The ecological importance of oceanic islands for cetaceans: the case study of Madeira archipelago

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ABSTRACT

Open ocean islands support resident cetaceans and are used seasonally as feeding/breeding areas by migrating populations. However, these usually small habitats are expected to have limited capacity to sustain many animals for long periods, especially in oligotrophic waters.

This study aimed at understanding how cetaceans use insular habitats, including their relevance to cetaceans' survival and life cycles, and how cetacean species may share or compete for local marine resources. The study combined data from multiple survey types (2001 – 2017) to model the temporal and spatial use of Madeira archipelago waters by 10 cetacean species, including baleen whales, dolphins and deep divers, and to identify their local habitat preferences. Photo-identification, capture-mark-recapture methods and satellite telemetry were used to investigate the role of Madeira in the survival and life cycle of Bryde's whales. Ecological niche partitioning among these cetacean species was studied using a multidisciplinary approach, where the trophic dimension was informed by stable isotopes and the spatial and temporal dimensions by habitat use models.

This study showed that open ocean islands are important for cetacean survival and play a role in many individuals' life cycles; however, their relevance is dependent on the species energetic requirements and on the islands' geographic context. Furthermore, the results suggest that Bryde's whales are recent to Madeira, using it seasonally to feed and calve in the context of a wider Atlantic distribution, and added further evidence on their income breeder strategy. The study also found that the limited local resources are shared among species through ecological niche partitioning and differences in their degree of ecological specialisation, to minimize competitive exclusion. Nevertheless, some degree of competition may exist among a few species, which together with other factors, may shape their local habitat use, the trophic level at which they feed and their local seasonal succession.

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My first words go to my family to thank them for the support over the years, not only during the PhD but also during the long path that took me to it. To my parents, Nicolau and Carmen, for their connection to nature, for their example of dedication to what they loved and perseverance in front of adversities, and for always having my back. To my brother Gabriel and sister Doli for being there when I needed and to my daughter Julia and son Rodrigo for being partners in this journey, not only for having patience with me when I got caught up in work at the end of the day or weekends but also for being my field assistants, always helpful and with a smile. To my partner Giulia for all her patience and support in these last three years, but especially in the last months of writing when I was fully dedicated to the PhD, including my spare time. You are all my inspiration. Father, I wish you were here to see what you helped me achieve.

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My journey in the research of marine mammals in Madeira, especially cetaceans, was mostly carried out at the Madeira Whale Museum, for over 25 years. As expected, my research work and the timing of my PhD has been intertwined with the research work, timing and objectives of the Museum. As such, I am very grateful to the whole Museum's team, which over the years have carried out or supported the research in the institution, and that directly or indirectly contributed to the work presented in this thesis. I am particularly grateful to Ana Nóbrega who, in several roles, has supported my work in the institution over the years, especially in the years of the PhD as director. I am also very grateful to the valuable support from Machico Municipality, through the Mayor Sr. Ricardo Franco, which over the last years has given words of encouragement and the necessary institutional support for this work to be carried out.

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ETHICAL STATEMENT

This study had the approval of the School of Biology Ethics Committee of the University of St Andrews regarding the deployment of satellite tags of Bryde's Whales (Biology SEC ref: SEC18009) in the context of project "MARCET: Red Macaronésica de Transferencia de Conocimientos y Tecnologías Interregional y Multidisciplinar para proteger, vigilar y monitorizar los cetáceos y el medio marino, y analizar y explotar de forma sostenible la actividad Turística associada" (MAC/1.1b/149) and the use of biopsy samples (Biology SEC ref: SEC18009) collected by the author for project "Oceanwebs: Redes tróficas oceânicas: utilização de dados espaciais, informação sobre dieta e biomarcadores de predadores de topo para revelear a estrutura e funcionamento de ecossistemas pelágicos subtropicais"(PTDC/MAR-PRO/0929/2014).

The deployment of satellite tags and collection of biopsy samples in the context of the above-mentioned projects required permits from the wildlife management authority in Madeira Autonomous Region (IFCN – Instituto de Florestas e Conservação da Natureza, IP-RAM) and from the competent national authority DGAV (Direcção Geral de Alimentação e Veterinária) regarding animal handling/sampling, in accordance with Portuguese (Decreto-Lei nº 113/2013, de 7 de Agosto) and EU legislation (2010/63/EU), with respect to animal handling and welfare.

The work in project MARCET was carried out under IFCN permit nº 544 dated 17-01-2018, and DGAV permit nº 015534, dated 16-08-2018.

The work in project OCEANWEBS was carried out under IFCN permit dated 07-12-2016, and DGAV permit nº 021819, dated 14-11-2016.

The author is certified by DGAV in Animal Handling skills to fulfil the requirements of the above-mentioned legislation (document 024962 dated 30-11-2018).

Chapter 1

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GENERAL INTRODUCTION

GENERAL INTRODUCTION

The oceans are complex, dynamic and diversified systems, in spite being a physically continuous environment and apparently homogeneous when looked at from the surface. Many factors contribute to such complexity, among them physical and chemical properties of the medium (water), latitudinal differences in sunlight incidence (equatorial, tropical, temperate and polar regions), rotation of the earth (Coriolis force), local physiography, influence of continental land masses, winds and currents (Mann and Lazier, 1991). Open ocean archipelagos are part of these systems and contribute to the complexity and diversity of marine habitats.

Krebs (1972) defined ecology as the scientific study of the interactions (biotic and abiotic) that determine abundance and distribution of organisms. Variations in environments define variations in animal distribution (how abundance of a species changes from place to place) (Begon *et al.*, 1990), whether these variations are physical (abiotic), biological (biotic) or the result of both.

As pointed out by Begon *et al.* (1990), “most species are absent from most places most of the time”, so it is important to explain not only how the properties of different sorts of species fit them for life in particular environments, but also how these properties come to exclude them from the majority of environments. The environment or locality in which a plant or animal lives is defined as habitat (McIntosh, 1989). Each locality has some favourable and some unfavourable characteristics relating to its suitability as habitat for the species. Preferred habitats are often environments that have an optimal balance between favourable and unfavourable characteristics (Bjørge, 2001).

Animals of a species have shared characteristics and individual characteristics that overall make them more adapted to survive and reproduce in certain habitats (Begon *et al.*, 1990). Among these are anatomical, physiological and behavioural characteristics and, for mammals, life history strategies (involving gestation, lactation and weaning periods, mating system, birth, growth and mortality rates, life spans, migration patterns) that can limit individual fitness and thus contribute to define the species overall habitat use and distribution of abundance (Evans and Stirling, 2001). Other limiting factors are availability/distribution of prey, shelter, sexual mates, and predators (Begon *et al.*, 1990; Heimlich-Boran *et al.*, 2001). Ultimately, these and other factors define the processes of birth, death and migration that shape distribution and abundance of populations.

Cetaceans are important components of marine ecosystems. Most of these species are predators at higher trophic levels that both are affected by the ecosystem of which they are a part and affect that same ecosystem (Estes, 2009). Thus, studying their ecology is important to understand how marine ecosystems work. As pointed out by Würsig (2009), morphological, physiologic and behavioural adaptations of marine mammals to marine environments are largely driven by their food and the habitats of their prey. One way of classifying those ecological adaptations is by considering several general habitat types where these animals live, namely, open ocean, semi-pelagic, coastal and riverine (Würsig, 2009). As the name implies, oceanic cetacean species utilize mostly or exclusively the open ocean waters (beyond the continental shelf). Typically, the open ocean is characterized by deep waters (>200m depth) within a pelagic environment.

Oceanic or open ocean cetaceans are an ecologically diverse group of species that include: most of the great baleen whales (families Balaenidae, Neobalaenidae and Balaenopteridae); oceanic dolphins, killer whales and related species (family Delphinidae); all beaked whales (family Ziphiidae); sperm whales (family Physeteridae), pygmy and dwarf sperm whales (family Kogiidae); and some species of porpoises (family Phocoenidae) (Perrin *et al.*, 2009a). Although many of these species are mainly or exclusively oceanic, some species like the minke whale *Balaenoptera acutorostrata*, the bottlenose dolphin *Tursiops truncatus* or the killer whale *Orcinus orca*, have animals that utilize both the open ocean and the coastal waters and/or populations that utilize mostly one of these provinces (Ford, 2009; Perrin and Brownell, 2009; Wells and Scott, 2009).

The open ocean cetaceans can be broadly divided into two categories: "surface dwellers" and "deep divers" (Würsig, 2009). Large baleen whales, smaller toothed whales and dolphins typically spend their entire lives within the first couple of hundred meters below the surface, where the near-surface open ocean environment usually has low primary and secondary productivity, except in higher latitudes in summer (above 40º). The smaller pelagic odontocetes travel great distances in search of food, often in large schools of hundreds to thousands. They feed on sporadically encountered near-surface fishes and squid, or at night on animals associated with the deep scattering layer (DSL). On the other hand, many of the larger toothed whales dive deep, routinely feeding on mid-sized deep waters fishes and squid at depths greater than 500m (MacLeod *et al.*, 2003; Würsig, 2009; Pereira *et al.*, 2011; Heithaus *et al.*, 2018; Perrin, 2018a).

Some open ocean cetaceans explore the zone between shallow and deep water, often at the edge of the continental shelf or some other underwater feature, broadly called semi-pelagic habitats by Würsig (2009). These animals are attracted by the high productivity caused by upwelling or current systems as the sea interacts with land. Some dolphin populations in abruptly rising volcanic islands or coral atolls can also be considered semi-pelagic. They seek out deep productive open waters in areas close to shore to feed but retreat to shallow waters, often into bays and inlets or onto expansive shoals to rest. Spinner dolphins of the tropical islands of the Pacific are an example. During the day, they rest and socialise within island bays and lagoons and at night head out to sea, often a few kilometres from land, to feed at the DSL when it is closer to the surface at depths accessible to them (Würsig, 2009).

The continuous and dynamic nature of the oceanic environment makes it difficult to define clear geographic limits to its structure, organization and processes. Unlike land, there are usually no visible boundaries or reference points, the species live in a three-dimensional environment difficult to access, probe and study, and the vastness of the oceans pose logistical and practical problems to its study and exploration. To complicate matters, phenomena happening hundreds or thousands of kilometres away (e.g. water mass formation; fronts; currents; upwelling areas and strength) may influence the local environment (habitat) that in turn influences or even determines the presence, recruitment, abundance and distribution of species, the existence and dynamics of communities and ultimately of ecosystems (Mann and Lazier, 1991). It is a challenge to study the ecology of highly mobile species, namely cetaceans, in such a context. It is important to have in mind the temporal and spatial scales of the different processes and phenomena (physiographic, oceanographic and biological) when studying cetacean ecology (Bjørge, 2001).

Oceanic islands provide the logistical support and opportunity to probe and study the open ocean, being important solid spatial references amidst the dynamic ocean and fixed sampling points that enable the study of oceanic phenomena evolving at different spatial and temporal scales. Oceanic islands also seem to be important habitats for highly mobile oceanic species such as cetaceans (Freitas *et al.*, 2004a; Silva *et al.*, 2014; Baird *et al.*, 2015).

1.1 OPEN OCEAN INSULAR MARINE ENVIRONMENTS

Islands are spread throughout the oceans of the world from the equator to the polar regions. In spite of having some common characteristics resulting from their insular condition, the islands' surrounding marine environments vary greatly with latitude (incidence of sunlight), geology, sea bottom composition, island physiography, proximity to continental land masses and local oceanography and meteorology. Such diversity of habitats results in a very wide range of ecological niches, biological communities and ecosystems that are too vast to encompass in a single study. Although this study may refer and make comparison to studies and knowledge derived from work carried out in insular and continental environments through the world, its geographic focus is mainly on the subtropical and warm temperate open ocean archipelagos.

Whittaker & Fernández-Palacios (2007) define oceanic islands "as those that have formed over oceanic plates and have never been connected to continental masses". They can have different geological origins that are related with the plate tectonic processes, namely plate boundary islands and islands at intraplate locations; all are of volcanic origin.

The Madeira archipelago is an example of islands at an intraplate location. They are roughly 700 km west of northwest Africa, in the Canary basin part of the Eastern Atlantic basin (Heezen *et al.*, 1959). Administratively, it comprises seven volcanic islands organized in two sub-archipelagos. The main sub-archipelago includes *Madeira*, *Porto Santo* and *Desertas* Islands (three smaller islands – *Búgio, Deserta Grande* and *Ilhéu Chão*), less than a kilometre to no more than 37 km apart (32º 46' N;16º 46' W). The *Selvagem Grande* and *Selvagem pequena* Islands make the second sub-archipelago located 290 km SSE of *Madeira* Island. Both Madeira and Porto Santo Islands are inhabited while the Desertas and Selvagens islands are uninhabited protected areas both on land and on the surrounding sea (Figure 1.1). These islands are part of a marine biogeographic region called webbinesia that comprises the Canary Islands as well, although in the context of this study we will also consider a wider biogeographical unit called Macaronesia, which also includes the Azores (Freitas *et al.*, 2019b).

These islands are surrounded by the Madeira abyssal plain characterised by flat bottoms covered by sediment with depths greater than 5400 m (Heezen *et al.*, 1959), with sea mounts (e.g. Seine, Unicorn, Dragon, Ampere and Madeira-Tore Rise) present mainly to the north and northeast of these islands, with some coming close to the surface (< 500 m)(Geldmacher *et al.*, 2000).

