S. (1981). Influence of diet on the distribution of nitrogen isotopes in animals. Geochim. Cosmochim. Acta 45, 341–351.

de Soto, N. A. & Alves, F. (2023) Short-Finned Pilot Whale *Globicephala macrorhynchus* Gray, 1846. In: Hackländer, Klaus; Zachos, Frank E. (Ed.): Handbook of the Mammals of Europe, pp. 1–32, Springer International Publishing, Cham, ISBN: 978-3-319-65038-8.

Dias, E., Dromby, M., Ferreira, R., Gil, A., Tejerina, R., Castro, L. F. C., Rosso, M., Sousa-Pinto, I., Hoffman, J. C., Teodósio, M. A., Dinis, A., Alves, F. (2023). Trophic ecology of common bottlenose dolphins in a pelagic insular environment inferred by stable isotopes. Hydrobiologia, 850, 4227–4241. https://doi.org/10.1007/s10750-023-05294-4

Días-Gamboa, R.E., Gendron, D., Guerrero-de la Rosa, F. (2022). Aggressive behavior of short-finned pilot whales towards sperm whales in the Gulf of California: Insight into food competition. Aquat. Mamm., 48(6), 529-532. https://doi.org/10.1578/AM.48.6.2022.529

Dinis, A., Alves, F., Nicolau, C., Ribeiro, C., Kaufmann, M., Cañadas, A., Freitas, L. (2016). Bottlenose dolphin *Tursiops truncatus* group dynamics, site fidelity, residency and movement patterns in the Madeira Archipelago (North-East Atlantic). Afr. J. Mar. Sci., 38, 151–160. https://doi.org/10.2989/1814232X.2016.1167780.

Dromby, M. (2018). Assessment of the ecophysiological conditions and trophic ecology of two cetacean species (*Tursiops truncatus* and *Globicephala macrorhynchus*) in Madeira Archipelago, using RNA/DNA ratios and Carbon/Nitrogen stable isotopes. MSc thesis, Faculdade de Ciências e Tecnologia, Universidade do Algarve.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., C. Jackson, J. B., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., . . . Wardle, D. A. (2011). Trophic Downgrading of Planet Earth. Science 333 (6040), 301-306. https://doi.org/10.1126/science.1205106

Falk-Petersen S., Haug, T., Nilssen, K. T., Wold, A., Dahl, T. M. (2004). Lipids and trophic linkages in harp seal (*Phoca groenlandica*) from the eastern Barents Sea. Polar Res., 23(1), 43-50. https://doi.org/10.3402/polar.v23i1.6265

Fernández, R., Santos, M. B., Carrillo, M., Tejedor, M., Pierce, G. J. (2009). Stomach contents of cetaceans stranded in the Canary islands 1996-2006. J. Mar. Biol. Assoc. U. K., 89(5), 873-883. https://doi.org/10.1017/S0025315409000290

Fernández, R., García-Tiscar, S., Santos, M.B., López, A., Martínez-Cedeira, J.A., Newton, J., Pierce, G.J. (2011). Stable isotope analysis in two sympatric populations of bottlenose dolphins *Tursiops truncatus*: evidence of resource partitioning? Mar. Biol. 158, 1043−1055. https://doi.org/10.1007/s00227-011-1629-3

Fernandez, M., Yesson, C., Gannier, A., Miller, P.I., Azevedo, J.M.N. (2018). A matter of timing: how temporal scale selection influences cetacean ecological niche modelling. Mar. Ecol. Prog. Ser. 595, 217-231. https://doi.org/10.3354/meps12551

Fernandez, M., Alves, F., Ferreira, R., Fischer, J., Thake, P., Nunes, N., Caldeira, R., Dinis, A. (2021). Modeling Fine-Scale Cetaceans' Distributions in Oceanic Islands: Madeira Archipelago as a Case Study. Front. Mar. Sci., 8, 688248. https://doi.org/10.3389/fmars.2021.688248

Ferreira, R., Alves, F., Gomes, C., Jardim, D., Kok, J., Dinis, A. (2017). First confirmed record of Northern Bottlenose Whale (Hyperoodon ampullatus) in Madeira Archipelago, Northeast Atlantic. Aquatic Mammals, 43(5), 474-478. https://doi.org/10.1578/AM.43.5.2017.474

Ferreira, R., Steiner, L., Martín, V., Fusar Poli, F., Dinis, A., Kaufmann, M., Fernandez, M., Alves, F. (2022). Unraveling site fidelity and residency patterns of sperm whales in the insular oceanic waters of Macaronesia. Front. Mar. Sci. 9:1021635. https://doi.org/10.3389/fmars.2022.1021635

Frisch, A.J., Ireland, M., Baker, R. (2014). Trophic ecology of large predatory reef fishes: energy pathways, trophic level, and implications for fisheries in a changing climate. Mar. Biol., 161, 61–73. https://doi.org/10.1007/s00227-013-2315-4

Freitas, L., Dinis, A., Nicolau, C., Ribeiro, C., and Alves, F. (2012). New records of cetacean species for Madeira Archipelago with an updated checklist. Bol. Mus. Mun. Funchal. 62, 25–43.

Friedlander, A. M., Ballesteros, E., Clemente, S., Gonçalves, E. J., Estep, A., Rose, P., Sala, E. (2017). Contrasts in the marine ecosystem of two Macaronesian islands: A comparison between the remote Selvagens Reserve and Madeira Island. PLoS ONE 12: e0187935. https://doi.org/10.1371/journal.pone.0187935.

García-Rivas, M. del C., Schmitter-Soto, J. J., & Pérez-Flores, J. (2013). Fatal predation of oilfish, *Ruvettus pretiosus* (Gempylidae), by a young short-finned pilot whale, *Globicephala macrorhynchus* (Delphinidae). UNED Research Journal, 5(2), 231–233. https://doi.org/10.22458/urj.v5i2.268

Geldmacher, J., Van Den Bogaard, P., Hoernle, K., Schmincke, H.U. (2000). The 40Ar/39Ar age dating of the Madeira Archipelago and hotspot track (eastern North Atlantic). *Geochem. Geophys. Geosystems,* 1(2), 1999GC000018. https://doi.org/10.1029/1999GC000018

Giménez, J., Ramirez, F., Almunia, J., Forero, M.G., Stephanis, R. (2016). From the pool to the sea: Applicable isotope turnover rates and diet to skin discrimination factors for bottlenose dolphins (*Tursiops truncatus*). J. Exp. Mar. Biol. Ecol. 475, 54–61. https://doi.org/10.1016/j.jembe.2015.11.001

Giménez, J., Marçalo, A., García-Polo, M., García-Barón, I., Castillo, J. J., Fernández-Maldonado, C., Saavedra, C., Santos, M. B. (2018). Feeding ecology of Mediterranean common dolphins: The importance of mesopelagic fish in the diet of an endangered subpopulation. Mar. Mamm. Sci., 34(1), 136-154. https://doi.org/10.1111/mms.12442

Gilbert, L., Jeanniard-du-Dot, T., Authier, M., Chouvelon, T., Spitz, J. (2023). Composition of cetacean communities worldwide shapes their contribution to ocean nutrient cycling. Nat. Commun., 14(1), 1-13. https://doi.org/10.1038/s41467-023-41532-y

González, A. F., López, A., Guerra, A., Barreiro, A. (1994). Diets of marine mammals stranded on the northwestern Spanish Atlantic coast with special reference to Cephalopoda. Fish. Res., 21, 179–191. https://doi.org/10. 1016/0165-7836(94)90103-1.

Haro, D., Riccialdelli, L., Blank, O., Matus, R., Sabat, P. (2018). Estimating the isotopic niche of males and females of false killer whales (*Pseudorca crassidens*) from Magellan Strait, Chile. Mar. Mamm. Sci., 35(3), 1070-1082. https://doi.org/ 10.1111/mms.12564

Hermida, M., Delgado, J. (2016). High Trophic Level and Low Diversity: Would Madeira Benefit from Fishing Down? Mar. Policy 73, 130–37. https://doi.org/10.1016/j.marpol.2016.07.013.

Hernández-García, V., Martín, V. (1994). Cephalopods in the diet of two short-finned pilot whales *Globicephala macrohynchus* Gray 1846 in the Canary Islands Area. ICES J. Mar. Sci. C.M. 1994/K: Shellfish 659 Committee.

Herzing, D. L. (1996). Vocalizations and associated underwater behavior of free ranging Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*). Aquat. Mamm. 22, 61–79. https://doi.org/10.12966/abc.02.02.2015

Jackson, A. L., Inger, R., Parnell, A. C., Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. J. Anim. Ecol., 80(3), 595-602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jackson, M. C., Donohue, I., Jackson, A. L., Britton, J. R., Harper, D. M., Grey, J. (2012). Population-Level Metrics of Trophic Structure Based on Stable Isotopes and Their Application to Invasion Ecology. Plos One, 7(2), e31757. https://doi.org/10.1371/journal.pone.0031757

Jackson, A., Parnell, A. (2023). SIBER: Stable Isotope Bayesian Ellipses in R. R package version 2.1.9

Kadin, M., Blenckner, T., Casini, M., Gårdmark, A., Torres, M. A., Otto, S. A. (2019). Trophic Interactions, Management Trade-Offs and Climate Change: The Need for Adaptive Thresholds to Operationalize Ecosystem Indicators. Front. mar. sci., 6, 451862. https://doi.org/10.3389/fmars.2019.00249

Kaufmann, M. J., Santos, F., Maranhão, M. (2015). Checklist of nanno- and microphytoplankton off Madeira Island (Northeast Atlantic) with some historical notes. Nova Hedwig. 101: 205-232. https://doi.org/10.1127/nova_hedwigia/2015/0265

Kiszka, J., Oremus, M., Richard, P., Poole, M., Ridoux, V. (2010). The use of stable isotope analyses from skin biopsy samples to assess trophic relationships of sympatric delphinids off Moorea (French Polynesia). J. Exp. Mar. Bio. Ecol., 395(1-2), 48-54. https://doi.org/10.1016/j.jembe.2010.08.010

Kiszka, J. J., Woodstock, M. S., Heithaus, M. R. (2022). Functional roles and ecological importance of small cetaceans in aquatic ecosystems. Front. mar. sci., 9:803173. https://doi.org/10..3389/fmars.2022.803173

Knoff A, Hohn A, Macko S (2008) Ontogenetic diet changes in bottlenose dolphins (Tursiops truncatus) reflected through stable isotopes. Mar. Mammal Sci. 24(1) 128-137 https://doi.org/10.1111/j.1748-7692.2007.00174.x

Koch, P. L. (2007). Isotopic study of the biology of modern and fossil vertebrates. In R. Michener & K. Lajtha (Eds.), Stable isotopes in ecology and environmental science (pp. 99–154). Blackwell Publishing.