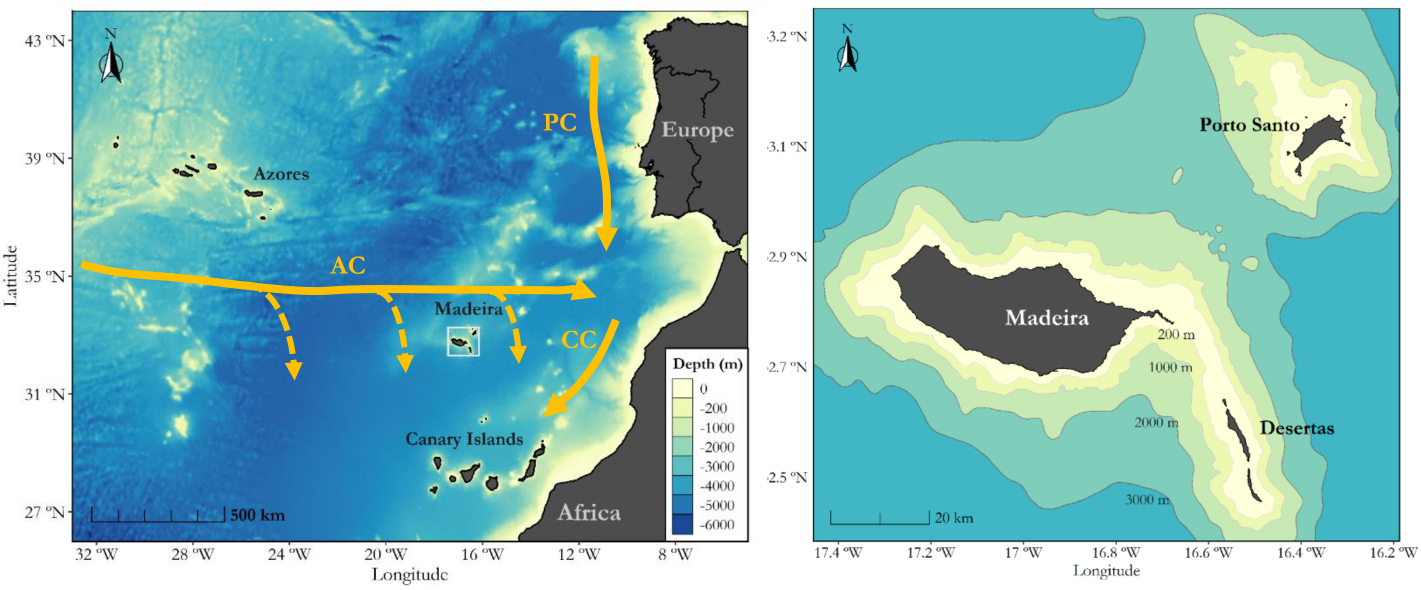

Figure 1.1. Left: location of the Madeira archipelago in the context of the Atlantic Ocean, with the identification of the study area (white box) and the main surface currents: AC – Azores Current; PC – Portugal Current; and CC – Canary Current (adapted from Narciso *et al.*, 2019 and Frazão *et al.*, 2022). Right: Madeira archipelago islands (except Selvagens islands) showing detailed bathymetry.

Open ocean islands are usually at considerable distances from continental coasts, beyond the continental shelf break. Thus, they are influenced mainly by the general oceanic circulation, which varies with their location in the oceanic basins, latitude and local physiographic constraints. In the case of oceanic islands in subtropical and warm temperate waters, they are strongly influenced by the subtropical gyres.

The Madeira archipelago is mostly influenced by the Azores current (AC), a branch of the subtropical North Atlantic Gyre originating in the Gulf Stream system (e.g. Klein and Siedler, 1989), that moves eastwards with its flow centred around latitude 34ºN (Juliano, 2002) (Figure 1.1). It transports warm and salty water over the mid-Atlantic Ridge, southwest of Azores (~ 34ºN; 37ºW)(Käse and Siedler, 1982), and continues eastwards to produce a thermohaline front (abrupt changes in temperature and salinity) with a convergence zone (Zhou *et al.*, 2000). This subtropical front is called the Azores front (Juliano, 2002), and it shows mesoscale phenomena activity with intensive meander formation (Käse *et al.*, 1985; Kielmann and Kase, 1987), where eddies and filaments promote a turbulent mixing between subtropical waters in the south and temperate waters in the north (Caldeira *et al.*, 2002; Sala *et al.*, 2013) (Figure 1.1).

The Madeira archipelago islands, as all oceanic islands, are the visible part (above sea level) of mountains rising from the ocean floor, in this case from the Madeira abyssal plain at depths greater than 5 400 m (Heezen *et al.*, 1959). The sections above sea level are a barrier to the prevailing northeast trade winds, that speed up when reaching the islands, especially Madeira due to its high-altitude mountain chain, producing atmospheric phenomena that affect the surrounding sea surface waters. In turn, the underwater sections of these islands are natural barriers to oceanic circulation at different depths generating, together with currents and winds, oceanographic phenomena such as local coastal upwelling or island induced eddies (Caldeira *et al*, 2002). These phenomena have also been observed and studied widely in other archipelagos such as Hawai'i, the Canary Islands or the Galapagos (e.g. Barton *et al.*, 2001; Holland and Mitchum, 2001; Palacios, 2003; Bakun, 2006).

The islands' induced turbulent flow processes, together with nutrient-rich land run-off and benthic processes in shallow waters contribute to the increase in primary productivity around oceanic islands (Doty and Oguri, 1956; Caldeira *et al.*, 2002; Palacios, 2002), called the "island mass effect" (after Doty & Oguri 1956). These processes contribute to the primary production in the oceans because they promote the vertical transport of nutrients from the deeper rich layers of the ocean to the superficial layers where there is enough light for photosynthesis to take place – the euphotic zone (Mann and Lazier, 1991) (Figure 1.2).

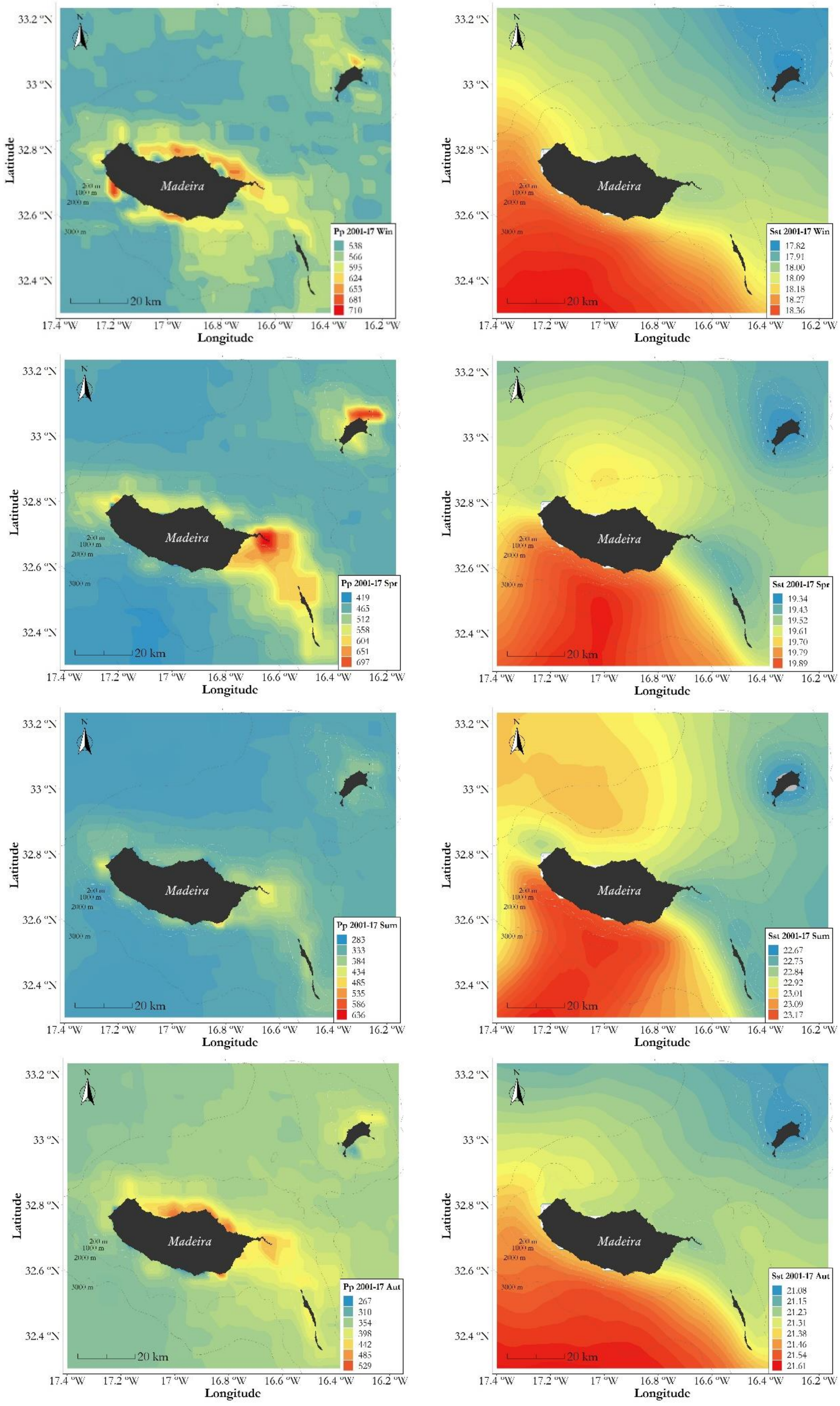

Figure 1.2. Maps of the average seasonal primary productivity (mg C m^{-2} day^{-1}) and sea surface temperature (ºC) in Madeira archipelago for the period 2001 – 2017, presented on the left and right, respectively. The maps for winter, spring, summer, and autumn for each variable are ordered from top to bottom. These maps were obtained from satellite telemetry readings (Table 4.1).

However, islands offer limited coastal marine habitats when compared with the surrounding wide pelagic environment. Unlike continents, they usually do not have extensive shelfs tens or hundreds of kilometres wide where nutrients can easily be brought to the euphotic zone by mixing processes, but rather small insular shelfs that may be absent in many islands (Heezen *et al.*, 1959; Mann and Lazier, 1991; Neall and Trewick, 2008). Nevertheless, oceanic islands like Madeira tend to be areas of higher primary productivity in the midst of a generally oligotrophic sub-tropical and warm temperate oceanic domain (Longhurst *et al.*, 1995; Caldeira *et al.*, 2002), often showing seasonal patterns (Figure 1.2).

It is difficult to determine the boundaries of an insular marine environment because of the continuous and usually dynamic nature of an island's surrounding waters. However, an insular marine environment can be broadly defined as the coastal marine waters surrounding the island(s) and the contiguous oceanic waters under the influence of the island mass effect. It includes all the oceanic body of water surrounding the island(s) that is affected (positively or negatively) by the atmospheric, oceanographic and biological phenomena generated by the presence of the island that otherwise would not take place. This definition can be further narrowed by identifying (if possible) the boundaries of specific features (e.g. coastal upwelling; warm water wakes; island generated eddies; bottom topography; areas of higher primary productivity) that affect the biological processes being studied.

The static nature of islands combined with higher productivity and their prey aggregating effect (Fiedler, 2009) seems to play in favour of cetaceans. For example, Baird *et al.* (2008) suggested that the range and movements of rough-toothed dolphins can be influenced by oceanic islands, potentially as a result of increased predictability of food resources in these ecosystems.

1.2 CETACEANS AND OPEN OCEAN ISLANDS

Ideally, and from an energetic point of view, it makes sense for animals to use an area that fulfils all their life cycle demands such as, feeding, socialisation, mating, reproduction, calving and resting, as well as minimization of predation and other sources of mortality (e.g. anthropogenic), and thus avoiding spending energy on displacements. Resident groups, or populations, find in one place an acceptable balance between all these conditions thus allowing a certain number of animals to live and reproduce in the same place (Bjørge, 2001). However, many species populations need to migrate as a whole or partially to fulfil their life cycle demands in different areas, or to make wide displacements in search for prey or following prey migrations (Ballance, 2018; Stern and Friedlaender, 2018). Oceanic islands in many cases are among the habitats used by both resident and migratory groups or populations (e.g. Silva *et al.*, 2014; Freitas and Penry, 2021; Esteban *et al.*, 2022).

Oceanic islands tend to have a high diversity of cetacean species (e.g. Palacios, 2003; Carrillo *et al.*, 2010; Prieto and Silva, 2010; Freitas *et al.*, 2012; Baird *et al.*, 2013a). The rapid increase in depth with distance from the coast creates the conditions for the existence, in a relatively small area, of marine coastal habitats and oceanic habitats, bringing together or in close proximity cetacean species that prefer one or the other type of habitats (Kiszka *et al.*, 2007).

Ecological theory says that the coexistence of sympatric species with similar ecological requirements need some degree of habitat and resource differentiation to minimize competition (Pianka, 1974). This differentiation may have a temporal dimension, with species using the same habitat and exploring the same resources at different times of the year. For co-existing species, that differentiation can be temporal (e.g. diel patterns - different species exploring the same resources at different times of the day), spatial (differentiated use of areas and habitats), differential exploration of local resources (e.g. through prey species or size specialization)(Pianka, 1973; Ballance, 2018), or some combination of the previous dimensions.

Furthermore, the usually limited size of oceanic islands offers smaller coastal marine habitats and limited productivity (especially in warm temperate, subtropical and tropical areas of the oceans), when compared with continental habitats. As a result, although cetacean diversity may be high, one would expect that the size of cetacean species populations or sub-populations dependent on these habitats to be smaller, or to be dependent for shorter periods of time, when compared with populations exploring equivalent continental habitats (e.g. continental slope, shelf and coastal waters). Nevertheless, the combination of multiple oceanic island habitats (multiple archipelagos) or of oceanic islands and continental habitats may be crucial to sustain wide ranging oceanic cetacean populations.

Consequently, to understand the ecology of cetacean species, it is important to study and understand the role that oceanic islands play in cetacean life cycles and in their populations' structure and distribution of abundance in the wider oceanic context. It is also important to study and understand how different, apparently competing, species utilize and share limited resources (space, food, shelter, etc.) in such usually small insular habitats. This is particularly relevant for cetacean species, which are mostly predators at higher trophic levels.

1.3 THE CASE STUDY OF MADEIRA ARCHIPELAGO: MAIN OBJECTIVES AND OUTLINE OF THE THESIS

Twenty-eight cetacean species have been recorded in Madeira archipelago, of which two are unconfirmed records (Freitas *et al.*, 2012; Ferreira *et al.*, 2017). All but three species were recorded in the archipelago in the last 20 years, although with very different sighting frequencies; some common, some occasional and some rare (Freitas *et al.*, 2004b, 2012).

The present study aims to improve our understanding of the ecological importance of insular environments for oceanic cetaceans by using Madeira archipelago as a case study and addressing the two following questions:

1. How do cetacean species (populations) use insular marine environments in the wider context of their oceanic distribution, including the relevance of those habitats to their survival and their role in the life cycle of individuals of those populations?
2. How do cetacean species (populations) use and share (or compete for) those islands marine habitats and resources?

Chapter 2 is a review of the current knowledge and understanding of cetacean ecological patterns in oceanic island archipelagos. Firstly, the importance of oceanic islands in the wider context of cetacean species oceanic distribution is explored, together with the role that oceanic islands habitats may have in the life cycle of individuals of those species (question 1). Furthermore, the importance and use of oceanic islands by cetaceans is discussed considering other marine habitats available to them, such as continental and open ocean waters, and how they may use those habitats complementarily. Secondly, the perspective of how cetacean species use and share island marine habitats and resources is reviewed (question 2), considering aspects such as interspecific competition or niche partitioning.