Kratofil, M. A., Ylitalo, G. M., Mahaffy, S. D., West, K. L., Baird, R. W. (2020). Life history and social structure as drivers of persistent organic pollutant levels and stable isotopes in Hawaiin false killer whales (*Pseudorca crassidens*). Sci. Total Environ., 733, 138880. https://doi.org/10.1016/j.scitotenv.2020.138880

Layman, C. A., Arrington, D. A., Montaña, C. G., & Post, D. M. (2007). Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology, 88(1), 42-48. https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2

Lebon, M., Colaço, A., Prieto, R., Cascão, I., Oliveira, C., Tobeña, M., Planque, Y., Spitz, J., & Silva, M. A. (2024). Isotopic niches reveal the trophic structure of the cetacean community in the oceanic waters around the Azores. Frontiers in Marine Science, 11, 1283357. https://doi.org/10.3389/fmars.2024.1283357

Lopes, X. M., Santos, M. C., Silva, E., Bassoi, M., Santos, R. A. (2012). Feeding habits of the Atlantic spotted dolphins, *Stenella frontalis*, in Southeastern Brazil. Braz. J. Oceanogr., 60(2), 189-198. https://doi.org/10.1590/S1679-87592012000200009

Luna, A., Escánez, A., Marrero, J., Íñiguez, E., Pérez, J. A., & Sánchez, P. (2024). Early prey intake of a short-finned pilot whale (*Globicephala macrorhynchus* Gray, 1846, Cetacea: Delphinidae) in the Canary Islands. Ecol. Evol., 14(3), e11139. https://doi.org/10.1002/ece3.11139

McCutchan, J. H., Lewis, W. M. J., Kendall, C., McGrath, C. C. (2003). Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos, 102, 378–390. https://doi.org/10.1034/j.1600-0706.2003.12098.x

Melo, C. L. C., Santos, R. A., Bassoi, M., Araújo, A. C., Lailson-Brito, J., Dorneles, P. R., Azevedo, A. F. (2010). Feeding habits of delphinids (Mammalia: Cetacea) from Rio de Janeiro State, Brazil. J. Mar. Biol. Assoc. U. K., 90(8), 1509-1515. https://doi.org/10.1017/S0025315409991639

Méndes, S., Newton, J., Reid, R. J., Zuur, A. F., Pierce, G. J. (2007). Stable carbon and nitrogen isotope ratio profiling of sperm whale teeth reveals ontogenetic movements and trophic ecology. Oecologia, 151, 605-615. https://doi.org/10.1007/s00442-006-0612-z

Mendez-Fernandez, P., Bustamante, P., Bode, A., Chouvelon, T., Ferreira, M., López, A., Pierce, G.J., Santos, M.B., Spitz, J., Vingada, J.V., Caurant, F. (2012). Foraging ecology of five toothed whale species in the Northwest Iberian Peninsula, inferred using carbon and nitrogen isotope ratios. J. Exp. Mar. Bio. Ecol., 413, 150-158. https://doi.org/10.1016/j.jembe.2011.12.007

Mintzer, V.J., Gannon, D.P., Barros, N.B., Read, A.J. (2008). Stomach contents of mass-stranded short-finned pilot whales (*Globicephala macrorhynchus*) from North Carolina. Mar. Mamm. Sci., 24(2), 290-302. https://doi.org/10.1111/j.1748-7692.2008.00189.x

Naito, Y., Costa, D. P., Adachi, T., Robinson, P. W., Fowler, M., Takahashi, A. (2013). Unravelling the mysteries of a mesopelagic diet: a large apex predator specializes on small prey. Funct. Ecol., 27, 710-717. https://doi.org/10.1111/1365-2435.12083

Noren, D. P., & Mocklin, J. A. (2012). Review of cetacean biopsy techniques: Factors contributing to successful sample collection and physiological and behavioral impacts. Marine Mammal Science, 28(1), 154-199. https://doi.org/10.1111/j.1748-7692.2011.00469.x

Odell, D. K. & McClune, K. M. (1999). *Pseudorca crassidens* (Owen, 1846). In S. H. Ridgway & R. Harrison (Eds.), Handbook of marine mammals: Vol. 6. The second book of dolphins and porpoises (pp. 213-244). London: Academic Press.

Palacios, D. M., Salazar, S. K., Day, D. (2004). Cetacean remains and strandings in the Galapagos islands 1923-2003. Lat. Am. J. Aquat. Mamm. 3, 127–150. https://doi.org/10.5597/lajam00058

Palacios, D.M., Cantor, M. (2023). Priorities for ecological research on cetaceans in the Galápagos Islands. Front. Mar. Sci., 10:1084057. https://doi.org/10.3389/fmars.2023.1084057

Perrin, W. F., Caldwell, D. K., Caldwell, M. C. (1994). Atlantic spotted dolphin *Stenella frontalis*. (G. Cuvier, 1829). In: Ridgway, S. H., Harrison, R. (Ed.). Handbook of Marine Mammals. v. 5: The First Book of Dolphins. New York: Academic Press, p. 173-190.

Peters, K.J., Bury, S.J., Betty, E.L., Parra, G.J., Tezanos-Pinto, G., Stockin, K.A. (2020). Foraging ecology of the common dolphin *Delphinus delphis* revealed by stable isotope analysis. Mar. Ecol. Prog. Ser., 652, 173-186. https://doi.org/10.3354/meps13482

Peters, K. J., Bury, S. J., Hinton, B., Betty, E. L., Casano-Bally, D., Parra, G. J., Stockin, K. A. (2022). Too Close for Comfort? Isotopic Niche Segregation in New Zealand's Odontocetes. Biology, 11 (8), 1179. https://doi.org/10.3390/biology11081179.

Pinela, A.M., Borrell, A., Cardona, L., Aguilar, A. (2010). Stable isotope analysis reveals habitat partitioning among marine mammals off the NW African coast and unique trophic niches for two globally threatened species. Mar. Ecol. Prog. Ser., 416, 295-306. https://doi.org/10.3354/meps08790

Pirotta, E., Vighi, M., Brotons, J. M., Dillane, E., Cerdà, M., Rendell, L. (2020). Stable isotopes suggest fine-scale sexual segregation in an isolated, endangered sperm whale population. Mar. Ecol. Prog. Ser., 654, 209-218. https://doi.org/10.3354/meps13502

Plint, T., ten Doeschate, M. T. I., Brownlow, A. C., Davison, N. J., Hantke, G., Kitchener, A. C., Longstaffe, F. J., McGill, R. A. R., Simon-Nutbrown, C., Magill, C. R. (2023). Stable isotope ecology and interspecific dietary overlap among dolphins in the Northeast Atlantic. Front. Mar. Sci., 10:1111295. https://doi.org/10.3389/fmars.2023.1111295

Post, D.M. (2002). Using stable isotopes to estimate trophic position: models, methods and assumptions. Ecology 83, 703-718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Pusineri, C., Magnin, V., Meynier, L., Spitz, J., Hassani, S., Ridoux, V. (2006). Food and feeding ecology of the common dolphins (Delphinis delphis) in the oceanic Northeast Atlantic and comparison with its diet in neritic areas. Mar. Mamm. Sci., 23 (1), 30-47. https://doi.org/10.1111/j.1748-7692.2006.00088.x

Quay, P., Sonnerup, R., Westby, T., Stutsman, J., McNichol, A. (2003). Changes in the $^{13}C/^{12}C$ of dissolved inorganic carbon in the ocean as a tracer of anthropogenic CO_2 uptake. Glob. Biogeochem. Cycles, 17:1004. https://doi.org/10.1029/2001GB001817

Quérouil, S., Kiszka, J., Cordeiro, A.R., Cascão, I., Freitas, L., Dinis, A., Alves, F., Santos, R. S., Bandarra, N. M. (2013). Investigating stock structure and trophic relationships among island-associated dolphins in the oceanic waters of the North Atlantic using fatty acid and stable isotope analyses. Mar. Biol., 160, 1325–1337. https://doi.org/10.1007/s00227-013-2184-x

Rastgoo, A. R., Navarro, J. (2017). Trophic levels of teleost and elasmobranch species in the Persian Gulf and Oman Sea. J. Appl. Ichthyol., 33(3), 403-408. https://doi.org/10.1111/jai.13249

Reisinger, R. R., Gröcke, D. R., Lübcker, N., McClymont, E. L., Hoelzel, A. R., de Bruyn, P. N. (2016). Variation in the diet of killer whales *Orcinus orca* at Marion Island, Southern Ocean. Mar. Ecol. Prog. Ser., 549,263–274. https://doi.org/10.3354/meps11676

Romero, J., Alonso, H., Freitas, L., Granadeiro, J. P. (2024). Food web of the oceanic region of the archipelago of Madeira: The role of marine megafauna in the subtropical northeast Atlantic ecosystem. Mar. Environ. Res., 195, 106382. https://doi.org/10.1016/j.marenvres.2024.106382

Rosel, P. E. (2003). PCR-based sex determination in Odontocete cetaceans. Conserv. Genet., 4: 647–649. https://doi.org/10.1023/A:1025666212967

Sanders, D., Vogel, E., Knop, E. (2015). Individual and species-specific traits explain niche size and functional role in spiders as generalist predators. J. Anim. Ecol., 84(1), 134-142. https://doi.org/10.1111/1365-2656.12271

Santos, M. B., Pierce, G. J., Reid, R. J., Patterson, L. A. P., Ross, H. M., Mente, E. (2001). Stomach contents of bottlenose dolphins (*Tursiops truncatus*) in Scottish waters. J. Mar. Biol. Assoc. U. K. 81, 873–878. https://doi.org/10.1017/S0025315401004714

Santos, M.B., Pierce, G.J., Lopez, A., Martinez, M.T., Fernandez, M.T., Ieno, E., Mente, E., Porteiro, P., Carrera, P., Meixide, M. (2004). Variability in the diet of common dolphins (*Delphinus delphis*) in Galician waters 1991–2003 and relationships with prey abundance. ICES Conference and Meeting (CM) Document 2004/Q:09. Copenhagen, Denmark: International Council for the Exploration of the Sea. https://doi.org/10.17895/ices.pub.25349722.v1

Santos, M. B., Fernandez, R., López, A., Martínez, J. A., Pierce, G. J. (2007). Variability in the diet of bottlenose dolphin, *Tursiops truncatus*, in Galician waters, north-western Spain, 1990–2005. J. Mar. Biol. Assoc. U. K., 87(2), 31–241. https://doi.org/10.1017/S0025315407055233

Seagars, D. J., Henderson, J. R. (1985). Cephalopod remains from the stomach of a short- finned pilot whale collected near Santa Catalina Island, California. J. Mammal., 66(4), 777-779. https://doi.org/10.2307/1380806.

Shearer, J.M., Jensen, F.H., Quick, N.J., Friedlaender, A., Southall, B., Nowacek, D.P., Bowers, M., Foley, H.J., Swaim, Z.T., Waples, D.M., Read, A.J. (2022). Short-finned pilot whales exhibit behavioral plasticity in foraging strategies mediated by their environment. Mar. Ecol. Prog. Ser., 695, 1-14. https://doi.org/10.3354/meps14132

Silva, M.A. (1999). Diet of common dolphins, *Delphinus delphis*, off the Portuguese continental coast. J. Mar. Biol. Assoc. U. K., 79(3), 531-540. https://doi.org/10.1017/S0025315498000654

Simonis, A.E., Roch, M.A., Bailey, B., Barlow, J., Clemesha, R. E. S., Iacobellis, S., Hildebrand, J. A., Baumann-Pickering, S. (2017). Lunar cycles affect common dolphin Delphinus delphis foraging in the Southern California Bight. Mar. Ecol. Prog. Ser., 577, 221-235. https://doi.org/10.3354/meps12247

Teixeira, C.R., Troina, G.C., Daura-Jorge, F.G., Simões-Lopes, P.C., Botta, S. (2022). A practical guide on stable isotope analysis for cetacean research. Mar. Mamm. Sci., 38, 1200-1228. https://doi.org/10.1111/mms.12911

Tejerina, R., Hermida, M., Faria, G., Delgado, J. (2019). The purse-seine fishery for small pelagic fishes off the Madeira Archipelago. Afr. J. Mar. Sci., 41 (4), 373–83. https://doi.org/10.2989/1814232X.2019.1678520.

Thorne, L.H., Foley, H.J., Baird, R.W., Webster, D.L., Swaim, Z.T., Read, A.J. (2017). Movement and foraging behavior of short-finned pilot whales in the Mid-Atlantic Bight: importance of bathymetric features and implications for management. Mar. Ecol. Prog. Ser., 584, 245-257. https://doi.org/10.3354/meps12371

Tieszen, L. L., Boutton, T. W., Tesdahl, K. G., Slade, N. A. (1983). Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}C$ analysis of diet. Oecologia, 57, 32–37. https://doi.org/10.1007/bf00379558

Troina, G.C., Botta, S., Dehairs, F., Di Tullio, J. C., Elskens, M., Secchi, E. R. (2020). Skin $\delta^{13}C$ and $\delta^{15}N$ reveal spatial and temporal patterns of habitat and resource use by free-ranging odontocetes from the southwestern Atlantic Ocean. Mar. Biol., 167, 186. https://doi.org/10.1007/s00227-020-03805-8

Van Cise, A. M., Switzer, A. D., Apprill, A., Champagne, C. D., Chittaro, P. M., Dudek, N. K., Gavery, M. R., Hancock-Hanser, B. L., Harmon, A. C., Jaffe, A. L., et al. (2024). Best practices for collecting and preserving marine mammal biological samples in the ‘omics era. Marine Mammal Science, e13148. https://doi.org/10.1111/mms.13148

Vander Zanden, M. J., Rasmussen, J. B. (2001). Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: implications for aquatic food web studies. Limnol. Oceanogr., 46, 2061–2066. https://doi.org/10.4319/lo.2001.46.8.2061.

Vianna-Gatts, F., Montanini, G., Azevedo, A. F., Lailson-Brito, J., Bisi, T. L. (2023). Feeding ecology based on stable carbon and nitrogen isotopes: A comparative study on different Guiana dolphin tissues. Mar. Environ. Res., 192: 106234. https://doi.org/10.1016/j.marenvres.2023.106234

Whitehead, H. (2018). "Sperm whale," in Encyclopedia of marine mammals, 3rd Editions. Eds. B. Würsig, J. G. M. Thewissen and K. M. Kovacs (London, UK: Academic Press), 919–924

CHAPTER VI - General Discussion and Future Steps

CHAPTER VI

CHAPTER VI - General Discussion and Future Steps

General Discussion

Oceanic islands, such as those where the present study was developed, are recognized as biodiversity hotspots, hosting a high density of top predators, including cetaceans (Afonso et al., 2020; McIvor et al., 2022; Alves et al., 2023a). Cetaceans play a crucial role in maintaining the structure and function of marine habitats, providing essential ecosystem services, and serving as sentinel species, informing the ecological status of less visible marine ecosystems (Kiszcka, Woodstock and Heithaus, 2022; Pearson et al., 2023). Despite their importance, cetaceans face intense and cumulative pressures globally (Nelms et al., 2021), and their low fecundity and long generation times limit their capacity for population recovery (Authier et al., 2021).

One of the main challenges in studying pelagic cetacean populations is their highly dynamic nature, characterized by extensive home ranges, long migrations across remote areas, and deep-diving behaviors (Kaschner et al., 2012; Horton et al., 2017; Thums et al., 2018; Afonso et al., 2020). These factors challenge research efforts, as ecological studies at individual and population levels require long-term datasets (e.g., Laran et al., 2024). However, oceanic islands serve as valuable platforms for accessing pelagic species, mitigating some of the logistical constraints typically associated with offshore research campaigns. Moreover, integrating data from platforms of opportunity and scientific surveys is a valuable method to increase the datasets (e.g., MacLeod et al., 2006), and has been used worldwide in numerous studies on cetacean ecology (e.g., Moura, Sillero and Rodrigues, 2012; Hupman et al., 2014; Vinding et al., 2015), and as supported by this study.

Nevertheless, a significant portion of these animals' lives occurs on the high seas, beyond national jurisdictions, requiring transboundary collaboration between countries involved in the distribution of these animals to establish effective conservation measures (Harrison A-L et al., 2018; Correia et al., 2020). This is one of the primary principles of the Convention on the Conservation of Migratory Species of Wild Animals, signed by 133 parties in 2022 (as indicated on its homepage), including by the countries focused on the present study. This convention declares that States are the protectors of migratory species within or passing through their jurisdictions and that international cooperation is essential for the conservation of migratory species. Presently, Portugal has taken a leading step in biodiversity conservation by extending the Selvagens Island Nature Reserve, creating Europe's largest marine reserve (Alves, Monteiro and Oliveira, 2022). This measure contributes to the 30x30 Biodiversity Goal, established at the 2023 United Nations Climate Change Conference, that vows to protect 30% of the ocean by 2030.

The estimation of distribution patterns and abundance remains critical not only for many species worldwide, but also for specific populations (Authier et al., 2021). Accurately measuring biodiversity over time at a single location can be challenging, and biodiversity trends can vary significantly between locations (Buckland et al., 2005). Consequently, monitoring population dynamics in the long term is essential to detect significant changes, especially in long-lived species such as those focused on this study (Boyd and Punt, 2021).

As such, this thesis contributes with innovative information on several species of cetaceans in Macaronesia, not only by establishing essential baselines for species' distribution and movements but also by providing valuable insights into social structure and oceanic ecosystem traits. By addressing the challenges of cetacean conservation and using oceanic islands as strategic monitoring sites, this research provides a foundation for an improved understanding and management of these critical marine species.

One of the most enigmatic baleen whale species worldwide is the Bryde's whale (*Balaenoptera edeni*). Although first recorded in the Madeira Archipelago in 2003, it is now one of the most observed species in the area (Alves et al., 2018). However, before this study, only one investigation into its foraging ecology was conducted (Alves et al., 2010). In Chapter II, I developed the first photographic catalogue of this species in the Madeira Archipelago, identifying a high percentage of individuals that used these waters on an inter-annual basis. Additionally, many of these individuals were observed with calves, including neonates, and engaged in feeding, underscoring the area's significance for essential behaviors. The long-term dataset used in this study incorporated data collected from both platforms of opportunity and scientific surveys, highlighting the value of integrating multiple data sources to increase datasets on pelagic species. Using likelihood techniques, I provided the first assessment of residency times for the species, demonstrating that individuals spent a considerable amount of time in this area during their seasonal stay (from June to November). Given that inter-archipelago connectivity in Macaronesia is expected and documented for several cetacean species (e.g., Alves et al., 2019; Dinis et al., 2021), including a baleen whales species (sei whale, *Balaenoptera borealis*; Prieto et al., 2014), I compared the Madeira catalogue with an open-access catalogue from the Canaries, where this species is regularly observed due to its tropical and subtropical habitat preferences. This comparison identified, for the first time, the movement of individuals between these archipelagos, which are separated by more than 500 km. Consequently, this species regularly explores and moves within Macaronesia, encompassing a wide habitat range that includes international waters. Recently, a study using satellite telemetry in the Madeira Archipelago supported these findings, documenting the wide-ranging movements of the species within the archipelagos of Macaronesia (Freitas, 2024). This information is particularly crucial considering that this species is regarded as one of the most vulnerable to climate change in the Madeira Archipelago (Sousa et al., 2019) and is exposed to numerous threats that may go unnoticed or unreported in the high seas. One such case was documented in the Madeira Archipelago in 2020, where a very thin and emaciated individual was observed for several days entangled in fishing lines that prevented it from opening its mouth. This individual was identified as a female, as it had been observed with calves on several occasions and had been a frequent visitor to the area for over 10 years. The animal disappeared after a few days and was never resighted, and there was little to no expectation of survival. This study highlights the importance of the Macaronesian archipelagos of Madeira and the Canaries for this species and the importance of transborder cooperation between all the countries involved in its distribution.

Chapter III focused on a historically important species, the sperm whale (*Physeter macrocephalus*), aggregating quantitative data on residency and movements from the three archipelagos of Macaronesia. Sperm whales are globally classified as Vulnerable by the IUCN (Taylor, 2019) and are the subject of numerous studies worldwide. In the Azores Archipelago, the sperm whale is the species that presents a higher number of scientific studies (Cartagena-Matos et al., 2021), covering a wide range of thematics, from whaling records (e.g., Clarke, Martins and Pascoe, 1993), to genetics (e.g., Pinela et al., 2009; Violi et al., 2023), acoustic (e.g., Pérez-Jorge et al., 2023), abundance (e.g., Boys et al., 2019), behavior (e.g., Magalhães et al., 2002), among others. In the Madeira Archipelago, previous research was limited to whaling records (Freitas et al., 2012), a documented birth (Correia-Fagundes & Romano, 2011), long-term occurrence patterns (Alves et al., 2018), spatio-temporal distribution with the use of modeling techniques (Fernandez et al., 2021) and genomics (e.g., Violi et al., 2023). In the Canaries, sperm whales have been the subject of a few studies that encompass mainly distribution and abundance (e.g., Fais, 2015; Herrera et al., 2021), ship-strike mortality (e.g., Carrillo and Ritter, 2010; Fais et al., 2016), data from strandings (e.g., Fernandez et al., 2009, 2020) and genomics (e.g., Violi et al., 2023). In the present study, photographic catalogues covering several years of sperm whale identifications in subareas of the Azores, Madeira, and the Canaries were compiled using photographs from platforms of opportunity and scientific surveys. Movements of individuals between these archipelagos had been previously identified (Steiner et al., 2015), indicating a high degree of connectivity and suggesting the presence of a single pelagic population in Macaronesia, as supported from a genomic study (Violi et al., 2023). Although the Canaries dataset was small and spatially limited, it provided a preliminary evaluation of habitat use, which is crucial due to the identified ship strike mortality in this region (Fais et al., 2016). The Azores presented a much higher number of captured individuals than Madeira, but the percentage of recaptured individuals was similar in both archipelagos (≈25%), indicating a comparable habitat use by this pelagic population. This suggests that, while most of the population remains in pelagic habitats, these oceanic archipelagos are essential for a subset of the population that returns regularly over several years. In this chapter, I used a composite index to quantify site fidelity, with low results reflecting this species' expected pelagic habitat use. Despite similar site fidelity between the archipelagos, residency times differed, with the Azores showing a higher number of individuals residing for longer periods. This could be attributed to a higher abundance of individuals in the Azores and/or the possibility of the Madeira Archipelago's most suitable habitats being further from shore and not covered by whale-watching boats or scientific surveys (Fernandez et al., 2021). Overall, the importance of the oceanic Macaronesian islands for this species is clear.

The family Ziphiidae includes some of the least studied species worldwide, primarily due to their cryptic nature, and the importance of studying these species has been highlighted in top-ranked publications (namely “Science”, Li and Rosso, 2021). In fact, this is the second most speciose family of cetaceans with 24 extant species – of which only four have available information on their ecology, and several of which were never recorded alive (Alves et al., 2023a, b). Therefore, Chapter IV is dedicated to shedding light on the site fidelity and social ecology of the most abundant species of this family in the Madeira Archipelago, the Blainville's beaked whale *Mesoplodon densirostris*. This species was first described in Madeira in 1917 (Harmer, 1924) and is now the most frequently sighted species of beaked whale (Alves et al., 2018), suggested to occur preferably between the summer and early autumn months (Fernandez et al., 2021). Similarly to the species covered in previous chapters, there is limited information about the residency and social ecology of Blainville's beaked whale in Madeira, except for a preliminary study by Dinis et al. (2017) which provided insight into the existence of island-associated individuals. This study used a larger photographic dataset and revealed a high degree of site fidelity within this population, with a significant portion of individuals exhibiting inter-annual presence. As expected in a mammalian social structure, females comprised the majority of the resident population, indicating female philopatry. The residency analysis reflected this high female site fidelity, with a greater number of adult females and immatures spending more time in the area than adult and subadult males, but also leaving for longer periods. This pattern was also reflected in the social network analyses, where the main cluster included all the resident individuals and almost all the visitors. Strong dyadic associations were observed between adult females and immatures, but not between males. These analyses strongly support female defense polygyny as the social structure for this population, consistent with findings in other areas/oceanic islands worldwide (Bahamas, Claridge, 2006; Hawai'i, McSweeney et al., 2007; Canaries, Suárez, 2018), and underscore the importance of Madeira Archipelago for this population. This study constitutes, to the best of our knowledge, the most complex study on the social ecology of this species worldwide.

Finally, Chapter V was dedicated to a comprehensive study of the foraging ecology of six species of odontocetes in Madeira Archipelago: the short-beaked common dolphin (*Delphinus delphis*), Atlantic spotted dolphin (*Stenella frontalis*), common bottlenose dolphin (*Tursiops truncatus*), false killer whale (*Pseudorca crassidens*), short-finned pilot whale (*Globicephala macrorhynchus*), and sperm whale (*Physeter macrocephalus*). These species exhibit different seasonality, residency patterns and forage in various pelagic layers (Alves et al., 2018), providing an overview of the oceanic ecosystem. By analyzing stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), the species were classified into two groups. The first group, composed of the short-beaked common dolphin, Atlantic spotted dolphin, and common bottlenose dolphin, showed lower values of both isotopes, as well as a lower trophic position, reflecting their generalist diet and predation on lower trophic levels (González et al., 1994; Férnandez et al., 2009; Mendez-Fernandez et al., 2021). The second group, consisting of false killer whale, short-finned pilot whale, and sperm whale, exhibited higher values of both isotopes and a higher trophic position, indicating that they feed on prey at higher trophic levels and, in the case of the latter two species, also in deeper habitats. These findings align with research conducted throughout their distribution range (Bode et al., 2022; Días-Gamboa, Gendron and Guerrero de la Rosa, 2022; Lebon et al., 2024). This difference in foraging ecology was also evident in the size of their isotopic niches. The three species with more generalist predatory behavior exhibited wider trophic niches when compared to the more specialized species. While generalist predatory behaviors are typically associated with wider trophic niches, other factors may also influence these results, such as inter-individual differences in feeding habits, the presence of different ecotypes and/or residency patterns, and variations related to prey seasonality (e.g., Fernández et al., 2011; Dias et al., 2023). The common bottlenose dolphin presented the widest trophic niche, overlapping with several other species, such as short-beaked common dolphin, Atlantic spotted dolphin, and short-finned pilot whale. Overlapping isotopic niches can indicate interspecific competition; however, it may also simply reflect the broad trophic niche of common bottlenose dolphins (Plint et al., 2023). No isotopic differences were found between sexes for the five evaluated species. This finding aligns with some studies (e.g., Kiszka et al., 2010; Quérouil et al., 2013) but contrasts with others (e.g., Haro et al., 2018; Pirotta et al., 2020), highlighting the need for further evaluation. The investigation of the foraging habitats of these species based on their isotopic composition provided an exploratory approach to understanding diet in an area where strandings are rare or difficult to access. Although the results for the short-beaked common dolphin, Atlantic spotted dolphin, common bottlenose dolphin, and false killer whale aligned with previous studies (e.g., Lopes et al., 2012; Giménez et al., 2018; Kratofil et al., 2020; Dias et al., 2023), there was a noticeable lack of prey sampling for short-finned pilot whale and sperm whale due to the challenges in obtaining such samples.