In chapter 3, question one of the thesis is addressed through the study of Bryde's whale use of Madeira archipelago inshore waters in the context of its wider oceanic distribution and the archipelago's role in the life cycle of individuals in the population. The Madeira Whale Museum's long-term Bryde's whale photo-identification dataset (2002 – 2021) is used to estimate abundance and survival rates (using mark-recapture methodology) of the species over time in Madeira inshore waters. Bryde's whales use of Madeira archipelago waters and of the corresponding wider ocean basin (movements and migration patterns), is investigated by exploring the animals' site fidelity patterns to the archipelago, by broadening the photo-identification study to include the Azores, the Canary Islands, mainland Portugal and Northwest Africa, and by the deployment of satellite tags on animals using Madeira coastal waters.

For cetacean species using Madeira archipelago inshore waters most frequently or regularly, it can be hypothesized that they occupy their own distinct local niches, which are characterized by different or partially different spatial and/or temporal patterns of habitat use and by the exploitation of different or partially different food resources. As noted by Pianka (1974), sympatric species with similar ecological requirements can compete for resources and thus their coexistence requires some degree of habitat and resource segregation. To test this hypothesis and address the second question of this thesis, several complementary approaches are used, namely:

a. model spatial and temporal variation in distribution (chapter 4) of the most frequently sighted species;
b. stable isotope analysis to study relative trophic levels to understand how food resources are shared by the different cetacean species (chapter 5);

In chapter 4, the species' relative importance is determined by comparison of encounter rates on multiple surveys to understand how frequently and when these species use the Madeira archipelago inshore waters. For the most common species, with more local ecological relevance, and for which there are enough data, General Additive Models (GAMs) are used to predict their overall and seasonal habitat preferences and to identify temporal patterns in their use of the study area, using a multi-survey multi-year dataset (2001-2017). Species with very few sightings over the years were excluded from the analysis. They probably use the Madeira archipelago opportunistically and thus are of small local ecological relevance.

In chapter 5, information about the trophic niches of several important cetacean species is investigated through carbon and nitrogen stable isotope analysis of skin biopsies of live animals collected in the wild and from animals stranded over the years along Madeira archipelago shores. The local ecological niches of the main cetacean species using Madeira inshore waters are then described and compared using three variables: trophic niche (Chapter 5), temporal distribution and spatial distribution (Chapter 4). The results of chapters 3 to 5 are then combined, interpreted and discussed to give a more comprehensive, integrated and multispecies view of how cetaceans use and share insular marine environments, their relevance in the wider oceanic context and hopefully shed light on the importance of some of the ecological processes that may be at play in these marine ecosystems.

Chapter 6 is the conclusion chapter of the thesis presenting final remarks with a summary of the most relevant findings of this study.

Chapter 2

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THE ECOLOGY OF CETACEANS IN OCEANIC ISLANDS

A COMPARATIVE REVIEW

THE ECOLOGY OF CETACEANS IN OCEANIC ISLANDS – A COMPARATIVE REVIEW

2.1 INTRODUCTION

Pompa *et al.* (2011) made a global analysis of distribution patterns for 129 marine mammals, describing their geographic ranges, assessing patterns of species richness and composition, and identifying key conservation sites based on a set of criteria. Figure 2.1 shows the distribution patterns of species richness for mysticetes and odontocetes, as presented by Pompa *et al.* (2011). These two cetacean families show broadly different patterns, with mysticetes having a clear latitudinal distribution with the highest species richness at around 30º S, whereas odontocetes have a highest species richness associated with the tropics, especially with continental coasts.

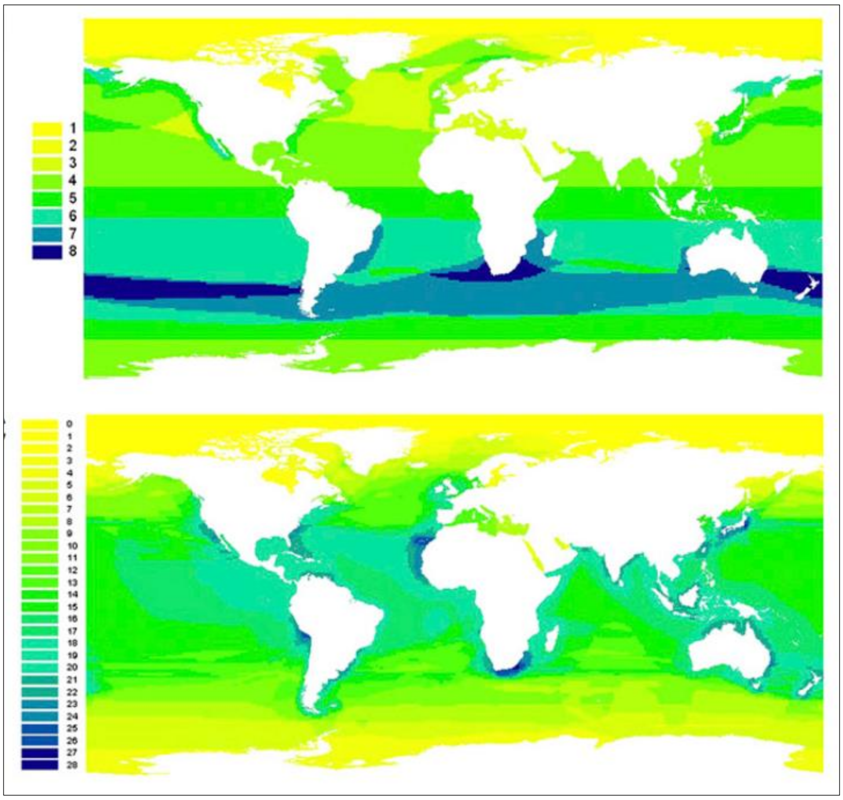

Figure 2.1. Patterns of geographic distribution of species richness of: top - Mysticetes (e.g., blue whale, Bryde's whale, right whale); bottom - Odontocetes (e.g., small dolphins, sperm whale, killer whale). The number of species in each cell is shown in the legend on the left. From Pompa *et al.* (2011).

As pointed out by the authors, areas especially rich in marine mammal species were found along the continental coasts apparently correlated with ocean currents and known upwelling areas of high productivity (e.g. California, Baja California, Peruvian coasts and Northwest Africa); good feeding areas for marine mammals. The same study identified nine key conservation sites selected because of their species richness all located in continental waters, mostly at temperate latitudes. Oceanic islands were only selected as key conservation sites when they were deemed irreplaceable because of local endemic species, e.g. the Hawaiian Islands (Hawaiian monk seal *Monachus schauinslandi*). However, using species richness and irreplaceability because of local endemisms may be an overly simplistic view of the role islands play as key ecosystems for cetaceans and marine mammals in general.

To understand the role of oceanic islands in the ecology and life cycles of cetaceans it is important to bear in mind the factors determining their distribution. Forcada (2018) grouped those factors in five types: demographic (e.g. abundance, age and sex structure of the populations, and the reproductive status and life cycle of individuals); evolutionary (e.g. morphological, physiological, and behavioural aspects of the species' adaptations), ecological (e.g. biological production and use of prey, distribution of prey and predators, and competitors), habitat-related (e.g. water temperature, thermocline depth, and bathymetry) and anthropogenic (e.g. pollutants, human-induced sounds, global warming, and incidental and direct kills). As pointed out by the author, the distribution results from some or all these factors acting on each species, and sometimes on groups of species, over different scales of space and time.

Other aspects to consider are the islands' location, context and characteristics. For example, islands at different latitudes have different roles for baleen whales and may have different species diversity, which may result in more or less competition for resources. The size, shape and height of oceanic islands, the number of islands (and sea mounts) and distance between them in an archipelago are also important as they result in more or less habitat available at different depths, higher or lower productivity (and prey availability) generated by local upwellings and the island mass effect, and more or less fragmented habitats according to each species needs. The distance of oceanic islands to continental masses and to other oceanographic features (e.g. fronts, divergences), are expected to influence cetacean diversity, abundance and their use of these open ocean insular environments.

2.2 ENERGETICS OF CETACEAN SPECIES AND HOW THEY RELATE TO THEIR USE OF OPEN OCEAN ISLANDS

Energy is crucial for animals' maintenance, growth and reproduction. Costa and Maresh (2018) give a robust account of the energetics of marine mammals in the context of their ecology, physiology, movements, behaviour and strategies to achieve energetic balance. In synthesis, animals obtain energy from their diet (prey intake) and spend energy in their basal metabolism, body repair, thermoregulation and activity, losing energy as well through waste (faecal energy, urinary energy, heat output and heat increment of feeding). To survive and succeed (grow and reproduce), animals need to achieve an overall energetic balance where the energy acquisition compensates the energetic expenditure. To grow and reproduce, they must have a positive energy balance, i.e. obtain more energy than needed to survive. Energy acquisition is dependent on the caloric value of the prey and on the assimilation efficiency of those prey by the predator (assimilation efficiency is highest in a high lipid diet). Conversely, energy expenditure is related with maintenance costs (e.g. basal metabolism, thermoregulation), locomotion and foraging costs (energetics of locomotion, energetics of foraging behaviour, energetics of prey choice), and growth and reproduction costs (e.g. variation in milk composition or breeding strategy) (Costa and Maresh, 2018).

Different strategies are used by different species, and even by different individuals of the same species, to achieve an overall energetic balance. The species and individual characteristics (e.g. anatomy, physiology and behaviour) limit the habitats and food they are able to exploit, and when they are able to exploit them. Some species, including sea otters and sea lions, have high energy expenditure rates that need to be balanced by high rates of energy acquisition (Costa and Williams, 2000; Costa and Maresh, 2018). They live preferentially in upwelling areas or close to shore environments where prey is abundant, obtaining energy balance at smaller spatial and temporal scales of tens to hundreds of kilometres and days to weeks, respectively (Williams and Maresh, 2016; Costa and Maresh, 2018). In contrast, baleen whales have low energy expenditure rates and follow a strategy with variations in energy balance. They gain energy while feeding in seasonal highly productive environments to build energy reserves to use when food is not available, and fast during migration and/or reproduction (capital breeders). These animals achieve energy balance over large spatial scales of hundreds to thousands of kilometres and temporal scales of months to years, when compared to other marine mammals (Costa and Maresh, 2018). Bryde´s whales may be to some extent an exception to this general pattern, considering that they do not have large geographic resource partitioning nor accumulate large amounts of stored energy in the form of thick blubber layers, as do most migratory baleen whales (Freitas and Penry, 2021). According to these authors, Bryde's whales appear to be more similar to income breeders than to capital breeders, and, therefore, may have lactation periods much longer than currently believed (6 to 12 months), possibly up to 2 years.

Overall, the strategies used by odontoceti species to achieve energy balance seem to be closer to sea otters and sea lions than to baleen whales. Odontoceti species distributions are mostly restricted to temperate and tropical waters of the world, especially in high productivity areas (Figure 2.1, bottom). In general, they do not have the long distance seasonal migrations that are found among mysticetes and they feed more continuously throughout the year than baleen whales (Hooker, 2018). They follow an income breeding strategy which involves alternate foraging and provisioning their young in short intervals of minutes to hours (Costa and Maresh, 2018). They probably obtain their energy balance over smaller spatial (tens to hundreds of kilometres) and temporal (weeks to months) scales. Overall, odontoceti species energy expenditure rates should be higher than baleen whales. For example, the total cost of transport, defined as the amount of fuel it takes to transport one unit of body weight over a unit distance (Schmidt-Nielsen, 1972), decreases linearly with increase in body mass. This indicates a higher energetic cost with locomotion of smaller dolphins when compared with larger whales (Williams, 1999, 2018).

The description above of the general strategy odontocetes follow to achieve energy balance is probably an oversimplification of reality, considering the diversity of species in the suborder, the different habitats they explore and the factors at play to achieve that energy balance. Nevertheless, it is probably a valid model to understand the role of oceanic islands in their life cycles, especially of oceanic species. Mannocci *et al.* (2014a) hypothesised that predators with high energetic demands might be constrained to select the most productive habitats to fulfil their high energetic requirements, while less active predators would be able to sustain their needs by exploiting habitats of either high or low productivity. To overcome the scarcity of data on cetacean metabolic requirements, Mannocci *et al.* (2014a) classified odontoceti species in their study based on their diving performances, which are closely related to their capacity to save oxygen by reducing their energetic costs. As such, three guilds were considered, the sperm whales and beaked whales with the lowest energy requirements among odontoceti species, followed by the Globicephalinae with intermediate energetic requirements and finally the Delphininae with the highest energetic requirements.

The role of open ocean insular environments in the life cycle of many open ocean cetacean species is expected to be determined by the trade-off between energetic benefits and energetic costs to access and use those habitats, at the spatial and temporal scale at which those species achieve energy balance. From an energetic point of view, it makes sense for animals to use an area that fulfils all their life cycle needs, without energetic costs with long displacements; however, many times that is not possible.

It can be hypothesised that open ocean cetaceans are attracted or drawn (i.e. they will approach and stay) to oceanic islands (or any other habitat within the diversity of habitats they use) as long as the insular environment gives them an advantage in achieving an energy balance in relation to open ocean habitat, both in terms of energy acquisition and minimization of energy costs, not only to survive but also to grow and reproduce (positive energy balance) (hypothesis 1). Furthermore, it is expected that the effect of attraction to those open ocean insular environments will be stronger in more isolated open ocean islands located in more oligotrophic seas and closer to the limits of the spatial and temporal scales at which these animals achieve energy balance (hypothesis 2).

The fixed predictable location of islands and their usually higher productivity when compared with surrounding offshore waters, especially in oligotrophic seas, should help open ocean cetacean species find prey more easily and thus increase their energetic acquisition. The higher availability and predictability in finding prey, enhanced by the islands' prey aggregating effect (Fiedler, 2009), should provide an energetic advantage to these species when compared with the energetic cost to search, find and capture more scattered prey in the much larger open ocean, especially for smaller species that have higher energetic costs with locomotion or lactating females with higher energetic needs (Reddy *et al.*, 1994; Srinivasan *et al.*, 2018; Williams, 2018). The islands can also offer sheltered areas (e.g. leeward side, bays and atolls) more benign to calves and where animals can rest, socialize and be more protected from predators (Srinivasan *et al.*, 2018) and adverse sea conditions, reducing energetic costs. Additionally, open ocean islands may be aggregating areas for cetacean groups where animals more easily find opportunities to mate with conspecifics.