Overall, the present thesis underscores the importance of Macaronesia, particularly the Madeira Archipelago, for cetacean conservation, a critical component of many marine conservation strategies. Moreover, conservation efforts targeting marine megafauna often benefit lower trophic level species, thereby enhancing the protection of the entire ecosystem (Hooker and Gerber, 2004). Despite national and international legislation protecting cetaceans, there is limited data to assess the conservation status of many species on a regional basis, leading to their classification as either “Data Deficient” or “Least Concern” in Macaronesia (Cartagena-Matos et al., 2021). Assessing regional conversation status is of the utmost importance, as biodiversity trends can vary significantly between locations, and conservation measures may not be appropriate for local populations. Additionally, the growing whale-watching industry in the Macaronesian archipelagos, specifically in the Madeira Archipelago (Krasovskaya, 2018), exerts pressure on the populations of cetaceans and should be monitored, especially having in consideration the resident populations that are targeted more frequently (Sambolino et al., 2022).

Future steps

As with all scientific research, the analyses conducted in this study were constrained by challenges and limitations, prompting further questions. Consequently, I have outlined suggestions that future studies could follow to address the limitations of the current research and to expand our knowledge on these taxa and on the marine ecosystem in general:

● Expand sampling efforts. Increasing the geographical and temporal scope of data collection is essential for a deeper understanding of cetacean populations and their ecosystems. Including both coastal and offshore regions would significantly enhance the robustness of the datasets, and while results from small areas can be extrapolated, broader sampling provides a more accurate picture of the existing ecological dynamics. The current limited sampling of this study may not reliably represent other regions, emphasizing the need for a wider geographic scope. Plus, long-term studies are vital to accurately reflect the realities of long-living cetaceans. While this study used long-term data, continued efforts to build decadal datasets are imperative to track ecological changes and shifting human pressures (Cantor et al., 2019; Plint et al., 2023).

● Animal tracking technologies. Since the distributions of migratory species in the ocean span local, national, and international jurisdictions, there is a growing need for connectivity knowledge, particularly insights from animal tracking studies (Dunn et al., 2019). Satellite telemetry is a cutting-edge methodology that allows for data collection over extended periods and distances, providing near real-time information (Hays et al., 2016). These transmitters collect data on the position and depth of individuals and habitat characteristics, offering insights into depths beyond the reach of conventional satellite remote sensing (Priede, 2003). When transmitters are deployed on multiple individuals, valuable insights into social structure can also be obtained (Aguilar de Soto et al., 2006). One of the initial aims of the present study was to investigate the habitat use and movements of sperm whales using satellite transmitters. However, the application of low-invasive SPOT LIMPET tags on this species did not yield significant results due to their short temporal durability, with a maximum placement duration of only nine days. While transdermal satellite transmitters can overcome this temporal limitation, their large size and invasiveness can restrict their use, due to ethical concerns (Goley et al., 2023). The development of smaller transdermal transmitters would be desirable and expected with technological advances. This evolution is expected to provide a valuable opportunity for improving knowledge on sperm whales in the Macaronesia region.

- Unmanned aerial systems. Drones provide a unique aerial perspective that enables to observe submerged individuals and detect markings that are not visible from the surface, facilitating the identification of individuals (Torres et al., 2018). This capability is particularly valuable for studying species that spend a significant portion of their lives underwater, where they are difficult to observe directly. Moreover, drones allow for the detailed observation of interactions, social hierarchies, and group dynamics from a vantage point that minimizes animal disturbance (Hartman et al., 2020). Additionally, drones can measure the individuals' size, evaluate nutritive condition and collect biological samples, gathering important biological data with low disturbance of the animals (Cantor et al., 2019; Hooker et al., 2019).

- Passive and active acoustics. Passive acoustics is particularly effective in determining stock status, assessing the presence of species and their movement patterns, and evaluating potential levels of anthropogenic acoustic threats (Constantine et al., 2018; Hooker et al., 2019). Furthermore, it can also provide detailed information on prey capture and foraging behavior, as well as indicate social associations, providing insight into the social structure and communication of these animals (Madsen et al., 2005; Hooker et al., 2019). On the other hand, active acoustic techniques, particularly echosounders, have increasingly been used to detail the distribution and behavior of both predators and prey. This technique provides information in depths that cannot be observed from the surface, offering a more complete picture of the underwater ecosystem (e.g., Benoid-Bird et al., 2019).

- Biochemical markers. To gain a more comprehensive understanding of the trophic ecology of marine species, integrating fatty acid profiles with stable isotope analysis of several elements, such as hydrogen, sulfur, and oxygen (e.g., Clementz and Koch, 2001; Pinzone et al., 2019; Shipley and Matich, 2020), proves to be more effective and yields more detailed insights (Young et al., 2018). Ideally, these analyses should be complemented by stomach content analysis of by-caught or stranded individuals (Plint et al., 2023). Particular attention should be given to the temporal collection of samples to distinguish differences in trophic ecology between seasons while also considering the residency patterns of the sampled individuals (Dias et al., 2023). To accurately identify prey, stable isotope mixing models should be employed to estimate the contribution of different prey sources. This requires sampling a diverse range of potential prey species, with special attention given to deep-diving species, for which sampling prey may be more challenging (Parra et al., 2022).

- Genetic markers. Genetic and genomic methods enable the identification and tracking of individuals and their kin, offering insights into relatedness and social structure of species for which this information is difficult to obtain through direct observation (Hooker et al., 2019). Additionally, DNA samples can be collected from both live and dead animals using various methods, facilitating these analyses. In recent years, environmental DNA analysis has increasingly been employed in distribution studies, providing a cost-effective tool for gathering information on species presence and distribution (Valsecchi et al., 2021).

In conclusion, a comprehensive and multi-faceted research approach is essential for a detailed understanding of marine ecosystems. Integrating advanced methodologies and technologies with standard methods will enhance the accuracy and efficiency of future studies, providing critical insights for the conservation of these top predators amidst present anthropogenic threats and global environmental changes.

REFERENCES

Afonso, Pedro, Jorge Fontes, Eva Giacomello, Maria C. Magalhães, Helen R. Martins, Telmo Morato, Verónica Neves, et al. 2020. “The Azores: A Mid-Atlantic Hotspot for Marine Megafauna Research and Conservation”. *Frontiers in Marine Science*, 6:826. https://doi.org/10.3389/fmars.2019.00826

Aguilar de Soto, Natacha. 2006. "Acoustic and Foraging Behavior of Short-Finned Pilot Whales (*Globicephala macrorhynchus*) and Blainville’s Beaked Whales (*Mesoplodon densirostris*) in the

Canary Islands: Implications for Impacts of Man-Made Noise and Ship Collisions." PhD dissertation, La Laguna University.

Alves, Filipe, Ana Dinis, Irma Cascão, and Luís Freitas. 2010. "Bryde's Whale (*Balaenoptera brydei*) Stable Associations and Dive Profiles: New Insights into Foraging Behavior." *Marine Mammal Science*, 26(1), 202-212. https://doi.org/10.1111/j.1748-7692.2009.00333.x

Alves, Filipe, Anita Alessandrini, Antonella Servidio, Ana Sofia Mendonça, Karin L. Hartman, Rui Prieto, Simon Berrow, et al. 2019. "Complex Biogeographical Patterns Support an Ecological Connectivity Network of a Large Marine Predator in the Northeast Atlantic." *Diversity and Distributions*, 25(2), 269–284. https://doi.org/10.1111/ddi.12848

Alves, Filipe, João Monteiro, and Paulo Oliveira. 2022. “Portugal Leads with Europe’s Largest Marine Reserve”. *Nature*, 601, 18. https://doi.org/10.1038/d41586-022-00093-8

Alves, Filipe, Nuno Queiroz, and Patrick G. R. Jodice. 2023a. “Editorial: Ecological and Behavioral Traits of Apex Predators in Oceanic Insular Ecosystems: Advances and Challenges in Research and Conservation”. *Frontiers in Marine Science*, 10:1252360. https://doi.org/10.3389/fmars.2023.1252360

Alves, Filipe, Rita Ferreira, Miguel Fernandes, Zofia Halicka, Luís Dias, and Ana Dinis. 2018. "Analysis of Occurrence Patterns and Biological Factors of Cetaceans Based on Long-Term and Fine-Scale Data from Platforms of Opportunity: Madeira Island as a Case Study." *Marine Ecology*, 39(2), e12499. https://doi.org/10.1111/maec.12499

Alves, Filipe, Sarah L. Mesnick, Massimiliano Rosso, and Robert L. Pitman. 2023b. “Beaked Whale Sexual Dimorphism, Mating Strategies, and Diversification”. In *Sex in Cetaceans*, 385-413. Edited by Bernd Würsig, and Dara N. Orbach, 327-351. Springer eBooks. https://doi.org/10.1007/978-3-031-35651-3

Authier, Matthieu, Jérôme Spitz, Aurélie Blanck, and Vincent Ridoux. 2017. “Conservation Science for Marine Megafauna in Europe: Historical Perspectives and Future Directions”. *Deep Sea Research Part II: Topical Studies in Oceanography*, 141, 1-7. https://doi.org/10.1016/j.dsr2.2017.05.002

Benoit-Bird, Kelly J., Brandon L. Southall, and Mark A. Moline. 2019. “Dynamic Foraging by Risso's Dolphins Revealed in Four Dimensions”. *Marine Ecology Progress Series*, 632, 221-234. https://doi.org/10.3354/meps13157

Bode, Antonio, Camilo Saavedra, Miguel Álvarez-González, Marina Arregui, Manuel Arbelo, Antonio Fernández, A., Luis Freitas, et al. 2022. “Trophic Position of Dolphins Tracks Recent Changes in the Pelagic Ecosystem of the Macaronesian Region (NE Atlantic)”. Marine Ecology Progress Series, 699, 167-180. https://doi.org/10.3354/meps14176

Boyd, Charlotte, and André E. Punt. 2021. “Shifting Trends: Detecting Changes in Cetacean Population Dynamics in Shifting Habitat”. *PLoS ONE*, 16(5), e0251522. https://doi.org/10.1371/journal.pone.0251522

Boys, Rebecca, Cláudia Oliveira, Sergi Pérez-Jorge, Rui Prieto, Lisa Steiner, and Mónica A. Silva. 2019. “Multi-State Open Robust Design Applied to Opportunistic Data Reveals Dynamics of

Wide-Ranging Taxa: The Sperm Whale Case". *Ecosphere*, 10(3), e02610. https://doi.org/10.1002/ecs2.2610

Buckland, Steve T., Anne E. Magurran, Richard E. Green, and R. M. Fewster. 2005. "Monitoring Change in Biodiversity Through Composite Indices". *Philosophical Transactions of the Royal Society of London B, Biological Science*, 360(1454), 243-54. https://doi.org/10.1098/rstb.2004.1589

Cantor, Mauricio, Shane Gero, Hal Whitehead, and Luke Rendell. 2019. "Sperm Whale: The Largest Toothed Creature on Earth". In *Ethology and Behavioral Ecology of Marine Mammals*. Edited by Bernd Würsig, 261–80. Springer Nature Switzerland AG. https://doi.org/10.1007/978-3-030-16663-2

Carrillo, Manuel, and Fabian Ritter. 2010. "Increasing Numbers of Ship Strikes in the Canary Islands: Proposals for Immediate Action to Reduce Risk of Vessel-Whale Collisions". *Journal of Cetacean Research and Management*, 11, 131–138. https://doi.org/10.47536/jcrm.v11i2.618

Cartagena-Matos, Bárbara, Klervi Lugué, Paulo Fonseca, Tiago A. Marques, Rui Prieto, and Filipe Alves. 2021. "Trends in Cetacean Research in the Eastern North Atlantic". *Mammal Review,* 51 (3), 436–453. https://doi.org/10.1111/mam.12238

Claridge, Diane E. 2006. "Social Structure of Blainville's Beaked Whale in Bahamas". M.Sc. thesis, University of Aberdeen, Aberdeen, Scotland.