However, the usually small size of open ocean islands, and the related marine insular environments, are expected to have limited prey biomass available to sustain many cetaceans for a long time. Seasonal change in local productivity will further restrict the number of cetaceans using open ocean islands, including resident groups or populations. As such, some animals may fulfil their energetic needs (survive, grow and reproduce) around specific oceanic islands (resident animals), but most animals will need to complement their energy acquisition requirements in other habitats as well (e.g. nearby islands, neighbouring archipelagos or sea mounts, offshore open ocean waters or continental waters). The need to move away will have energetic costs associated with travel, finding food in open ocean and diminished energy acquisition during those shorter or longer transiting periods (depending on the travelling distance) to habitats with higher prey predictability and availability. The different patterns of cetacean use of oceanic islands (e.g. residents, island associated, seasonal visitors, nomads) can be seen as the result of the different trade-offs animals of different species make or are forced to make to maintain their energy balance in open ocean environments. These may involve changing prey through the year in the same oceanic island habitat (e.g. Villegas-Amtmann *et al.*, 2011; Quérouil *et al.*, 2013), switching seasonally or opportunistically to other higher abundance prey habitats (e.g. Silva *et al.*, 2008; Tobeña *et al.*, 2016) or taking the chance in the open ocean because islands do not have enough prey during parts of the year. Those trade-offs may also include switching regularly between inshore and offshore waters (e.g. Karczmarski *et al.*, 2005; Baird *et al.*, 2011a; Woodworth *et al.*, 2012) or opportunistically and only for short periods passing by open ocean insular environments (e.g. Acevedo-Gutiérrez, 1999) because they do not offer them particular energetic advantages in relation to open ocean or other habitats. All these options are expected to have energetic costs, such as periodically switching to lower caloric value prey, displacements or higher effort to find and capture prey. These energetic costs may force animals sometimes, or periodically, to prioritize survival over growth and reproduction because of energy constraints (Lockyer, 2007), the latter expressed possibly as a seasonal breeding trend.

It can also be hypothesised that more isolated open ocean islands/archipelagos, especially in oligotrophic seas, will have lower density of cetaceans than equivalent islands/archipelagos much closer to other major predictable sources of food (e.g. major islands, archipelagos or seamount chains, more predictable (stable over time) fronts and upwelling areas, and continental masses) (hypothesis 3), which can be used more regularly by animals without compromising for long periods the energy balance necessary to survive, grow and reproduce. Isolated open ocean islands/archipelagos should be interpreted as islands/archipelagos at distances from other more predictable sources of food beyond the spatial and temporal scales at which those cetaceans achieve their energetic balance.

Hypotheses 1, 2 and 3 are not mutually exclusive. Hypothesis 1 assumes that cetaceans are attracted to open ocean islands if these habitats give them an energetic advantage when compared to the surrounding open ocean habitat (e.g. more food available). In practical terms, this means that densities are expected to be higher closer to the islands than in further offshore waters. Hypothesis 2 assumes that attraction will be greater to open ocean islands located in more oligotrophic seas, especially if they are far away from other reliable source of food, i.e. close to or beyond the energetic capacities of the animals. In this case, higher differential in densities between inshore and offshore waters is expected in those islands. This means that, for example, in Hawaii (in oligotrophic seas and far away from continents and the equatorial high productive areas) it would be expected to find much higher densities of animals closer to the islands, their only easily accessible and reliable source of food, than in nearby offshore waters. That would not be the case in islands closer to continental waters, where animals could easily travel from the islands to continental waters to feed and back, without serious energetic constraints. Hypothesis 3 assumes that more isolated open ocean islands/archipelagos, especially in oligotrophic seas, will have lower density of cetaceans than equivalent islands/archipelagos much closer to other major predictable sources of food (e.g. major islands, archipelagos or seamount chains, fronts and upwelling areas, and continental masses). In this case, the inshore/offshore densities in the islands are not being compared as in hypotheses 1 and 2. Instead, the densities between isolated islands far from other predictable sources of food are being compared to islands close to other predictable sources of food. The latter can be used more regularly by animals to feed without compromising for long periods their energy balance. The lack of data on densities or other evidence of higher or lower presence of a species in inshore/offshore waters in most open ocean archipelagos makes a systematic approach to support or refute the above-mentioned hypotheses impossible. For archipelagos for which data is available the comparison is hampered by comparability issues among studies. Thus, the objective of the comparison exercise of densities among open ocean archipelagos in the next section is not to obtain strong evidence to support or refute the hypotheses formulated, but to debate the cetacean species ecological patterns of use among open ocean islands and in comparison with other habitats (e.g. insular inshore and offshore waters, continental waters and open ocean, at different latitudes), contextualized by the hypotheses, which consider the species' general energetic requirements.

2.3 THE ROLE OF OCEANIC ISLANDS IN THE CONTEXT OF CETACEAN DISTRIBUTION AND LIFE CYCLES

The high cetacean species diversity seen around open ocean islands and archipelagos, especially in subtropical and tropical waters, could be an indication of their importance for these species. However, this is not sufficient because their presence could be solely the consequence of much larger spatial scale processes influenced for example by latitude or oceanography. It is important to understand which advantages open ocean insular marine environments can offer (or not) to cetaceans in the context of their energetic requirements and life cycle demands, when compared with other habitats such as open ocean waters and continental slope and shelf waters. Furthermore, efforts should be made to contextualize the observed and inferred ecological patterns in open ocean islands with the energetic requirements of the different species or groups of species and their ecological/biological characteristics and limitations, and to present evidence to support or refute the hypotheses raised in Section 2.2 to explain the observed and inferred ecological patterns in open ocean islands.

As well described in the literature, and shown by Pompa *et al.* (2011), latitude and distance to continental masses are important variables explaining the distribution of cetacean species in the world's oceans. In simple terms, latitude is related to changes in primary productivity and stability of the water column because of latitudinal differences in sunlight incidence, and distance to continental masses is related to higher productivity in neritic waters and continental upwelling areas, and the availability and size of shelf and slope continental habitats when compared with open ocean marine environments. Additionally, the seasonal change in sunlight incidence in subtropical, warm temperate and higher latitude oceans results in seasonal changes in primary productivity (spring bloom) which in turn promotes seasonal fluctuations in prey availability in the open ocean at those latitudes. The role of open ocean islands should be considered in the context of these two major large-scale influences and their seasonal fluctuations.

Another important aspect to consider is the general habitat preferences of cetacean species. Some species are predominantly coastal, living in continental neritic waters (< 200m depth), like the harbour porpoise *Phocoena phocoena* (Bjørge and Tolley, 2018) or humpback dolphins (Parra and Jefferson, 2018). Other species are predominantly oceanic, living in pelagic habitats beyond the continental shelf (> 200 m depth), including the continental slope, shelf break, open ocean islands, seamounts and the deep offshore seas (e.g. beaked whales, the sperm whale *Physeter macrocephalus* or the striped dolphin *Stenella coeruleoalba*). Other species explore both coastal habitats and open ocean habitats, with some of them having populations, ecotypes or subspecies living in either continental neritic waters or open ocean habitats. Such is the case for the bottlenose dolphin *Tursiops truncatus*, the Atlantic spotted dolphin *S.*

frontalis, the pantropical spotted dolphin *S. attenuata* or the Bryde's whale (e.g. Perrin *et al.*, 2009b; Louis *et al.*, 2014; Viricel and Rosel, 2014; Freitas and Penry, 2021). For the purpose of this review, most emphasis will be given to oceanic species or oceanic populations of species living in both neritic and pelagic environments. To facilitate the comparison between open ocean islands/archipelagos and cetacean use of those insular marine environments, some relevant characteristics of open ocean islands/archipelagos and some of the relevant local ecological characteristics of cetacean species are summarized in Table I.1.1 and Table I.1.2 (Appendix I), respectively. In Figure 2.2, some of the characteristics of open ocean islands/archipelagos used in the study are represented graphically in relation to their latitudinal position and distance from the continents.

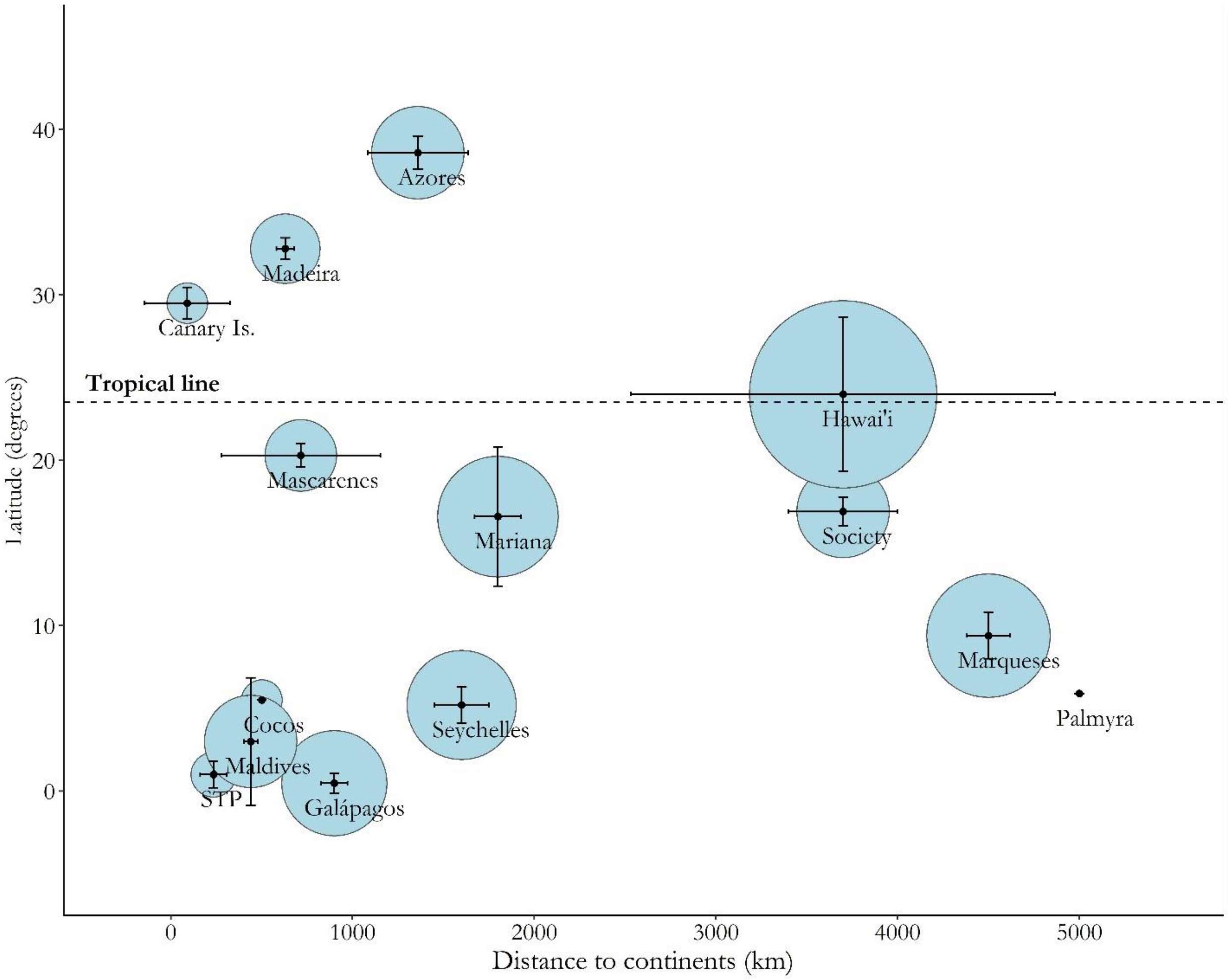

Figure 2.2. Representation of some of characteristics of the open ocean islands for which cetacean species were compared in this study. The location of each island, archipelago or atoll is represented by latitude on the y axis and distance to continents on the x axis. The vertical and horizontal error bars represent the latitudinal and longitudinal span, respectively, of these insular features, while the blue circle represent the distance to the closest islands or seamounts, in km (degree of isolation).

Baleen whales

Open ocean islands do not seem to be particularly important in the lives of baleen whales, except for humpback whales and, possibly, Bryde's whales. In general, their distributions and seasonal migrations seem to be determined by processes that are dynamic in time (seasonal productivity associated with higher latitudes and continental waters) and have a much larger spatial scale (hundreds to thousands of kilometres) than the spatial scale of islands (tens to hundreds of kilometres). This is possible because baleen whales are able to achieve and maintain energetic balance over large spatial (hundreds to thousands of kilometres) and temporal (months to years) scales by following a strategy with variations in energy balance, i.e. they gain energy through the build-up of energy reserves while feeding in seasonally highly productive grounds at higher latitudes, followed by fasting during migration and reproduction in low latitude breeding grounds (Costa and Maresh, 2018). Bryde's whales might be an exception due to their more restricted tropical distribution and to their possibly more income-breeder-like strategy. Nevertheless, open ocean islands and continental islands habitats falling within the higher productivity areas associated with the feeding grounds are expected to be used by these species to forage as much as the surrounding offshore waters (e.g. Ví-kingsson *et al.*, 2015; Bestley *et al.*, 2019; Todd and Williamson, 2022).

Open ocean islands are, however, important in the life cycle of humpback whales. Many winter grounds of this species are around oceanic islands in tropical waters where they mate, calve and nurse their young (Clapham, 2018). Open ocean islands may also be important for Bryde's whales as is shown by their occurrence around islands like the Galapagos, Maldives, Bonin Islands, Hawaiian Islands and the Macaronesia archipelagos (Omura, 1962; Palacios, 2003; Anderson, 2005; Barlow, 2006; Steiner *et al.*, 2007; Freitas *et al.*, 2012; Bradford *et al.*, 2017). However, Bryde's whales in the Hawaiian Islands have mostly been seen in offshore waters, indicating they might not be particularly drawn to the inshore waters of the archipelago (Barlow, 2006; Bradford *et al.*, 2017). The seasonal presence (spring-summer-autumn) of the species in Madeira and the Canary Islands, where the animals have been seen with calves and feeding close to shore (Freitas and Penry, 2021), is an indication that these archipelagos might be feeding grounds or part of much wider feeding grounds of the species in the Central East Atlantic.

Oceanic dolphins

Open ocean islands closer to productive equatorial waters do not seem to be particularly attractive to open ocean dolphins (e.g. pantropical dolphin, spinner dolphin, common dolphin, and striped dolphin) and the bottlenose dolphin when compared with offshore waters, as suggested by their wide distribution of abundance in the equatorial waters of the Eastern Tropical Pacific (ETP), West Tropical Indian Ocean and French Polynesia (FP) (e.g. Wade and Gerrodette, 1993; Ballance and

Pitman, 1998; Mannocci *et al.*, 2014a, 2014b)(Figure 2.3 - Figure 2.6). The information available on the presence and use of open ocean islands near the equator (e.g. Cocos Island, Galápagos, Maldives, Marquese Islands) by these species (Acevedo-Gutiérrez, 1999; Smith and Whitehead, 1999; Anderson, 2005; Gannier, 2009), supports the idea that they take advantage of both insular and offshore waters to feed and thus cover their energetic needs, without a particular dependence on the islands. Nevertheless, open ocean islands close to the equator may be important for dolphin species for reasons other than feeding, such as socialising, mating, calving and protection from predators (Karczmarski *et al.*, 2005).