Clarke, Malcom R., H. R. Martins, and P. Pascoe. 1993. "The Diet of Sperm Whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores". *Philosophical Transactions of the Royal Society of London B,* 33967–82. http://doi.org/10.1098/rstb.1993.0005

Clementz, Mark T., and Paul L. Koch. 2001. "Differentiating Aquatic Mammal Habitat and Foraging Ecology with Stable Isotopes in Tooth Enamel". *Oecologia*, 129, 461–472. https://doi.org/10.1007/s004420100745

Constantine, Rochelle, Takashi Iwata, Sharon L. Nieukirk, and Gwenith S. Penry. 2018. "Future Directions in Research on Bryde's Whales". *Frontiers in Marine Science*, 5, 333. https://doi.org/10.3389/fmars.2018.00333

Correia, Ana Mafalda, Ágatha Gil, Raul Valente, Massimiliano Rosso, Isabel Sousa-Pinto, and Graham John Pierce. 2020. "Distribution of Cetacean Species at a Large Scale: Connecting Continents with the Macaronesian Archipelagos in the Eastern North Atlantic". *Diversity and Distributions*, 26(10), 1234-1247. https://doi.org/10.1111/ddi.13127

Correia-Fagundes, Catarina, and Hugo Romano. 2013. "Observation of a Birth of a Sperm Whale *Physeter macrocephalus* at Madeira (NE Atlantic)". *Bocagiana*, 236, 1–3.

Dias, Ester, Morgane Dromby, Rita Ferreira, Ágatha Gil, Raquel Tejerina, Luis F. C. Castro, Massimiliano Rosso, Isabel Sousa-Pinto, J. C. Hoffman, M. Alexandra Teodósio, Ana Dinis, and Filipe Alves. 2023. "Trophic Ecology of Common Bottlenose Dolphins in a Pelagic Insular Environment Inferred by Stable Isotopes". *Hydrobiologia*, 850, 4227–4241. https://doi.org/10.1007/s10750-023-05294-4

Días-Gamboa, Raúl E., Diane Gendron, and Fabiola Guerrero de la Rosa. 2022. "Aggressive Behavior of Short-Finned Pilot Whales Towards Sperm Whales in the Gulf of California: Insight into Food Competition". *Aquatic Mammals*, 48(6), 529-532. https://doi.org/10.1578/AM.48.6.2022.529

Dinis, Ana, Carlota Molina, Marta Tobeña, Annalisa Sambolino, Karin Hartman, Marc Fernandez, Sara Magalhães. 2021. "Large-scale Movements of Common Bottlenose Dolphins in the Atlantic: Dolphins with an International Courtyard." *PeerJ*, 9:e11069. https://doi.org/10.7717/peerj.11069

Dinis, Ana, Raquel Marques, Luís Dias, Dinarte Sousa, Claudia Gomes, Nicolau Abreu, and Filipe Alves. 2017. "Site Fidelity of Blainville's Beaked Whale (*Mesoplodon densirostris*) off Madeira Island (Northeast Atlantic)." *Aquatic Mammals,* 43(4), 387–90. https://doi.org/10.1578/am.43.4.2017.387

Goley, P. Dawn, John Calambokidis, Pádraig Duignan, Frances M. D. Gulland, Barbie Halaska, Allison Lui, Margaret Martinez, et al. 2024. "Observations of tissue healing around an implanted "C" tag in a Pacific Coast Feeding Group gray whale (*Eschrichtius robustus*)". *Marine Mammal Science*, 40(1), 254-261. https://doi.org/10.1111/mms.13066

Dunn, Daniel C., Autumn-Lynn Harrison, Corrie Curtice, Sarah DeLand, Ben Donnelly, Ei Fujioka, Eleanor Heywood, et al. 2019. "The Importance of Migratory Connectivity for Global Ocean Policy". *Proceedings of the Royal Society Series B*, *Biological Sciences*, 286(1911), 20191472. https://doi.org/10.1098/rspb.2019.1472

Fais de Hierro, Andrea F. L. 2015. "Acoustic Behaviour of Sperm Whales (*Physeter macrocephalus*). PhD dissertation, Universidad de La Laguna.

Fais, Andrea, Tim P. Lewis, Daniel P. Zitterbart, Omar Álvarez, Ana Tejedor, and Natacha Aguilar De Soto. 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. https://doi.org/10.1371/journal.pone.0150660

Fernández, Antonio, Pedro Saavedra, Marisa Tejedor, Eva Sierra, Aina Xuriach, Miguel A. Rivero, Marisa Andrada, and Manuel Arbelo. 2020. "Retrospective Study of Traumatic Intra-Interspecific Interactions in Stranded Cetaceans, Canary Islands". *Frontiers in Veterinary Science*, 7, 512472. https://doi.org/10.3389/fvets.2020.00107

Fernandez, Marc, Filipe Alves, Rita Ferreira, Jan-Christopher Fischer, Paula Thake, Nuno Nunes, Rui Caldeira, and Ana Dinis. 2021. "Modeling Fine-Scale Cetaceans' Distributions in Oceanic Islands: Madeira Archipelago as a Case Study." *Frontiers in Marine Science,* 8. https://doi.org/10.3389/fmars.2021.688248

Fernández, Ruth, M. Begoña Santos, Manuel Carrillo, Marisa Tejedor, Graham J. Pierce. 2009. "Stomach Contents of Cetaceans Stranded in the Canary Islands 1996-2006". *Journal of the Marine Biological Association of the United Kigdom*, 89(5), 873-883. https://doi.org/10.1017/S0025315409000290

Fernández, Ruth, Susana García-Tiscar, M. Begoña Santos, Alfredo López, Jose A. Martínez-Cedeira, Jason Newton, and Graham J. Pierce. 2011. "Stable Isotope Analysis in Two Sympatric

Populations of Bottlenose Dolphins *Tursiops truncatus*: Evidence of Resource Partitioning?” *Marine Biology*, 158, 1043−1055. https://doi.org/10.1007/s00227-011-1629-3

Freitas, Luis. 2024. “The Ecological Importance of Oceanic Islands for Cetaceans: the Case Study of Madeira Archipelago”. PhD dissertation, University of St Andrews.

Freitas, Luis, Ana Dinis, Cátia Nicolau, Cláudia Ribeiro, and Filipe Alves. 2012. “New Records of Cetacean Species for Madeira Archipelago with an Updated Checklist”. *Boletim Do Museu Municipal Do Funchal*, 62, 25–43.

Giménez, Joan, Ana Marçalo, Manuel García-Polo, Isabel García-Barón, Juan J. Castillo, Carolina Fernández-Maldonado, Camilo Saavedra, et al. 2018. “Feeding Ecology of Mediterranean Common Dolphins: The Importance of Mesopelagic Fish in the Diet of an Endangered Subpopulation”. *Marine Mammal Science*, 34(1), 136-154. https://doi.org/10.1111/mms.12442

González, Ángel F., Alfredo López, Angel Guerra, and A. Barreiro. 1994. “Diets of Marine Mammals Stranded on the Northwestern Spanish Atlantic Coast with Special Reference to Cephalopoda”. *Fisheries Research*, 21, 179–191. https://doi.org/10.1016/0165-7836(94)90103-1

Harmer, S. F. (1924). “On Mesoplodon and other Beaked Whales”. *Proceedings of the Zoological Society*, 36, 541-587. https://doi.org/10.1111/j.1096-3642.1924.tb01515.x

Haro, Daniela, Luciana Riccialdelli, Olivia Blank, Ricardo Matus, and Pablo Sabat. 2018. “Estimating the Isotopic Niche of Males and Females of False Killer Whales (*Pseudorca crassidens*) from Magellan Strait, Chile”. *Marine Mammal Science*, 35(3), 1070-1082. https://doi.org/10.1111/mms.12564

Harrison, Autumn-Lynn, Daniel P. Costa, Arliss J. Winship, Scott R. Benson, Steven J. Bograd, Michelle Antolos, Aaron B. Carlisle, et al. 2018. “The Political Biogeography of Migratory Marine Predators”. *Nature Ecology & Evolution*, 2, 1571–1578. https://doi.org/10.1038/s41559-018-0646-8

Hartman, Karin, Pieter Van der Harst, and Raul Vilela. 2020. “Continuous Focal Group Follows Operated by a Drone Enable Analysis of the Relation Between Sociality and Position in a Group of Male Risso’s Dolphins (*Grampus griseus*)”. *Frontiers in Marine Science*, 7, 533103. https://doi.org/10.3389/fmars.2020.00283

Hays, Graeme C., Luciana C. Ferreira, Ana M. M. Sequeira, Mark G. Meekan, Carlos M. Duarte, Helen Bailey, Fred Bailleul, et al. 2016. “Key Questions in Marine Megafauna Movement Ecology”. *Trends in Ecology and Evolution*, 31, 463–475. https://doi.org/10.1016/j.tree.2016.02.015

Herrera, Irma, Manuel Carrillo, Marcial C. Esteban, and Ricardo Haroun. 2021. “Distribution of Cetaceans in the Canary Islands (Northeast Atlantic Ocean): Implications for the Natura 2000 Network and Future Conservation Measures”. *Frontiers in Marine Science,* 8, 669790. https://doi.org/10.3389/fmars.2021.669790

Hooker, Sasha K., and Leah R. Gerber. 2004. “Marine Reserves as a Tool for Ecosystem-Based Management: The Potential Importance of Megafauna”. *BioScience*, 54(1), 27-39. https://doi.org/10.1641/0006-3568(2004)054[0027:MRAATF]2.0.CO;2

Hooker, Sascha K., Natacha Aguilar De Soto, Robin W. Baird, Emma L. Carroll, Diane Claridge, Laura Feyrer, Patrick J. O. Miller, et al. 2019. “Future Directions in Research on Beaked Whales.” *Frontiers in Marine Science*, 5, 411237. https://doi.org/10.3389/fmars.2018.00514

Horton, Travis W., Nan Hauser, Alexandre N. Zerbini, Malcolm P. Francis, Michael L. Domeier, Artur Andriolo, Daniel P. Costa, et al. (2017). “Route Fidelity during Marine Megafauna Migration”. *Frontiers in Marine Science*, 4, 422. https://doi.org/10.3389/fmars.2017.00422

Hupman, Krista, Ingrid N. Visser, E. Martinez, and Karen A. Stockin. 2014. “Using Platforms of Opportunity to Determine the Occurrence and Group Characteristics of Orca (*Orcinus orca*) in the Hauraki Gulf, New Zealand”. *New Zealand Journal of Marine and Freshwater Research*, 49(1), 132–149. https://doi.org/10.1080/00288330.2014.980278

Kaschner, Kristin, Nicola J. Quick, Rebecca Jewell, Rob Williams, and Catriona M. Harris. 2012. “Global Coverage of Cetacean Line-Transects Surveys: Status Quo, Data Gaps and Future Challenges”. *PLoS ONE*, 7(9), e44075. https://doi.org/10.1371/journal.pone.0044075

Kiszka, Jeremy, Marc Oremus, Pierre Richard, Michael Poole, and Vincent Ridoux. 2010. “The Use of Stable Isotope Analyses From Skin Biopsy Samples to Assess Trophic Relationships of Sympatric Delphinids off Moorea (French Polynesia).” *Journal of Experimental Marine Biology and Ecology*, 395(1–2), 48–54. https://doi.org/10.1016/j.jembe.2010.08.010

Kiszka, Jeremy J., Matthew Woodstock, and Michael R. Heithaus. 2022. “Functional Roles and Ecological Importance of Small Cetaceans in Aquatic Ecosystems *Frontiers in Marine Science*, 9, 803173. https://doi.org/10.3389/fmars.2022.803173

Krasovskaya, Svetlana. 2018. “Economic Contribution of the Whale-Watching Industry for the Madeira Archipelago”. M.Sc. thesis, University of Madeira.