As other delphinids, short-finned pilot whales *Globicephala macrorhynchus* (henceforward called pilot whales) are usually found in tropical and subtropical waters of the world (Olson, 2018), being reported around many open ocean islands across their distributional range (e.g. Gannier, 2002; Anderson, 2005; Kiszka *et al.*, 2007; Freitas *et al.*, 2012; Baird *et al.*, 2013a; Servidio *et al.*, 2019). Their distribution around open ocean islands is further offshore, with preferential depths ranging from 1 000 to 2 500 m being consistently reported for these archipelagos (e.g. Dulau-Drouot *et al.*, 2008; Alves, 2013; Baird *et al.*, 2013a; Freitas *et al.*, 2014a; Servidio, 2014). However, little is known about pilot whales around open ocean islands closer to the equator (Figure 2.3, bottom, panels g – i).

The overall decrease in density of both Delphininae (rough-toothed dolphin, pantropical spotted dolphin, spinner dolphin, common bottlenose dolphin, Fraser's dolphin) and Globicephalinae (pygmy killer whale, melon-headed whale, pilot whale, false killer whale, Risso's dolphin, killer whale) with distance from equatorial waters has been found in both the Southwest Indian Ocean (SWIO) and French Polynesia (FP), and with distance from continents in the SWIO (Mannocci *et al.*, 2014b, 2014a). Furthermore, spinner dolphin, pantropical dolphin and pilot whale densities in the ETP were many times higher than in Hawai'i (Table I.1.2, Appendix I) (Wade and Gerrodette, 1993; Barlow, 2006), reflecting probably the confounding influence of latitude and distance to continents.

The densities of dolphin species (bottlenose dolphin, pantropical dolphin and spinner dolphin) and the pilot whale in the Main Hawaiian Islands inshore waters was several times higher than the density of these species in the offshore Hawaiian EEZ (Figure 2.3 - Figure 2.5, panel f ; Table I.1.2, Appendix I) (Barlow, 2006). The striped dolphin was the exception with a mostly offshore distribution (Figure 2.6). This evidence gives support to hypotheses 1 and 2 (Section 2.2), considering the geographic isolation of that archipelago, its oligotrophic waters and distance from more productive equatorial (> 1 800 km) and continental waters (~3 700 km).

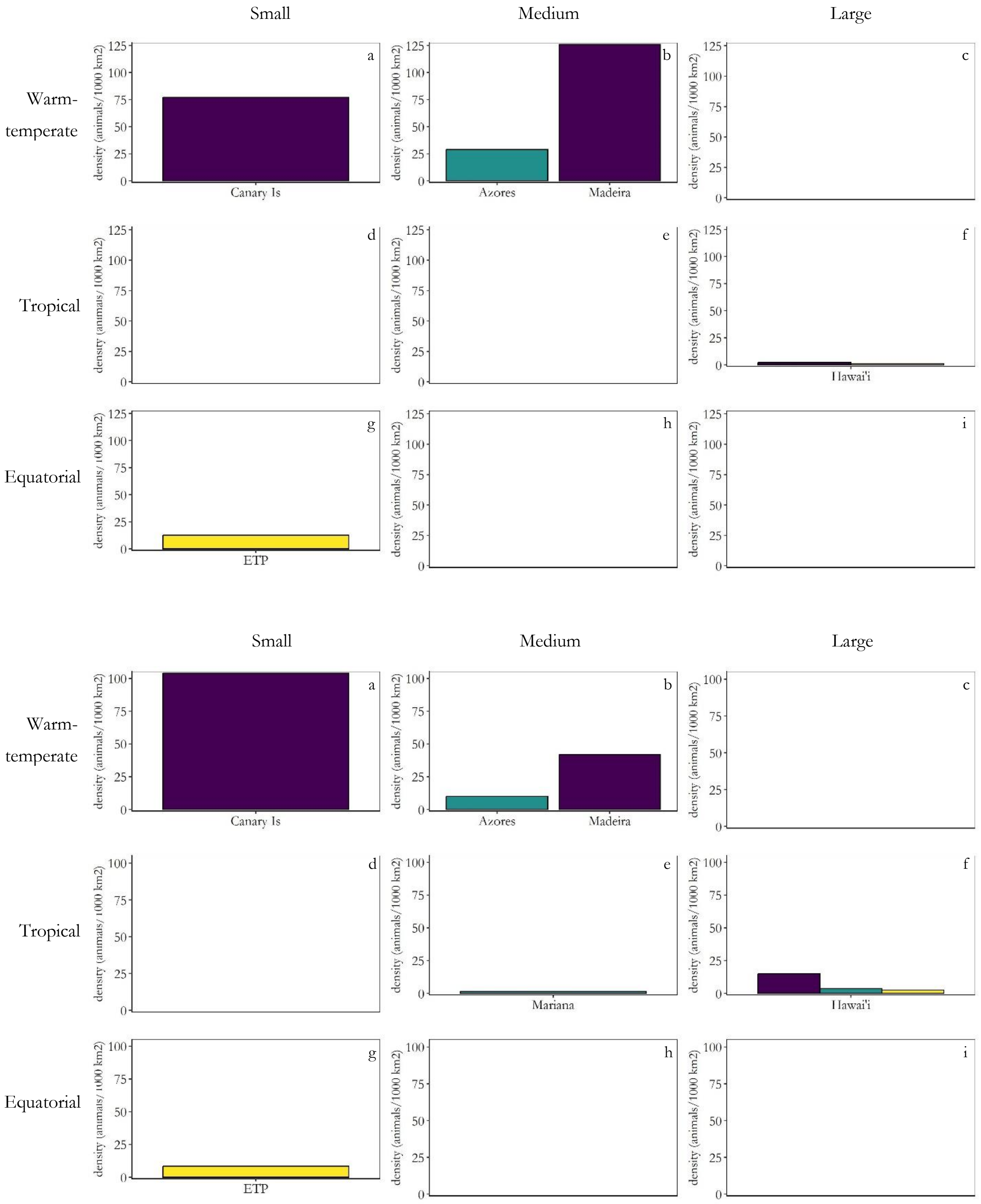

Figure 2.3. Densities of the bottlenose dolphin (top) and short-finned pilot whale (bottom) in locations (identified at the x axis of each barplot) at different latitudes (mean latitude of the locations: Equatorial – 0º - 10º S/N; Tropical – 10º - 24º S/N; Warm-temperate – > 24º S/N) and shortest distance from continents (Small – < 500 km; Medium – 500 - 2 000 km; Large > 2 000 km). The colours of the bars identify the local coverage of the surveys that generated the estimates: purple – inshore; green – inshore/offshore; yellow – offshore.

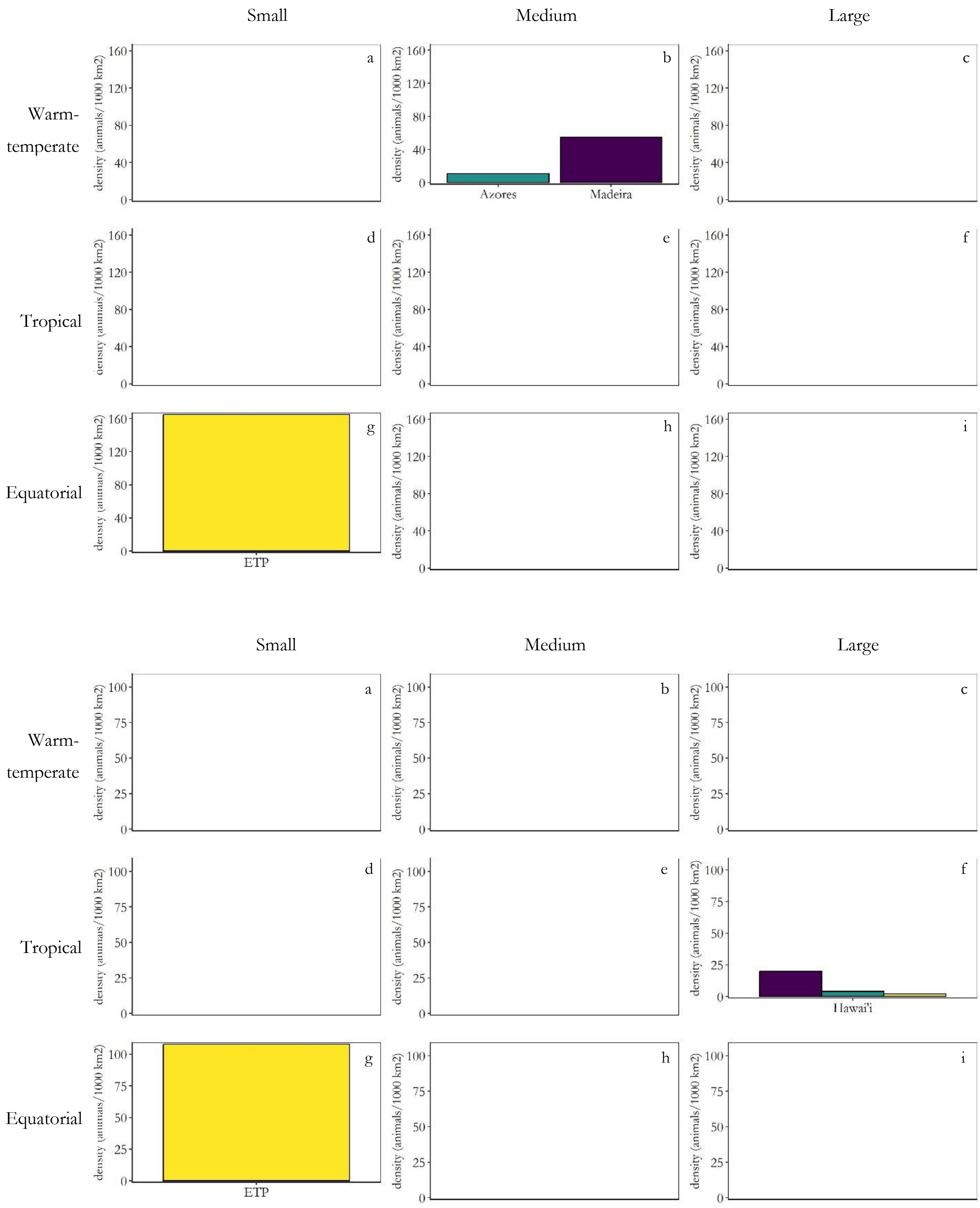

Figure 2.4. Densities of the common dolphin (top) and pantropical spotted dolphin (bottom) in locations (identified at the x axis of each barplot) at different latitudes (mean latitude of the locations: Equatorial – 0º - 10º S/N; Tropical – 10º - 24º S/N; Warm-temperate – > 24º S/N) and shortest distance from continents (Small – < 500 km; Medium – 500 - 2 000 km; Large > 2 000 km). The colours of the bars identify the local coverage of the surveys that generated the estimates: purple – inshore; green – inshore/offshore; yellow – offshore.

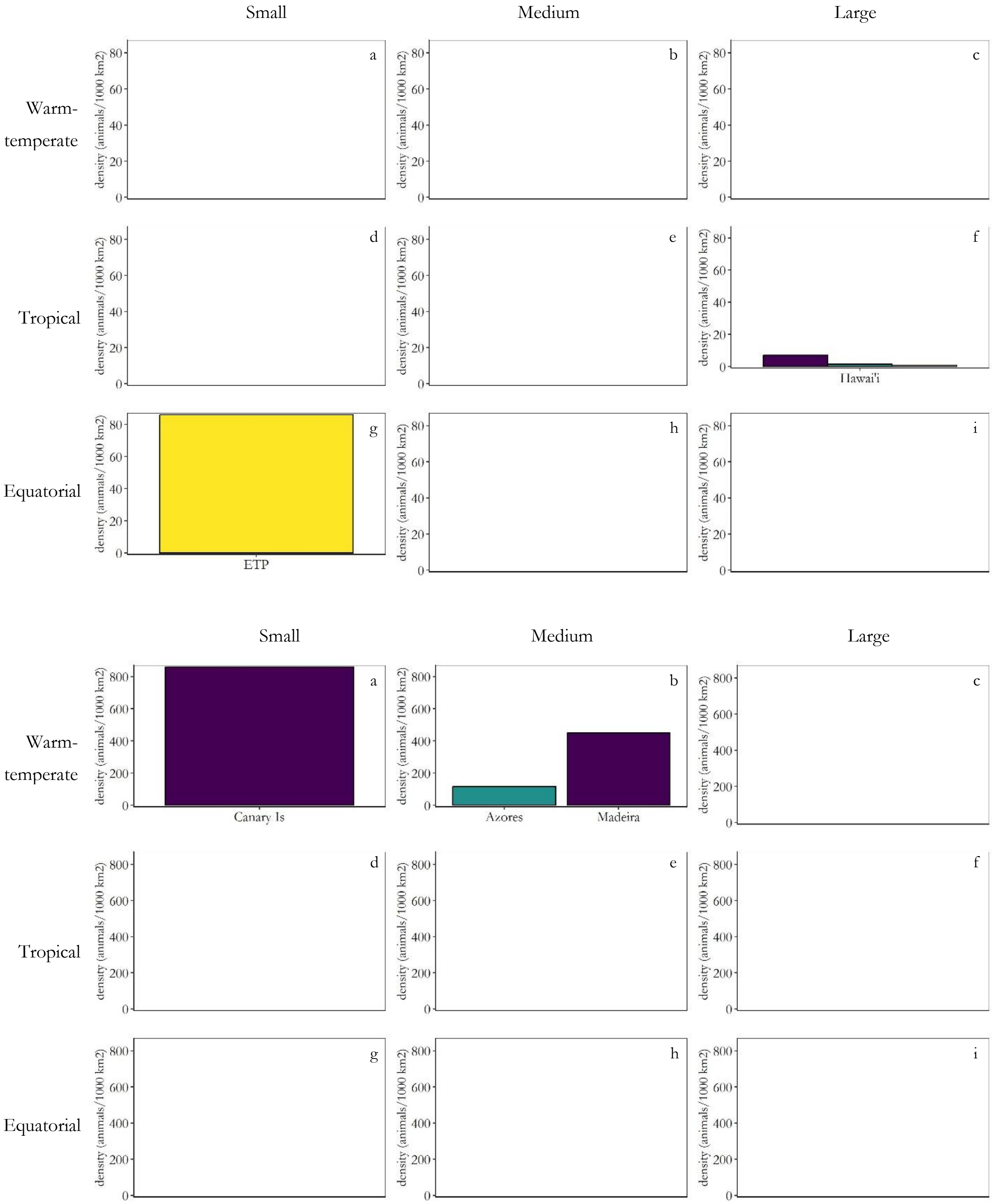

Figure 2.5. Densities of the spinner dolphins (top) and Atlantic spotted dolphin (bottom) in locations (identified at the x axis of each barplot) at different latitudes (mean latitude of the locations: Equatorial – 0º - 10º S/N; Tropical – 10º - 24º S/N; Warm-temperate – > 24º S/N) and shortest distance from continents (Small – < 500 km; Medium – 500 - 2 000 km; Large > 2 000 km). The colours of the bars identify the local coverage of the surveys that generated the estimates: purple – inshore; green – inshore/offshore; yellow – offshore.

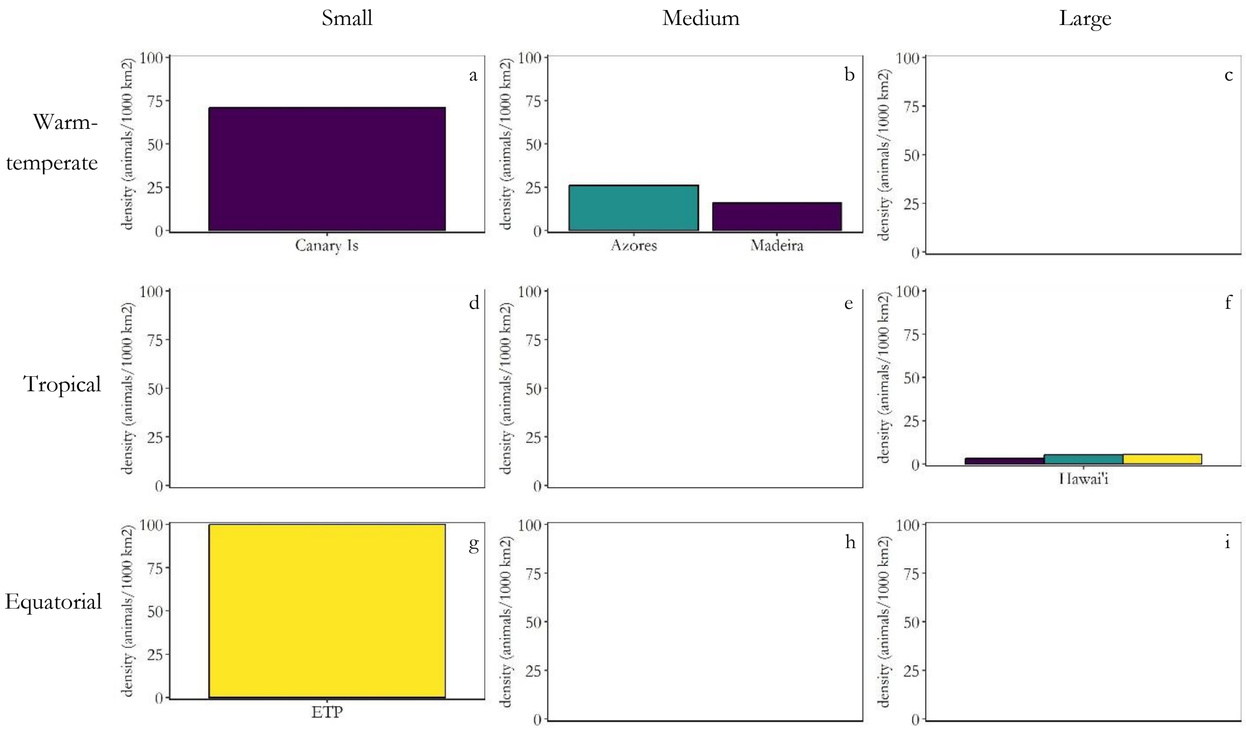

Figure 2.6. Densities of the striped dolphins in locations (identified at the x axis of each barplot) at different latitudes (mean latitude of the locations: Equatorial – 0º - 10º S/N; Tropical – 10º - 24º S/N; Warm-temperate – > 24º S/N) and shortest distance from continents (Small – < 500 km; Medium – 500 - 2 000 km; Large > 2 000 km). The colours of the bars identify the local coverage of the surveys that generated the estimates: purple – inshore; green – inshore/offshore; yellow – offshore.

Dolphin species also have an important presence in offshore waters of Macaronesia (Madeira, Azores and the Canary Islands), although it is not possible to compare with inshore waters because of the lack of abundance estimates for the former. However, a study using cargo ships as platforms of opportunity, covering mostly offshore waters of Macaronesia from April to October, showed the bottlenose dolphin's preference for coastal waters, but also recorded their presence frequently in the high seas (Correia *et al.*, 2020). According to the same study, the common dolphin and the Atlantic spotted dolphin had a relevant presence in Macaronesia offshore waters.

Dolphin species (bottlenose dolphin, pantropical dolphin, spinner dolphin and striped dolphin) and *Globicephala sp.* densities in the ETP (closer to the equator and to continental waters) were consistently higher than in the Hawaiian Islands, many times more for some species (Figure 2.3 – Figure 2.6, panels f and g; Table I.1.2, in Appendix I; Wade and Gerrodette, 1993; Barlow, 2006). The same pattern is also seen when the estimated densities of bottlenose dolphin, Atlantic spotted dolphin, striped dolphin, and pilot whales are compared among the Canary Islands, Madeira (both closer to African continental waters) and the Azores (~1 360 km from continental shores) (Figure 2.3, Figure 2.5 and Figure 2.6; Table I.1.2, Appendix I) (Freitas *et al.*, 2014b; Servidio, 2014; Freitas *et al.* in prep). According to hypothesis 3 (Section 2.2), the more isolated Hawaiian Islands in the Pacific and the Azores Islands in the Atlantic, are expected to have lower densities of animals when compared to equivalent habitats closer to continents (predictable source of food), such as the ETP in the Pacific and Madeira/Canary Islands in the Atlantic. The above evidence gives some support to this hypothesis for dolphin species and the pilot whale, but with a clear influence of continental masses.

Small delphinid species and the pilot whale are expected to be closer to the higher end of cetacean energy expenditure range when compared with beaked whales, sperm whales and baleen whales (Mannocci *et al.*, 2014b; Costa and Maresh, 2018). They are also income breeders which means they alternate between foraging and feeding their young in short intervals of minutes to hours (Costa and Maresh, 2018). As such, to maintain energy balance they need to find and consume prey more frequently while travelling less than baleen whales. It is advantageous for individuals/groups of these species to have their distributional range encompassing a network of more predictable sources of prey (e.g. islands, seamounts and persistent fronts) at distances from each other and with enough prey density to allow them to maintain energetic balance. Although open ocean dolphins may opportunistically find prey in the open ocean, it is probably neither frequently enough nor in the quantities needed to sustain them, otherwise their distribution would be more homogenous throughout the oceans of the world and open ocean dolphins would not be drawn to more predictable sources of food, such as open ocean islands. Furthermore, access to deeper ocean layers (mesopelagic and bathypelagic) has higher energetic costs to delphinids than to the deep diving species, limiting their access to these resources in deep open ocean waters. Consequently, oligotrophic open ocean seas may be an obstacle to the movement of open ocean dolphins between predictable habitats (able to provide food more reliably) that are located at larger spatial and temporal scales than those at which dolphins can maintain their energy balance. For example, although Palmyra Atoll (close to the equator) is much closer to the Hawaiian Islands (tropical oligotrophic waters) than to the western Pacific (closer to continental waters), the bottlenose dolphins sampled in the atoll shared more haplotypes with the western Pacific, suggesting higher gene flow between the atoll and the western Pacific than with the Hawaiian Islands (Martien *et al.*, 2012). This could be explained by the equatorial waters being a more reliable and consistent source of prey that would allow animals to travel longer distances without jeopardising their positive energetic budget. On the contrary, for animals to reach Hawaiian Islands from the Palmyra atoll, they would need to travel across large stretches of low productivity waters with much lower chances of finding prey in open waters, being more dependent on features, such as seamounts and islands as predictable sources of prey, that are however very far apart.

In contrast, the lack of genetic differentiation among bottlenose dolphins, common dolphins and spotted dolphins using the Macaronesia archipelagos (all part of large pelagic populations) (Quérouil *et al.*, 2007, 2010; Moura *et al.*, 2013; Louis *et al.*, 2014) could be explained by the movement of animals being energetically viable because of the much smaller distances (a few hundred kilometres) among archipelagos, and between archipelagos and other predictable sources of prey, such as seamounts, continental waters and the Azores current/front (Table I.1.1, Appendix I).

Unlike other small dolphin species, the striped dolphin does not seem to be so attracted to open ocean islands and so dependent on them to achieve energetic balance, not even in tropical oligotrophic seas. For example, in the Hawaiian Islands inshore waters they are seen mostly at depths greater than 3 000 m (Baird *et al.*, 2013a) and their average density in the offshore waters is almost twice that in waters further inshore around the main islands (Figure 2.6; Table I.1.2, Appendix I), contradicting hypotheses 1 and 2.

Deep divers

Beaked whales and sperm whales are among the deep diving species using open ocean islands marine habitats. However, open ocean islands do not seem to be, in general, more attractive to these deep diving species than open ocean habitats. Their wide distribution of abundance throughout the ETP and in offshore waters around Hawai'i, SWIO, FP and Macaronesia (e.g. Wade and Genodette, 1993; Barlow, 2006; Mannocci *et al.*, 2014a, 2014b; Correia *et al.*, 2020; Esteban *et al* in prep), suggests a relatively more homogeneous distribution in offshore waters of equatorial, tropical and warm temperate waters of the world when compared, for example, with delphinids. However, in the case of the sperm whale the evidence also supports a preference for more productive waters closer to the continents with higher relative abundances when compared with open ocean waters (Wade and Gerrodette, 1993; Whitehead *et al.*, 1997; Correia, 2020). The overall density of beaked whales and sperm whales is actually 3 times and <2 times higher, respectively, in the Hawaiian Islands EEZ than in the ETP (Figure 2.7; Table I.1.2, Appendix I) (Wade and Gerrodette, 1993). No evidence was found in the literature to suggest a similar preference of beaked whale species for continental waters near the equator. On the contrary, beaked whale echolocation signals were the most frequently detected group of species by passive acoustic monitoring in a remote seamount chain located in the Equatorial Central Pacific, near the Northern line islands (Baumann-Pickering *et al.*, 2016).

The distributions of sperm whale-beaked whale guild (Blainville's beaked whale, Cuvier's beaked whale, sperm whale, pygmy sperm whale, dwarf sperm whale) predicted by Mannocci *et al.* (2014b) for the SWIO and by Mannocci *et al.* (2014a) for FP, showed a pattern of higher densities closer to continents and the equator, as it did for the Delphinidae and Globicephalinae guilds, but with lower overall densities. However, the ratio between the two surveyed areas for sperm whales-beaked whales was 1.75, much lower than the ratio for Delphininae (15.6) and for Globicephalinae (7.6) (Lambert *et al.*, 2014). The sperm whale-beaked whale predicted distribution in the SWIO and FP had a much lower mean relative density than the Delphininae and Globicephalinae, with a more homogeneous distribution (Lambert *et al.*, 2014).

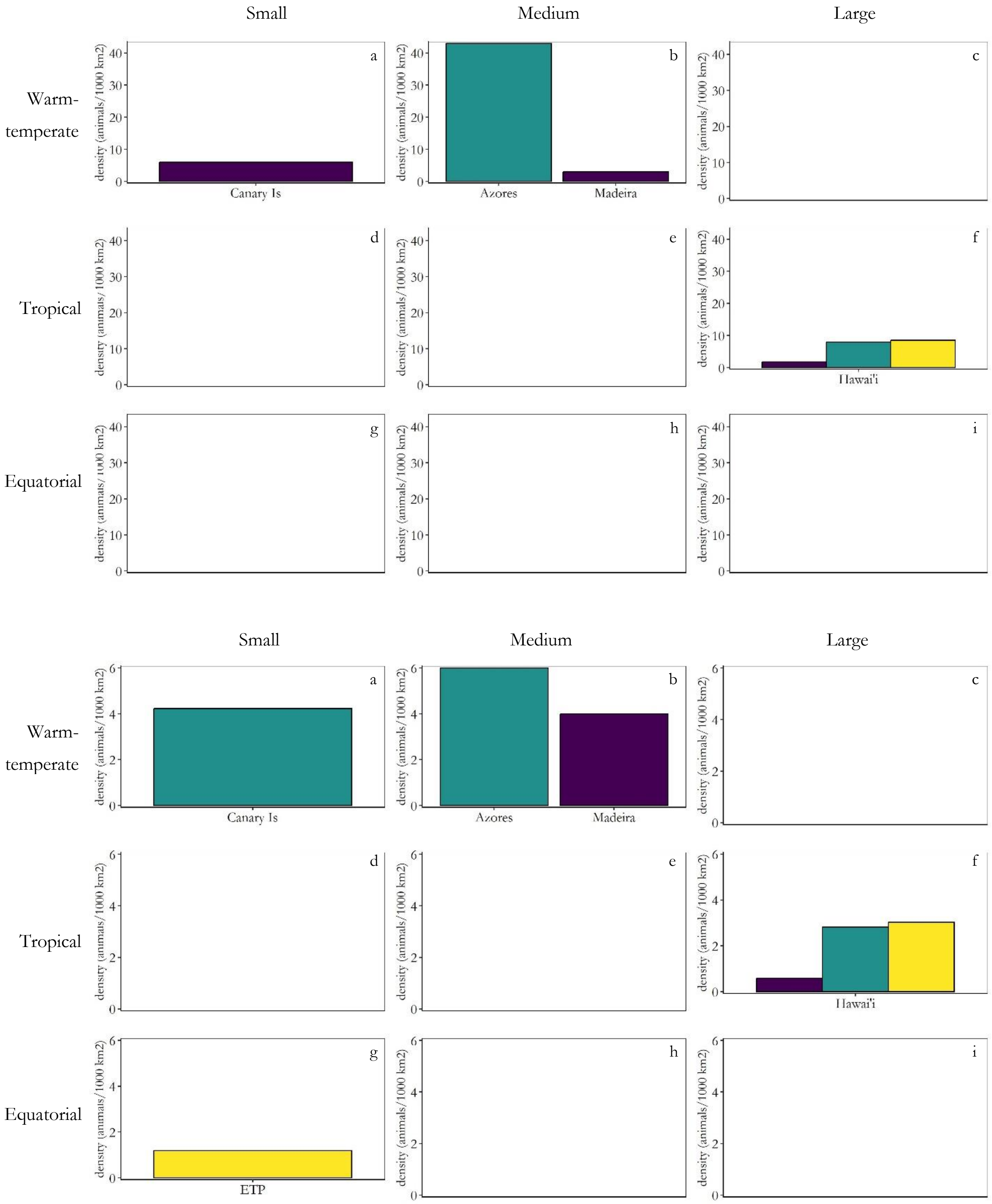

Figure 2.7. Densities of the beaked whales (Ziphiidae) (top) and sperm whales (bottom) in locations (identified at the x axis of each barplot) at different latitudes (mean latitude of the locations: Equatorial – 0º - 10º S/N; Tropical – 10º - 24º S/N; Warm-temperate – > 24º S/N) and shortest distance from continents (Small – < 500 km; Medium – 500 - 2 000 km; Large > 2 000 km). The colours of the bars identify the local coverage of the surveys that generated the estimates: purple – inshore; green – inshore/offshore; yellow – offshore.