Kratofil, Michaela A., Gina M. Ylitalo, Sabre D. Mahaffy, Kristi L. West, and Robin W. Baird. 2020. “Life History and Social Structure as Drivers of Persistent Organic Pollutant Levels and Stable Isotopes in Hawaiin False Killer Whales (*Pseudorca crassidens*)”. *Science of the Total Environment*, 733, 138880. https://doi.org/10.1016/j.scitotenv.2020.138880

Laran, Sophie, Olivier Van Canneyt, Ghislain Dorémus, Claire Garrigue, Tristan Berr, Hugo Bourgogne, Mathieu Genu, et al. 2024. “Who Lives in the Open Sea? Distribution and Densities of Surfacing Marine Megafauna in Three Subregions of the South Pacific (New Caledonia, Wallis and Futuna, and French Polynesia)”. *Pacific Conservation Biology*, 30, PC23023. https://doi.org/10.1071/pc23023

Lebon, Myriam, Ana Colaço, Rui Prieto, Irma Cascão, Cláudia Oliveira, Marta Tobeña, Yann Planque, Jérôme Spitz, and Mónica A. Silva. 2024. “Isotopic Niches Reveal the Trophic Structure of the Cetacean Community in the Oceanic Waters around the Azores”. *Frontiers in Marine Science*, 11, 1283357. https://doi.org/10.3389/fmars.2024.1283357

Li, Songhai, and Massimiliano Rosso. 2021. “Lack of Knowledge Threatens Beaked Whales”. *Science*, 371(6531), 791-791. https://doi.org/10.1126/science.abg8922

Lopes, Xênia M., Marcos Santos, Ednilson da Silva, Manuela Bassoi, and Roberta A. Santos. 2012. “Feeding habits of the Atlantic spotted dolphins, *Stenella frontalis*, in Southeastern Brazil”.

Brazilian Journal of Oceanography, 60(2), 189-198. https://doi.org/10.1590/S1679-87592012000200009

MacLeod, Colin D., William F. Perrin, Robert Pitman, Jay Barlow, Lisa Ballance, Angela D'Amico, Tim Gerrodette, et al. 2006. "Known and Inferred Distributions of Beaked Whale Species (Ziphiidae: Cetacea)". *Journal of Cetacean Research Management*, 7(3), 271–286.

Madsen, Peter T., Mark Johnson, Natasha Aguilar De Soto, Walter M. X. Zimmer, and Peter Tyack. 2005. "Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*). J. Exp. Biol. 208, 181–194. https://doi.org/10.1242/jeb.01327

Magalhães, Sara, Rui Prieto, Mónica A. Silva, João Gonçalves, Manuel Afonso-Dias, and Ricardo S. Santos. 2002. "Short-Term Reactions of Sperm Whales (*Physeter macrocephalus*) to Whale-Watching Vessels in the Azores". *Aquatic Mammals*, 28(3), 267-274.

Mendez-Fernandez, Paula, Paco Bustamante, Antonio Bode, Tiphaine Chouvelon, Marisa Ferreira, Alfredo López, Graham J. Pierce, et al. 2012. "Foraging Ecology of Five Toothed Whale Species in the Northwest Iberian Peninsula, Inferred using Carbon and Nitrogen Isotope Ratios". *Journal of Experimental Marine Biology and Ecology*, 413, 150-158. https://doi.org/10.1016/j.jembe.2011.12.007

McIvor, Ashlie, Collin Williams, Filipe Alves, Ana Dinis, Miguel Pais, and João Canning-Clode. 2022. "The Status of Marine Megafauna Research in Macaronesia: A Systematic Review". *Frontiers in Marine Science*, 9, 819581. https://doi.org/10.3389/fmars.2022.819581

McSweeney, Daniel J., Robin W. Baird, and Sabre D. Mahaffy. 2007. "Site Fidelity, Associations and Movements of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) Beaked Whales off the Island of Hawai'i". *Marine Mammal Science,* 23, 666–687. https://doi.org/10.1111/j.1748-7692.2007.00135.x

Moura, André E., Neftalí Sillero, and Ana Rodrigues. 2012. "Common Dolphin (*Delphinus delphis*) Habitat Preferences Using Data from Two Platforms of Opportunity." *Acta Oecologica*, 38, 24–32. https://doi.org/10.1016/j.actao.2011.08.006

Nelms, Sarah E., Joanna Alfaro-Shigueto, John P. Y. Arnould, Isabel C. Avila, Susan Bengtson Nash, Elizabeth Campbell, Matt I. D. Carter, et al. 2021. "Marine Mammal Conservation: Over the Horizon". *Endangered Species Research*, 44, 291-325. https://doi.org/10.3354/esr01115

Parra, Guido J., Zachary Wojtkowiak, Katharina J. Peters, and Daniele Cagnazzi. 2022. "Isotopic Niche Overlap Between Sympatric Australian Snubfin and Humpback Dolphins". *Ecology and Evolution*, 12(5), e8937. https://doi.org/10.1002/ece3.8937

Pearson, Heidi C., Matthew S. Savoca, Daniel P. Costa, Michael W. Lomas, Renato Molina, Andrew J. Pershing, Craig R. Smith, et al. 2023. "Whales in the Carbon Cycle: Can Recovery Remove Carbon Dioxide?" *Trends in Ecology and Evolution*, 38(3), 238-249. https://doi.org/10.1016/j.tree.2022.10.012

Pérez-Jorge, Sergi, Cláudia Oliveira, Esteban Iglesias Rivas, Rui Prieto, Irma Cascão, Paul J. Wensveen, Patrick J. O. Miller, et al. 2023. "Predictive Model of Sperm Whale Prey Capture Attempts from Time-Depth Data". *Movement Ecology*, 11, 33 (2023). https://doi.org/10.1186/s40462-023-00393-2

Pinela, Ana Maria, Sophie Quérouil, Sara Magalhães, Mónica A. Silva, Rui Prieto, J. A. Matos, and Ricardo S. Santos. 2009. “Population Genetics and Social Organization of the Sperm Whale (*Physeter macrocephalus*) in the Azores Inferred by Microsatellite Analyses”. *Canadian Journal of Zoology*, 87(9), 802-813. https://doi.org/10.1139/Z09-066

Pinzone, Marianna, France Damseaux, Loïc N. Michel, and Krishna Das. 2019. “Stable Isotope Ratios of Carbon, Nitrogen and Sulphur and Mercury Concentrations as Descriptors of Trophic Ecology and Contamination Sources of Mediterranean Whales”. *Chemosphere*, 237, 124448. https://doi.org/10.1016/j.chemosphere.2019.124448

Pirotta, Enrico, Morgana Vighi, José Maria Brotons, Eileen Dillane, Margalida Cerdà, and Luke Rendell. 2020. “Stable Isotopes Suggest Fine-Scale Sexual Segregation in an Isolated, Endangered Sperm Whale Population”. *Marine Ecology Progress Series*, 654, 209-218. https://doi.org/10.3354/meps13502

Plint, Tessa, Mariel T.I. ten Doeschate, Andrew C. Brownlow, Nicholas J. Davison, Georg Hantke, Andrew C. Kitchener, Fred J. Longstaffe, et al. 2023. “Stable Isotope Ecology and Interspecific Dietary Overlap Among Dolphins in the Northeast Atlantic”. *Frontiers in Marine Science*, 10, 1111295. https://doi.org/10.3389/fmars.2023.1111295

Priede, Imants G. 2014. “Biogeography of the Oceans: a Review of Development of Knowledge of Currents, Fronts and Regional Boundaries from Sailing Ships in the Sixteenth Century to Satellite Remote Sensing”. *Pure and Applied Geophysics*, 171, 1013–1027. https://doi.org/10.1007/s00024-013-0708-4

Prieto, Rui, Mónica A. Silva, Gordon T. Waring, And João M. A. Gonçalves. 2014. “Sei Whale Movements and Behavior in the North Atlantic Inferred from Satellite Telemetry”. *Endangered Species Research*, 26(2), 103–113. https://doi.org/10.3354/esr00630

Quérouil, Sophie, Jeremy Kiszka, Ana Rita Cordeiro, Irma Cascão, Luis Freitas, Ana Dinis, Filipe Alves, et al. 2013. “Investigating Stock Structure and Trophic Relationships among Island-Associated Dolphins in the Oceanic Waters of the North Atlantic using Fatty Acid and Stable Isotope Analyses”. *Marine Biology*, 160, 1325–1337. https://doi.org/10.1007/s00227-013-2184-x

Sambolino, Annalisa, Filipe Alves, Marc Fernandez, Anja Badenas Krakauer, Rita Ferreira, and Ana Dinis. 2002. “Spatial and Temporal Characterization of the Exposure of Island-Associated Cetacean Populations to Whale-Watching in Madeira Island (NE Atlantic)”. *Regional Studies in Marine Science*, 49, 102084. https://doi.org/10.1016/j.rsma.2021.102084

Shipley, Oliver N., and Matich, Philip. 2020. “Studying Animal Niches using Bulk Stable Isotope Ratios: An Updated Synthesis”. *Oecologia*, 193, 27–51. https://doi.org/10.1007/s00442-020-04654-4

Sousa, Andreia, Filipe Alves, Ana Dinis, Julia Bentz, Maria João Cruz, and João Pedro Nunes. 2019. “How Vulnerable Are Cetaceans to Climate Change? Developing and Testing a New Index.” *Ecological Indicators,* 98, 9–18. https://doi.org/10.1016/j.ecolind.2018.10.046

Steiner, Lisa, Monica Pérez, Miranda van der Linde, Luis Freitas, Raul Peres dos Santos, Vidal Martin, and Jonathan Gordon. 2015. “Long Distance Movements of Female/Immature Sperm

Whales in the North Atlantic". Poster presented at the 21st Biennial Conference of Society of Marine Mammalogy, San Francisco, USA, December.

Suárez, C.R. (2018). "Abundance estimate, survival and site fidelity patterns of Blainville's (*Mesoplodon densirostris*) and Cuvier's (*Ziphius cavirostris*) beaked whales off El Hierro (Canary Islands)". M.Sc. thesis, University of Saint Andrews.

Taylor, B. L., Robin Baird, J. Barlow, S. M. Dawson, J. Ford, J. G. Mead, G. Notarbartolo di Sciara, et al. 2019. *Physeter macrocephalus* (amended version of 2008 assessment). The IUCN Red List of Threatened Species. 2019, e.T41755A160983555. https://doi.org/10.2305/IUCN.UK.2008.RLTS.T41755A160983555.en

Thums, Michele, Juan Fernández-Gracia, Ana M. M. Sequeira, Victor M. Eguíluz, Carlos M. Duarte, and Mark G. Meekan. 2018. "How Big Data Fast Tracked Human Mobility Research and the Lessons for Animal Movement Ecology". *Frontiers in Marine Science*, 5, 21. https://doi.org/10.3389/fmars.2018.00021

Torres, Leigh G., Sharon L. Nieukirk, Leila Lemos, and Todd E. Chandler. 2018. "Drone up! Quantifying Whale Behavior from a New Perspective Improves Observational Capacity". *Frontiers in Marine Science*, 5, 394495. https://doi.org/10.3389/fmars.2018.00319

Valsecchi, Elena, Antonella Arcangeli, Roberto Lombardi, Elizabeth Boyse, Ian M. Carr, Paolo Galli, and Simon J. Goodman. 2021. "Ferries and Environmental DNA: Underway Sampling From Commercial Vessels Provides New Opportunities for Systematic Genetic Surveys of Marine Biodiversity". *Frontiers in Marine Science*, 8, 704786. https://doi.org/10.3389/fmars.2021.704786

Vinding, Katja, Marthán Bester, Stephen P. Kirkman, Wilfred Chivell and Simon H. Elwen. 2015. "The Use of Data from a Platform of Opportunity (Whale Watching) to Study Coastal Cetaceans on the Southwest Coast of South Africa". *Tourism in Marine Environments*, 11(1), 33-54. https://doi.org/10.3727/154427315X14398263718439

Violi, Biagio, Menno J. de Jong, Alexandros Frantzis, Paraskevi Alexiadou, Céline Tardy, Denis Ody, Renaud de Stephanis, et al. (2023). "Genomics Reveals the Role of Admixture in the Evolution of Structure among Sperm Whale Populations within the Mediterranean Sea". *Molecular Ecology*, 32(11), 2715-2731. https://doi.org/10.1111/mec.16898

Young, Talia, Jennifer Pincin, Phillip Neubauer, Sofía Ortega-Garcí, and Olaf P. Jensen. 2018. "Investigating Diet Patterns of Highly Mobile Marine Predators using Stomach Contents, Stable Isotope, and Fatty Acid Analyses". *International Council for the Exploration of the Sea, Journal of Marine Science*, 75, 1583–1590.