In Macaronesia archipelagos, the density of sperm whales was one-third higher in the Azores than in in Madeira and the Canary Islands (closer to continental waters), however the estimates in Azores were from a survey covering both inshore and offshore waters while in Madeira and the Canary Islands were from surveys covering mostly inshore waters (Figure 2.7, bottom ; Table I.1.2, Appendix I) (Fais *et al.*, 2016; Esteban *et al* in prep).

Like the striped dolphin, beaked whales and sperm whales do not seem to be particularly attracted to open ocean islands and thus dependent on them to achieve energetic balance, not even in more oligotrophic seas. For example, sperm whales in the Hawaiian Islands inshore waters are mostly seen at depths greater than 2 500 m (Baird *et al.*, 2013a) and their average density in the offshore waters of the archipelago is around five times higher than in further inshore waters around the main islands (Table I.1.2, Appendix I) (Barlow, 2006). The species mainly offshore distribution is supported by satellite telemetry evidence, which also associated the tracked animals with seamounts and cold core cyclonic eddies, presumably for foraging (Rone *et al.*, 2015). No consistent pattern was identified from the tracks that would indicate a particular association with the islands, thus suggesting the animals using Hawaiian waters are part of a wide-ranging population that likely extends across much of the Central Pacific (Rone *et al.*, 2015). Whaling and discovery tag data suggest that sperm whales in the North Pacific are nomadic (Mizroch and Rice, 2013).

The sperm whale is known to have a year-round presence in Azores, Madeira and the Canary Islands (e.g. Freitas *et al.*, 2004b; Martín *et al.*, 2011; Silva *et al.*, 2014). However, it seems to be an intermittent presence consistent with a nomadic behaviour as in the Pacific, with groups of animals passing by and staying in an area or archipelago from days to a few weeks. That is the case in the Azores and Madeira (Freitas *et al.*, 2004a; Silva *et al.*, 2014) and seems to be the case in the Canary Islands (Fais *et al.*, 2016).

In spite of the existence in the Main Hawaiian Islands of island associated populations of Blainville's and Cuvier's beaked whales, beaked whales were detected many times more in offshore waters than in the main islands in an equal coverage line-transect survey (Barlow, 2006), suggesting a higher density of these species offshore than closer to the islands. The results of surveys carried out from cargo ships connecting mainland Portugal and the Macaronesia archipelagos also indicate a preference of Cuvier's beaked whale for deep waters far from the coast, with a preference for seamounts (Correia *et al.*, 2020). These results are supported by other surveys in the area (Boisseau *et al.*, 2009; Silva *et al.*, 2014; Cunha and Freitas, 2017).

The more homogenous distribution of sperm whales and beaked whales in tropical and warm temperate open ocean waters when compared with delphinids, suggests that these species maintain their energy balance over larger spatial and temporal scales than the delphinids or have access to prey in the open ocean which are less available to the delphinids, or both. These deep diving species' larger size and thicker blubber layer could function as energy reserves that would allow them to endure longer periods and have wider displacements without feeding while moving between locations with more predictable prey. However, according to Koopman (2007) the main role of beaked and sperm whales' blubber is not to store energy, but may represent a physiological and mechanical adaptation to deep diving. Furthermore, as for the delphinids, these deep diving species are income breeders, needing to alternate between foraging and feeding their young over short time intervals (Costa and Maresh, 2018). As such, it seems more plausible that their ability to dive deep with lower energy costs (Mannocci *et al.*, 2014b) gives them easier and less costly access to mesopelagic and bathypelagic resources available in deep open ocean waters, than to delphinids.

Although, generally, both beaked whales and sperm whales do not seem to be particularly attracted to, or very dependent, on open ocean islands, there is still evidence that these habitats might be important in these species' life cycles. In the Azores, groups of female sperm whales accompanied by juveniles and calves were frequently observed, sometimes foraging, in the Central islands group every month of the year (Silva *et al.*, 2014), giving support to the suggestion that the Azores are a calving and possibly mating ground, as proposed by Clarke (1956). There is evidence of Madeira and Canary Islands coastal waters being used by the species to feed, socialize, rest and calve (e.g. Freitas *et al.*, 2004b; Carrillo *et al.*, 2010; Martín *et al.*, 2011). There is also evidence of several resident individuals or populations of beaked whales in open ocean islands. In the Canary Islands, the Blainville's beaked whale is present year-round (e.g. Carrillo and Tejedor, 2004; Carrillo *et al.*, 2010; Fais *et al.*, 2010; SECAC, 2014) and the archipelago may be a calving area (Tejedor *et al.*, 2011; SECAC, 2014). In the Hawaiian archipelago, the results of a photo-identification study of Cuvier's and Blainville's beaked whales spanning over a period of 21 years, suggest long-term site fidelity to the Island of Hawai'i, primarily from adult females of both species (McSweeney *et al.*, 2007).

2.4 HOW CETACEAN SPECIES USE AND SHARE ISLAND MARINE HABITATS AND RESOURCES

Open ocean islands tend to be relatively small but can have a wide variety of local marine habitats including coastal, insular shelf, inside lagoons in atolls, insular slopes, canyons, local upwelling areas, island induced eddies areas and nearby deep open ocean. This multitude of habitats have specific environmental characteristics and communities of organisms living in them, which provide a diversity of prey and conditions available to be explored by cetacean species with different characteristics and ecological needs. However, the limited size of those insular habitats, with limited productivity (especially in oligotrophic seas) and consequently prey availability, is expected to limit the density of animals of each cetacean species exploring and dependent on those habitats. As a result, local intra and interspecific competition among sympatric cetacean species is a possibility, especially among cetacean species with more similar ecological needs. As such, open ocean islands can be ideal locations to study and understand how cetacean species (populations) share (or compete for) resources, including minimizing competitive exclusion and niche partitioning among the species using those locations. Furthermore, the usually small size of open ocean marine environments make it more logistically feasible to collect data to study these processes.

Most studies in open ocean islands either focus on single species abundance, distribution, site fidelity and/or movements around oceanic islands (e.g. McSweeney *et al.*, 2007; Silva *et al.*, 2008; Baird *et al.*, 2011b; Tobeña *et al.*, 2014) or on cetacean diversity, relative abundance and general distribution (e.g. Gannier, 2000; Freitas *et al.*, 2004b; Carrillo *et al.*, 2010; 2011; Baird *et al.*, 2013a; Silva *et al.*, 2014). Some studies go one step further by investigating relationships between single species distribution and local habitat features (e.g. depth, distance from coast) and modelling habitat use, while others have studied particular aspects of how cetaceans' species explore marine habitats around islands, e.g. diving behaviour (e.g. Aguilar de Soto *et al.*, 2008; Johnson *et al.*, 2008; Servidio, 2014; Abecassis *et al.*, 2015). The results of these studies indicate that different groups of species have particular habitat preferences in open ocean islands, which imply some habitat segregation among them, such as preferential depths and distances from the coast, specific habitats (e.g. atolls, canyons) or sides of an island.

More recent research has started to study multispecies habitat preferences and modelling habitat suitability to understand how these species use open ocean marine environments (e.g. Tobeña *et al.*, 2016; Correia, 2020), including environmental niche analysis (Prieto *et al.*, 2017). For example, the latter authors using environmental niche models (MaxEnt) estimated the overlap between the habitat suitability predictions of baleen whales in the Azores. However, these models only consider the spatial dimension of the species' ecological niche thus producing an incomplete view of how sympatric cetacean species share local resources in oceanic islands.

Others studies have focused on the trophic dimension of the species' ecological niches by studying trophic niche overlap (or discrimination) among different cetacean species in oceanic islands using stable isotopes, fatty acids and stomach content analysis (e.g. Kiszka *et al.*, 2010; Quérouil *et al.*, 2013; Young *et al.*, 2017). These direct and indirect diet studies bring an important perspective on how cetaceans share and minimize competition for food resources in the small insular habitats. For instances, Quérouil *et al.* (2013) confirmed that the common dolphin and the Atlantic spotted dolphin in the Azores feed during summer on different resources, based on Fatty Acid (FA) and nitrogen Stable Isotopes (SI) profiles. Bode *et al.* (2022) studied the trophic positions of different delphinidae species in the Macaronesia archipelagos and their evolution over time.

To my knowledge, only two scientific multispecies studies bring together different methodological approaches to improve the ecological understanding of how cetaceans use oceanic islands' marine environments, both using Mayotte island in the Southwest Indian ocean as the case study (Gross *et al.*, 2009; Kiszka *et al.*, 2011). First, Gross *et al.* (2009) investigated habitat preferences of the Indo-Pacific bottlenose dolphin, the pantropical spotted dolphin, spinner dolphin and the melon-headed whale by analysing sighting data and the associated physiographic characteristics, as well as the resources partitioning among those species by analysing carbon and nitrogen stable isotope ratios from skin and blubber samples. Second, Kiszka *et al.* (2011), studied the ecological niche segregation within the local community of sympatric dolphins (same dolphin species as the previous study plus Fraser's dolphin *Lagenodelphis hosei*), using three dimensions to describe and compare the ecological niche of these species, namely physiography (habitat), diel behavioural budgets (time) and carbon and nitrogen stable isotopes (resources) from skin and blubber samples. Presently, most of the studies addressing the description and segregation (overlap) of cetaceans' ecological niches are in continental waters (e.g. Friedlaender *et al.*, 2009; Weir *et al.*, 2012; Méndez-Fernandez *et al.*, 2013; Giménez *et al.*, 2017a, 2018b).

Multispecies studies are important to improve the understanding of the ecological role and importance of different habitats to cetaceans, among them open ocean islands. Those studies should integrate several methodological approaches to address crucial aspects of cetacean biology and ecology, among them habitat use, temporal and spatial distribution, diet, trophic relationships and energy requirements. The combination of these aspects is expected to bring insights on how cetacean species deal with the challenges of limited resources in open ocean islands, including minimizing competitive exclusion and niche partitioning. The characteristics of open ocean islands, and their geographic context, are also crucial to understand cetacean species' patterns of use of those habitats (Section 2.1 and Section 2.3), as those patterns of use are expected to be determined by the trade-off between energetic benefits (prey intake) and energetic costs to access and use those habitats (Section 2.2).

Chapter 3

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THE ABUNDANCE, SURVIVAL, HABITAT USE OF BRYDE'S WHALES IN MADEIRA ARCHIPELAGO AND INDIVIDUAL MOVEMENTS IN THE SURROUNDING BASIN

THE ABUNDANCE, SURVIVAL, HABITAT USE OF BRYDE'S WHALES IN MADEIRA ARCHIPELAGO AND INDIVIDUAL MOVEMENTS IN THE SURROUNDING BASIN

3.1 INTRODUCTION

The Bryde's whale, *Balaenoptera edeni* Anderson, 1878, is a medium-sized baleen whale, reaching a total length between 12 – 15 m at full maturity (Freitas and Penry, 2021). Its size at birth is 3.81 – 3.96 m (Best, 2007). Bryde's whales sightings are normally of single individuals or small groups of up to 3 animals, although loose feeding aggregations of up to 20 individuals have been observed, spread over several kilometres (Best *et al.*, 1984; Wiseman, 2008; Penry *et al.*, 2011; Kato and Perrin, 2018).

Bryde's whales have a worldwide distribution in inshore and offshore tropical and warm-temperate waters (Kato and Perrin, 2018). There are smaller inshore forms and a larger offshore form with morphological and/or genetic differences, possibly reflecting a more complex population and ecological structure (Freitas and Penry, 2021). In general, the smaller forms of Bryde's whale have been associated with shallower neritic inshore habitats and seasonal displacements on the continental shelf and the larger form with deeper pelagic offshore habitats and seasonal migrations towards the equator along the west coast of Africa offshore waters (Best *et al.*, 1984; Best, 2001; Freitas and Penry, 2021).

The north-eastern limit of Bryde's whales in the Atlantic are the Macaronesia archipelagos of Madeira and the Canary Islands and, more rarely, the Azores (Martín *et al.*, 2003; Prieto and Silva, 2010; Freitas *et al.*, 2012). There are a few confirmed extralimital records of Bryde's whales further north of their normal distribution in European waters and in the east tropical and subtropical North Atlantic, there are records from the northwest African coast and adjacent offshore waters, including Guinea, Senegal, Cape Verde Islands, and Dakhla Bay in western Sahara (Freitas and Penry, 2021). The only available genetic data support that Bryde's whale in Madeira are part of a larger pelagic population in the Atlantic Ocean (Luksenburg *et al.*, 2015).

Bryde's whales do not make extensive latitudinal migrations like most other baleen whales and are presumably able to satisfy their nutritional and reproductive needs within their warm, temperate distribution (Bannister, 2002; Kato and Perrin, 2018). However, there is some evidence that pelagic populations have limited seasonal migrations that can cover distances of several thousand kilometres, although typically shorter than species moving between polar feeding grounds and tropical breeding areas (Best, 2001; Constantine *et al.*, 2018).

Studies of the ecology and habitat use of Bryde's whales have consistently associated a higher occurrence of these animals with areas of higher productivity, such as oceanic convergence areas, fronts, temporary or seasonal upwelling areas or the presence of islands (Freitas and Penry, 2021).

Oceanic islands seem to be important for Bryde's whales in offshore waters, as shown by their higher occurrence around islands like the Galapagos, Maldives, Bonin Islands, the Canary Islands, and the Madeira and Azores archipelagos (Omura, 1962; Palacios, 2003; Anderson, 2005; Steiner *et al.*, 2007; Carrillo *et al.*, 2010; Freitas *et al.*, 2012).