APPENDIX A – Supplementary Material to Chapter IV

Table S.IV.1 Capture histories of all Blainville's beaked whale individuals with distinctiveness ≥2 per month between 2011 and 2019.

	2011						2012			2013					2014					2015								2016										2017											2018								2019											
Individual	Apr	May	Jul	Aug	Sep	Oct	Apr	Jul	Aug	Jan	Jun	Jul	Aug	Sep	Jun	Jul	Aug	Sep	Nov	Apr	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Nov	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Dec	Jan	Mar	May	Jun	Jul	Aug	Sep	Oct	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	# of times seen
Md_001	■	■																																																																2
Md_002	■	■			■				■												■		■								■		■		■				■			■	■	■							■		■		■	■								■		■	24
Md_003																						■	■															■														■					■					■									10
Md_006			■	■	■																												■																																		5
Md_015								■	■																																											■			■													■	7
Md_016											■																																																									1
Md_017								■				■	■																																																								3
Md_020																								■																							■																					■				5
Md_025				■															■																																					■	■						■				■			7
Md_027																				■													■		■					■							■	■																						6
Md_029																				■																																																				1
Md_032																							■																																															1
Md_033																							■																																															1
Md_034																							■																																															2
Md_035																							■																																															4
Md_036				■																			■										■						■														■																				5
Md_038																							■																																															2
Md_039																							■																																															3
Md_040							■											■						■																■						■	■		■	■	■				■						■				■						13
Md_050																							■										■																					■																			3
Md_051																							■																																															1
Md_053																								■																																														1
Md_054																								■			■	■																																								■				4
Md_055																	■										■			■	■												■	■	■	■	■	■	■	■	■																					18
Md_058																							■																																															1
Md_059																	■						■											■																	■					■			■									■	8
Md_060				■						■																			■	■		■																																							5
Md_066																															■														■																									2
Md_068																■	■																																																				3
Md_073	■																																																																		1
Md_074	■																																																																		1
Md_076				■																																																																2
Md_077				■		■						■	■																																																								4
Md_081					■																																																															2
Md_086									■	■	■																																																										3
Md_087																						■																																																1
Md_090																					■																																																	1
Md_091																																	■																								■												2
Md_092											■																																																									1
Md_094																																		■																					■			■											4
Md_095																																		■												■																■									4
Md_096																																	■	■																							■						■									5
Md_097																■		■							■	■	■											■	■																							■								■	■				11
Md_098																																					■																															1
Md_099																																						■						■	■										■	■													■		■	10
Md_101																																		■		■							■		■	■	■							■							■				■			12
Md_103																																													■												■	■		■										■	6
Md_108																																														■	■																					2
Md_109				■	■	■		■								■	■	■	■	■				■											■		■															■								■	■				■			■	■			■			31
Md_112												■																																																								1
Md_113						■			■		■		■	■																																																										5
Md_116																															■																																					1
Md_117																																	■																																			2
Md_119																																												■		■		■	■		■	■	■														■			12
Md_120																																													■																									1
Md_121																																															■																							1
Md_130																																			■																																			1
Md_132																																																		■											■			■		■		5
Md_136																																																					■	■																2
Md_137																																																						■										■	■		■		4
Md_140																																																						■															2
Md_142																																																							■														1
Md_143																																																							■														1
Md_144																																																							■														1
Md_147																																																			■					■												2
Md_148																																																								■												1
Md_150																																																															■					1
Md_152																																															■					■		■	■														4
Md_154																																																											■									2
Md_155																																	■																																			2
Md_157																																												■																							1
Md_158																																																												■								2
Md_159																								■									■																											■						3
Md_160																																																													■						1
Md_162																																																														■					1
Md_163																																																													■				■			3
Md_164																																																																■				1
Md_166																														■																								■					■					■	■		■	6
Md_167																																																																■	■			3

Table S.IV.2 Mean (±SD) network measures of strength and clustering coefficient for the attributes of residency pattern and age-sex class. Individuals used in the network analysis were those with distinctiveness ≥2 and with linking information to at least one other individual.

	Attributes	Strength	Clustering Coefficient	Betweenness Centrality
Residency pattern	residents	2.21 (0.69)	0.06 (0.03)	101.76 (55.50)
	visitors	1.70 (0.60)	0.14 (0.14)	27.41 (7.50)
	transients	1.00 (0.71)	0.24 (0.00)	0.00 (4.35)
Age class	adult females	1.64 (0.81)	0.11 (0.17)	21.00 (25.33)
	adult males	1.36 (0.73)	0.13 (0.18)	0.00 (18.39)
	subadult males	1.39 (0.84)	0.19 (0.11)	0.00 (15.52)
	immatures	1.70 (0.75)	0.24 (0.21)	0.00 (19.76)

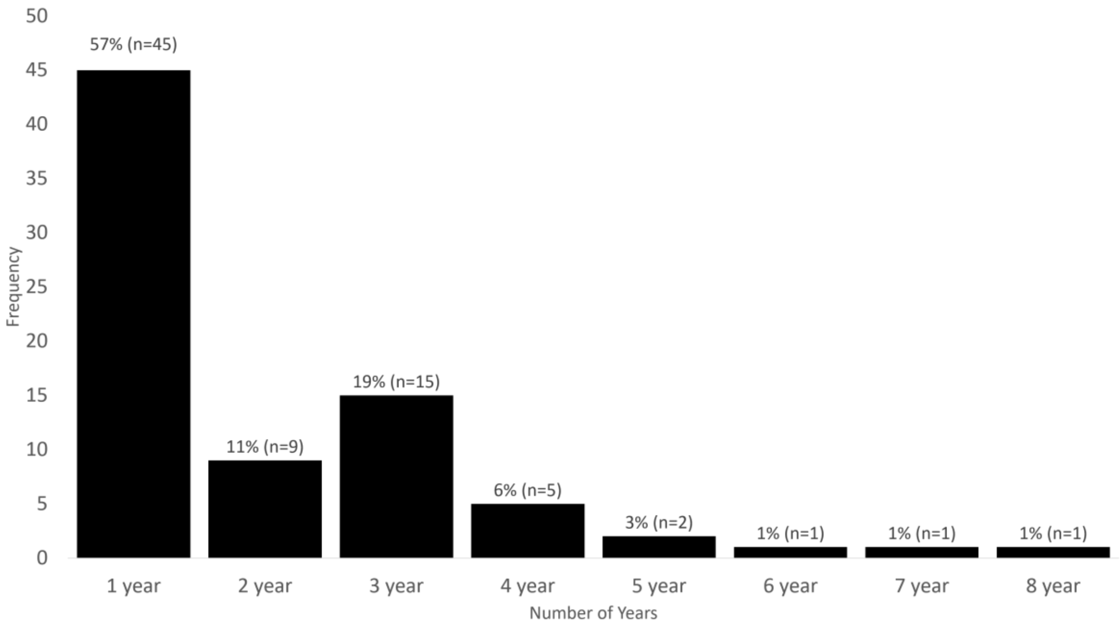

Figure S.IV.1 Frequency of individuals with distinctiveness ≥2 seen inter-annually between 2011-2019.

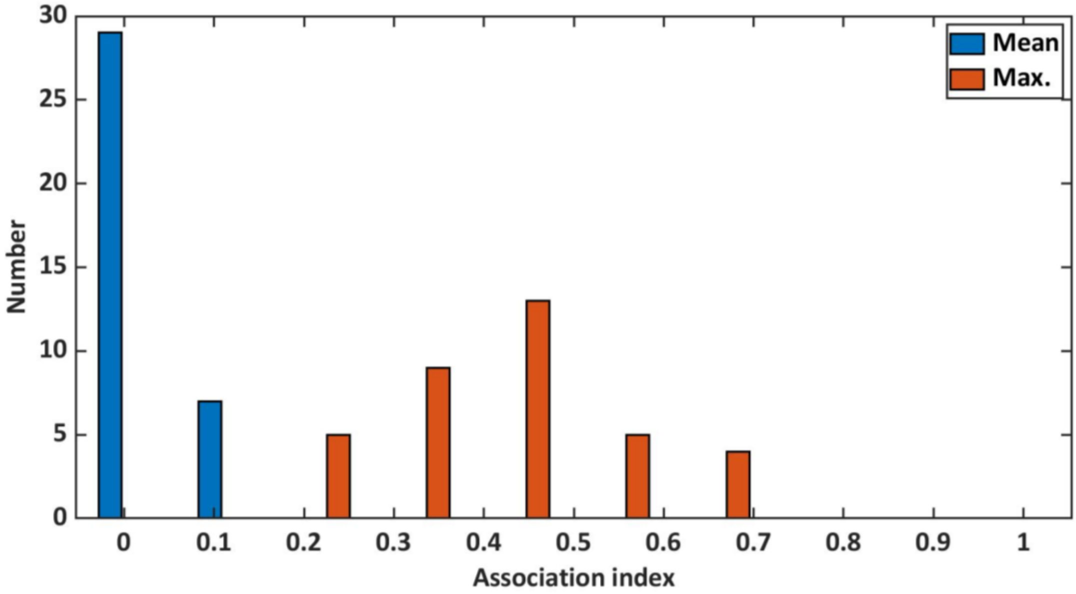

Figure S.IV.2 Distribution of mean (blue) and maximum (orange) HWI association indices for distinctive individuals captured on three or more occasions off Madeira Island.

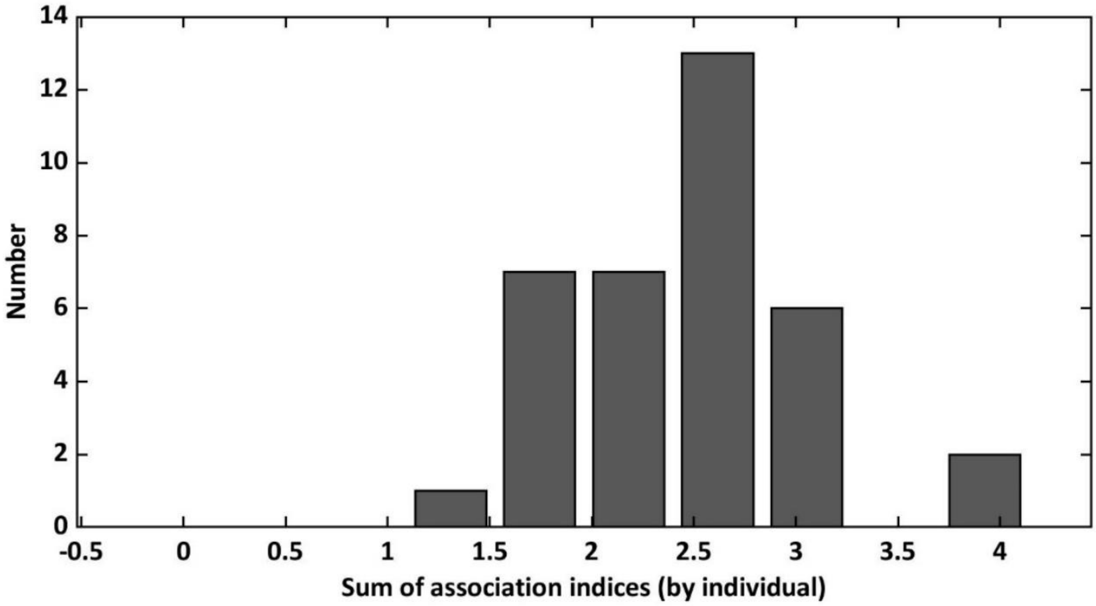

Figure S.IV.3 Sum of HWI association indices (average number of associates) for distinctive individuals captured on three or more occasions off Madeira Island.

APPENDIX B – Supplementary Material to Chapter V

Table S.V.1 Mean (± SD) δ13C and δ15N values of the prey species (Dias et al., 2023) and zooplankton (Dromby, 2018) used in this study. Prey species were divided by groups, general type and habitat of preys were based on fishbase.org and thecephalopodepage.org (Dias et al., 2023). n = number of samples.

Taxa/species	**General type**	**Main habitat**	**Group**	***n***	**δ^{13}C**	**δ^{15}N**
Prey						
Scomber colias	small-sized fish	epipelagic	Small pelagic fish A	18	-19.27 ± 0.35	7.94 ± 0.55
Sardina pilchardus	small-sized fish	benthopelagic	Small pelagic fish A	11	-19.23 ± 0.35	7.67 ± 0.43
Sardinella sp.	small-sized fish	benthopelagic	Small pelagic fish A	3	-19.49 ± 0.83	7.03 ± 0.13
Boops boops	small-sized fish	benthopelagic	Small pelagic fish A	2	-19.08 ± 0.20	8.29 ± 0.58
Macroramphosus gracilis	small-sized fish	benthopelagic	Small pelagic fish A	4	-19.08 ± 0.36	6.52 ± 0.42
Trachurus picturatus	small-sized fish	epipelagic	Small pelagic fish B	15	-17.91 ± 1.30	9.02 ± 0.33
Katsuwonus pelamis	medium-sized fish	epipelagic	Large pelagic fish	6	-18.64 ± 0.42	9.74 ± 0.29
Thunnus obesus	large-sized fish	epipelagic	Large pelagic fish	8	-17.66 ± 1.82	11.11 ± 0.38
Thunnus alalonga	large-sized fish	epipelagic	Large pelagic fish	8	-18.47 ± 0.37	11.08 ± 0.37
Loligo vulgaris	squid	demersal	Demersal squids	5	-18.92 ± 0.29	8.27 ± 0.47
Ommastrephes caroli	squid	mesopelagic	Pelagic squids A	5	-18.69 ± 0.27	6.85 ± 0.50
Sthenoteuthis pteropus	squid	mesopelagic	Pelagic squids B	6	-18.14 ± 0.23	9.89 ± 0.57
Baseline						
Zooplankton	NA	NA	NA	4	-18.8 ± 1.87	3.72 ± 0.30

Table S.V.2 Pairwise Wilcoxon *post hoc* tests with Bonferroni correction for δ^{13}C values for the six cetacean species, at 0.05 significance level. Significant differences (*p-value* < 0.05) are marked with bold.

	Short-beaked common dolphin	Atlantic spotted dolphin	Common bottlenose dolphin	False killer whale	Short-finned pilot whale
Short-beaked common dolphin	NA	NA	NA	NA	NA
Atlantic spotted dolphin	**1.46953e-09**	NA	NA	NA	NA
Common bottlenose dolphin	**1.53317e-12**	**8.19640e-06**	NA	NA	NA
False killer whale	**0.00011**	**0.00026**	**0.03082**	NA	NA
Short-finned pilot whale	**9.93338e-13**	**1.52794e-10**	**3.30044e-06**	1	NA
Sperm whale	**0.00036**	**0.00100**	1	0.43357	**0.01217**

Table S.V.3 Pairwise Wilcoxon *post hoc* tests with Bonferroni correction for $\delta^{15}N$ values for the six cetacean species, at 0.05 significance level. Significant differences (*p-value* < 0.05) are marked with bold.

	Short-beaked common dolphin	Atlantic spotted dolphin	Common bottlenose dolphin	False killer whale	Short-finned pilot whale
Short-beaked common dolphin	NA	NA	NA	NA	NA
Atlantic spotted dolphin	**0.01025**	NA	NA	NA	NA
Common bottlenose dolphin	0.10671	1	NA	NA	NA
False killer whale	**1.65083e-06**	**0.00073**	**0.00022**	NA	NA
Short-finned pilot whale	**1.00465e-11**	**4.32109e-09**	**1.20394e-10**	0.66339	NA
Sperm whale	**3.21851e-06**	**0.00181**	**0.0005**	0.20979	1

Table S.V.4 Mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values of females and males of all the species investigated in the study, except for sperm whales, since all the sampled individuals were females.

Cetacean species		**$\delta^{13}C$**	**$\delta^{15}N$**
Short-beaked common dolphin			
	Females	-19.50 ± 0.38	10.05 ± 0.95
	Males	-19.42 ± 0.57	9.62 ± 0.57
Atlantic spotted dolphin			
	Females	-19.05 ± 0.35	10.19 ± 0.85
	Males	-19.21 ± 0.50	10.51 ± 0.92
Common bottlenose dolphin			
	Females	-17.11 ± 0.46	10.15 ± 0.77
	Males	-16.99 ± 0.30	10.16 ± 0.64
False killer whale			
	Females	-17.50 ± 0.31	12.19 ± 0.13
	Males	-17.70 ± 0.49	11.95 ± 0.11
Short-finned pilot whale			
	Females	-15.82 ± 0.35	12.21 ± 0.69
	Males	-15.70 ± 0.24	12.70 ± 0.56

Table S.V.5 Pairwise Wilcoxon *post hoc* tests with Bonferroni correction for trophic position values for the six cetacean species, at 0.05 significance level. Significant differences (*p-value* < 0.05) are marked with bold.

	Short-beaked common dolphin	**Atlantic spotted dolphin**	**Common bottlenose dolphin**	**False killer whale**	**Short-finned pilot whale**
Short-beaked common dolphin	NA	NA	NA	NA	NA
Atlantic spotted dolphin	**0.01025**	NA	NA	NA	NA
Common bottlenose dolphin	0.10671	1	NA	NA	NA
False killer whale	**1.65083e-06**	**0.00073**	**0.00022**	NA	NA
Short-finned pilot whale	**1.00465e-11**	**4.32109e-09**	**1.20394e-10**	0.66339	NA
Sperm whale	**3.21851e-06**	**0.00181**	**0.0005**	0.20979	1

Table S.V.6 δ^{13}C and δ^{15}N stable isotope values used in the present study, without corrections, for all sampled individuals of the six species.

Cetacean species	δ^{13}C	δ^{15}N
Short-beaked common dolphin		
Dd1	-18,539	8,891
Dd2	-19,131	8,586
Dd3	-17,910	10,977
Dd4	-19,723	9,900
Dd5	-18,849	9,179
Dd6	-20,114	9,625
Dd7	-19,950	9,480
Dd8	-19,257	11,573
Dd9	-18,965	9,389
Dd10	-19,336	11,403
Dd11	-19,491	10,624
Dd12	-19,718	9,407
Dd13	-19,219	10,492
Dd14	-18,708	9,124
Dd15	-18,708	9,644
Dd16	-19,613	9,505
Dd17	-18,838	8,824
Dd18	-18,941	12,722
Dd19	-19,464	9,296
Dd20	-19,984	9,966
Dd21	-19,524	9,207
Dd22	-19,152	9,967
Dd23	-18,954	9,827
Dd24	-19,854	9,000
Dd25	-19,612	9,403
Dd26	-19,855	9,472
Dd27	-18,843	9,523
Dd28	-19,391	9,936
Dd30	-20,185	9,482
Dd31	-20,143	9,925
Dd32	-19,839	9,126
Dd33	-19,248	8,970
Dd34	-19,700	9,987
Dd35	-19,851	9,279
Dd36	-19,469	9,738
Dd37	-20,178	9,774
Dd38	-19,857	9,450
Dd39	-20,404	9,636
Dd40	-19,644	10,045
Dd41	-19,757	9,886
Dd42	-19,499	9,284
Dd43	-19,699	10,696
Dd44	-19,901	9,864
Dd45	-19,239	9,610
Dd46	-19,407	9,603

Dd47	-19,315	10,869
Dd48	-19,232	10,076
Atlantic spotted dolphin		
Sf2	-19,333	10,152
Sf3	-18,487	9,632
Sf4	-18,835	9,898
Sf5	-18,672	9,097
Sf6	-19,096	11,610
Sf8	-18,843	9,763
Sf9	-19,194	9,803
Sf10	-19,888	9,831
Sf11	-19,679	10,486
Sf12	-18,616	13,291
Sf13	-19,000	11,376
Sf14	-19,415	11,206
Sf15	-19,783	10,049
Sf16	-19,407	10,141
Sf17	-19,674	9,482
Sf18	-19,346	9,783
Sf19	-19,086	10,955
Sf20	-18,616	11,401
Sf21	-19,453	10,092
Sf22	-19,568	10,955
Sf23	-18,041	11,071
Sf25	-19,148	10,393
Sf26	-18,930	9,609
Sf27	-18,681	9,963
Sf29	-20,046	11,658
Sf30	-19,128	10,233
Sf31	-19,186	9,914
Sf32	-18,809	11,002
Sf33	-19,399	9,330
Sf34	-18,668	9,970
Sf35	-19,375	9,797
Sf36	-19,081	9,196
Sf37	-19,194	11,163
Common bottlenose dolphin		
Tt3	-18,856	10,456
Tt4	-18,712	9,294
Tt5	-17,926	9,515
Tt6	-18,912	9,531
Tt7	-18,561	9,259
Tt8	-18,146	9,901
Tt9	-17,832	11,463
Tt10	-18,203	9,178
Tt11	-17,794	9,416
Tt12	-18,575	9,412
Tt13	-18,539	10,429
Tt14	-18,384	9,457

Tt15	-18,559	9,787
Tt16	-18,193	10,312
Tt18	-18,352	11,454
Tt19	-18,487	11,187
Tt20	-18,884	9,272
Tt21	-18,686	9,616
Tt22	-17,740	11,230
Tt23	-18,572	10,024
Tt24	-18,784	10,279
Tt25	-18,503	10,265
Tt26	-18,583	10,251
Tt27	-19,011	10,093
Tt28	-19,101	9,968
Tt29	-19,524	9,740
Tt30	-18,452	10,611
Tt31	-18,825	9,159
Tt32	-19,310	10,914
Tt33	-18,668	9,984
Tt34	-18,593	10,265
Tt35	-18,695	10,791
Tt36	-18,243	10,578
Tt37	-18,300	9,890
Tt41	-18,910	11,990
Tt42	-18,600	10,260
Tt43	-18,310	10,170
Tt44	-18,540	10,440
False killer whale		
Pcr1	-17,729	11,798
Pcr2	-17,628	12,243
Pcr3	-17,659	12,001
Pcr4	-17,100	12,932
Pcr5	-17,675	12,239
Pcr6	-17,696	11,938
Pcr7	-17,035	12,283
Pcr8	-18,291	12,045
Short-finned pilot whale		
Gma2	-17,084	13,375
Gma3	-16,681	14,042
Gma4	-17,476	11,929
Gma5	-15,795	13,043
Gma6	-17,400	12,586
Gma7	-17,443	12,928
Gma8	-17,776	12,356
Gma9	-17,027	12,466
Gma10	-17,876	12,899
Gma12	-17,329	12,558
Gma13	-17,063	12,449
Gma14	-17,213	13,261
Gma15	-17,222	12,682

	Gma17	-16,628	12,581
	Gma18	-17,907	12,439
	Gma19	-17,427	12,803
	Gma20	-17,433	11,981
	Gma21	-18,778	11,930
	Gma23	-17,260	12,805
	Gma25	-17,620	12,793
	Gma26	-17,250	12,511
	Gma27	-17,220	12,290
	Gma30	-17,000	12,040
	Gma31	-17,220	12,040
	Gma33	-17,160	11,950
	Gma34	-17,040	11,880
	Gma35	-17,630	12,050
	Gma36	-17,500	12,080
	Gma38	-18,120	11,210
	Gma39	-17,000	12,020
	Gma43	-18,310	10,170
	Gma44	-17,390	12,530
Sperm whales			
	Pm2	-17,992	13,235
	Pm3	-18,249	12,232
	Pm5	-17,659	12,962
	Pm6	-18,395	12,272
	Pm7	-18,288	12,165
	Pm8	-17,907	12,665
	Pm9	-18,012	12,297