Bryde's whales have a seasonal presence (spring-summer-autumn) in the Macaronesia archipelagos, where the animals have been seen with calves and feeding close to shore (Freitas and Penry, 2021), both at the surface on schooling fish and lunge feeding at depth (Steiner *et al.*, 2007; Alves *et al.*, 2009; Brederlau *et al.*, 2011). The seasonal pattern is an indication that these archipelagos might be feeding grounds or part of much wider feeding grounds of the species in the Central East Atlantic, although no information is available on the relative importance of these archipelagos' inshore waters versus offshore waters. Bryde's whale movements between Madeira and the Canary Islands have been confirmed as well as the existence of animals with different patterns of use of Madeira inshore waters (short-term or long-term site fidelity) (Ferreira *et al.*, 2021). The abundance estimates available for Madeira inshore waters are from line-transect surveys carried out in 2017-2018, which estimated 30 animals (CV=0.28; 95%CI=21 – 43) using, on average, the study area during summer (Freitas *et al.*, 2019a).

It is unclear if the presence of Bryde's whales in the Macaronesia archipelagos is a recent event or they simply went unnoticed (Freitas and Penry, 2021). The oldest record of the species in the Macaronesia archipelagos is from 1997 in the Canary Islands (Urquiola *et al.*, 1997), although there are a couple of extralimital records at higher latitudes in continental European waters around the same time (Kinze, 2006; Gutiérrez-Expósito *et al.*, 2012). The most reliable prior reference to Bryde's whales in Macaronesia refers to the catch of Bryde's whales by the M.V. Sierra catcher (and associated vessels) in 1976 in the waters between Madeira and the Canary Islands (Best, 1992; Freitas and Penry, 2021). The species' first record in Madeira is from 2003 (Freitas *et al.*, 2012).

Questions posed by the study

This chapter addresses the two overarching questions of the thesis (Section 1.3) by shedding light on some aspects of the biology and ecology of Bryde's whales in Macaronesia archipelagos of Madeira, Azores and the Canary Islands and surrounding waters. The study focussed on Madeira and the specific objectives were:

- Investigate the movements and migration patterns of the Bryde's whales in Madeira archipelago waters and the surrounding ocean basin, to shed light on how Bryde's whales in the Eastern North Atlantic use insular marine environments in the wider context of their oceanic distribution;
- Investigate the site fidelity patterns of the Bryde's whales in Madeira archipelago to better understand the relevance and use of this insular marine habitat by the species;
- Estimate population parameters (apparent survival, abundance and calving rates) of Bryde's whales in Madeira archipelago to increase the understanding of the role of this archipelago in their survival and life cycle.

The study used photo-identification data and capture-mark-recapture methods as well as satellite telemetry to address the objectives stated above. Other types of data (e.g. stranding records, sightings information) were used whenever available and relevant to shed light on the importance of these archipelagos in the life cycle of Bryde's whales.

3.2 METHODOLOGY

3.2.1 Study area

The study encompassed the waters of the East Central and Tropical Atlantic from Latitude 38º N (Azores) south to 10º N (Guinea-Bissau). However, the study was focused mostly on the Macaronesia archipelagos of Madeira, Azores and the Canary Islands, especially in the former where most of the data were collected (Figure 3.1).

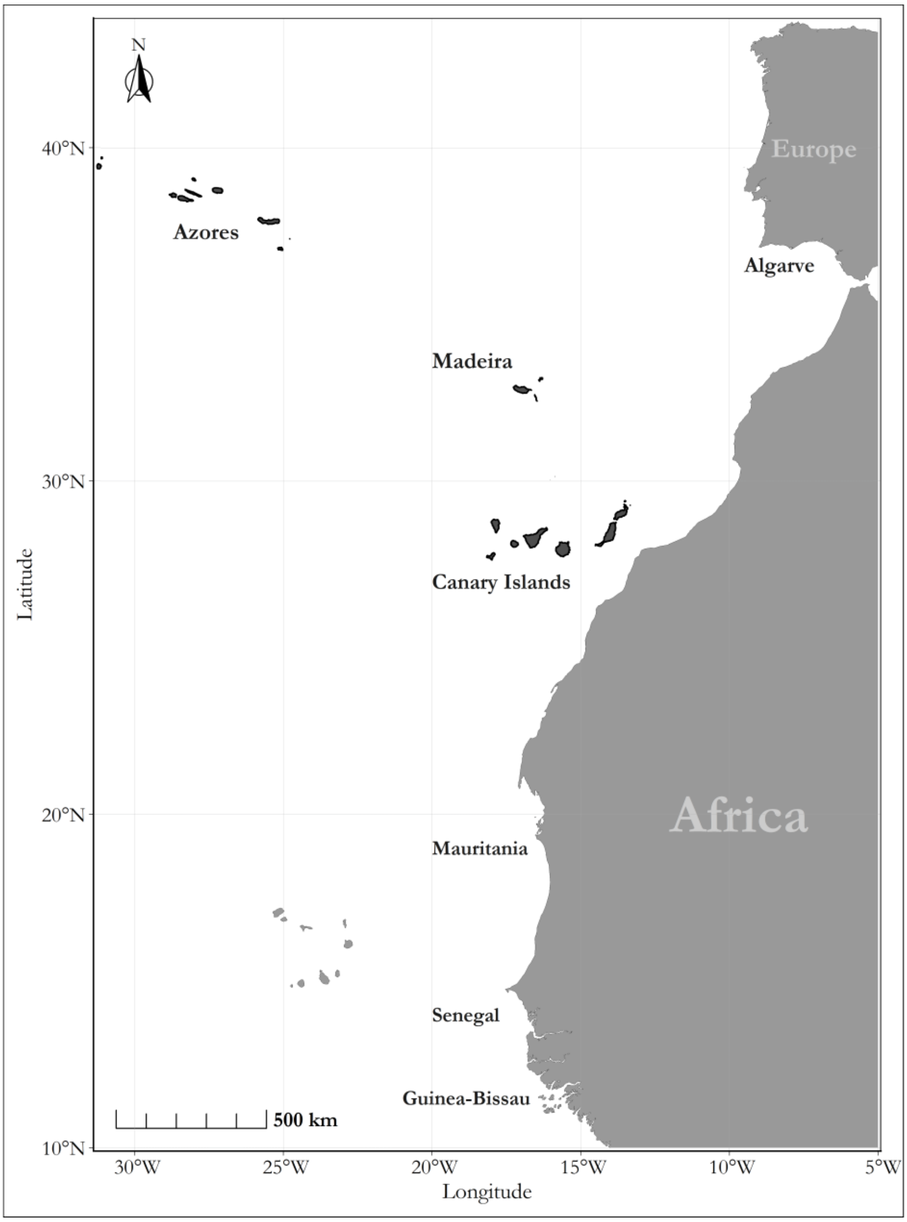


Figure 3.1. Map of the overall study area, including the core area of interest (Madeira archipelago), the surrounding Macaronesia archipelagos of Azores and the Canary Islands, and relevant neighbouring areas of Algarve, and offshore Mauritania, Senegal and Guinea-Bissau.

3.2.2 Photo-identification

3.2.2.1 Data collection

A total of over 50 000 pictures of confirmed and unconfirmed Bryde's whale encounters, collected in the study area by multiple sources, were compiled and organized into a dataset, covering a period from 2002 to 2021. The photo-identification data collection was heterogeneous among the different locations considered in the study in terms of temporal and spatial coverage, effort and survey type. In the Canary Islands, Madeira and the Azores archipelagos the majority of images were collected by commercial whale-watching companies, although the dataset also included images from the three archipelagos obtained by dedicated research surveys, such as non-systematic surveys for photo-identification and biopsy sampling studies (NSS) and shipboard line-transect surveys (SLS), and from opportunistic encounters (OE) and other types of surveys (OS; e.g. seismic surveys). In the Canary Islands and Madeira archipelago, the effort to collect images was year-round while in the Azores it was concentrated in late spring, summer and early autumn, when most whale-watching companies operate in the archipelago. In the case of Madeira, the research surveys contributed to the year-round effort as well and to a wider geographical coverage of the waters around Madeira archipelago. Figure 3.2 shows the area of operation of the whale-watching companies in Madeira that contributed to this study as well as the area covered by the SLS surveys, which encompassed the areas of other research surveys (NSS) that also collected images for the study in the archipelago. For further information on the effort and coverage of the research surveys see Appendix III, Section II.2.1. In general, the whale-watching operations in all archipelagos were concentrated on the leeward side of the islands, protected from the prevailing winds.

The collection of photo-identification pictures from other locations was more opportunistic and isolated, with a few encounters from whale-watching boats in Algarve, and one sighting from each of the locations off west Africa (Mauritania, Senegal and Guinea-Bissau), obtained in OE or OS.

Photo-identification images prior to 2004 were taken with single lens reflex (SLR) 35 mm cameras using colour slides. From 2004 onwards, images were taken mostly with digital SLR cameras using a variety of lenses (e.g. 70-200 mm; 75-300 mm; 100-400 mm). Many of the photographs submitted by third parties to the Madeira Whale Museum (MWM) catalogue or to this study were not accompanied by information on the sighting, apart from the general location of the encounter (e.g. the archipelago) and date, usually also embedded in the image.

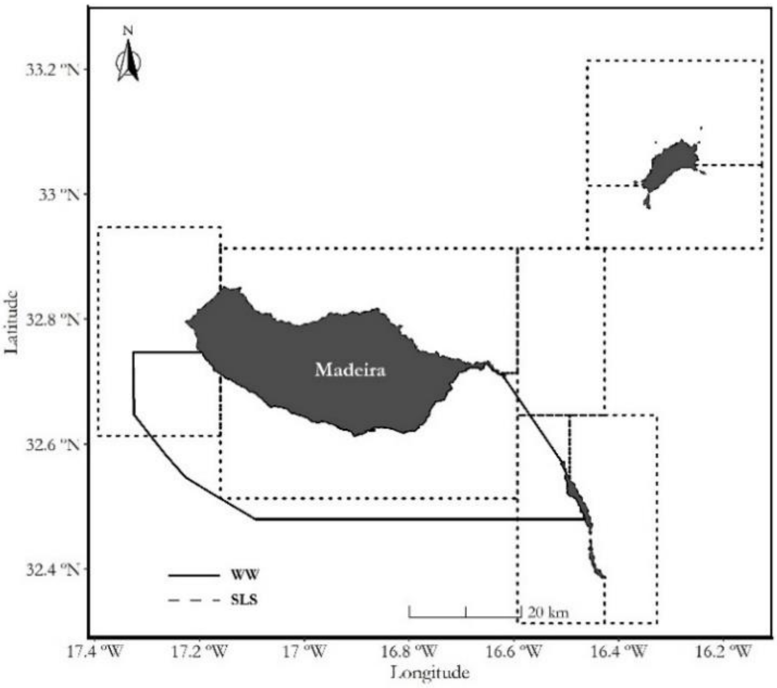


Figure 3.2. Map with the areas, in Madeira archipelago, covered by the systematic line-transect surveys (SLS; 2001-2012), other research surveys (NSS) and whale-watching companies (WW), during which photo-identification pictures of Bryde's whales were taken. The solid and the dotted lines encompass the areas covered by the SLS/NSS and WW, respectively.

3.2.2.2 *Data organization and processing*

All images of Bryde's whales were initially organized into daily folders, named by date, species and source of the images. With the exception of a small number of images already processed prior to this study, the images were also named as the daily folders and ending with the original name submitted by the contributors, for easier backtracking to the sources. Within the daily folders, the best photo-identification images of the animals by encounter (defined as the images with best framing of the dorsal fin and better photo quality, as defined below, among the batch of images with similar embedded times from the same source/boat) were selected into subfolders named with the time of the encounter, number of animals seen in the encounter and, whenever was the case, the presence of mother-calf pairs. Animals were classified as calves when they were less than half of an adult body length and were usually accompanied by an adult, presumably the mother. The remaining animals were classified as non-calves, here referred to as adults. Whenever available, multiple images were selected of the dorsal fin, back and flank from both sides of all the animals identified in an encounter to be compared with the catalogue, irrespective of their markings, so that a proportion of marked individuals could be estimated (see below). Whenever necessary, the images were cropped and edited to adjust light and contrast. For Madeira archipelago, the general location of the encounter was also established from the images with land on the background taken during the encounter, whenever those images were available.

Due to the similarities in size and shape between Bryde's and sei whales, and their co-occurrence in the study area, it was necessary to confirm the species for as many encounters as possible to minimize the incorporation of sei whales in the Bryde's whale catalogue and analysis. Bryde's whales can be identified at sea by the three prominent rostral ridges (Freitas and Penry, 2021). As such, for every encounter, images of the animals' heads confirming the species were also included in the encounter folder. In sightings with multiple animals, the species of all animals in the group was assumed to be the same as the animals for which there were head images. No encounters with both species were identified in the dataset, although that cannot be totally ruled out because a minority of sightings with multiple animals did not include images of the head of all animals. For consistency, this procedure was applied to all images of the overall dataset, regardless of the availability of metadata confirming the species identity.

All images used for photo-identification were rated for their photographic quality and distinctiveness of the dorsal fin, used for individual identification. The photo-quality rating criteria and dorsal fin distinctiveness criteria were adapted from Ashe (2015) and Penry (2010), respectively.

Photo quality was assessed based on the dorsal fin focus, its relative size in the picture, how much of the dorsal fin could be seen in the picture, angle of the fin relative to the camera; and lighting. The images were classified from 0 to 3, with 0 being a poor-quality image and 3 a very good quality image, defined by the following criteria:

- 0 – dorsal fin is small in the image (<= 5% of total image size), fin out of focus and/or fin at an angle > 20° to the camera;
- 1 – dorsal fin in focus, but most of it is not seen in the image;
- 2 – dorsal fin in focus, but at an angle 5°-20° to the camera, and it size is >5% of total image size;
- 3 – dorsal fin in focus, its size is >5% of total image size, most or all the fin is seen, and at an angle of 0-5° to the camera. This criterion was further divided based on the lighting (3.1 dull, 3.2 back-lit, and 3.3 well lit).

Further details on the photo-quality grading criteria are presented in Appendix II.1.

The level of markings varied among the dorsal fins of Bryde's whales using the study area, some were well-marked, some moderately marked and some unmarked. Furthermore, Bryde's whales dorsal fin can have very distinctive shapes and many of them, although unmarked, can still be identified with a considerable degree of confidence. Because of these different levels of markings (Figure 3.3), the dorsal fin distinctiveness was rated according to the following criteria:

0. Slightly distinctive - Uniquely shaped dorsal fin, no nicks or notches but fits into one of the following ‘shape’ categories:

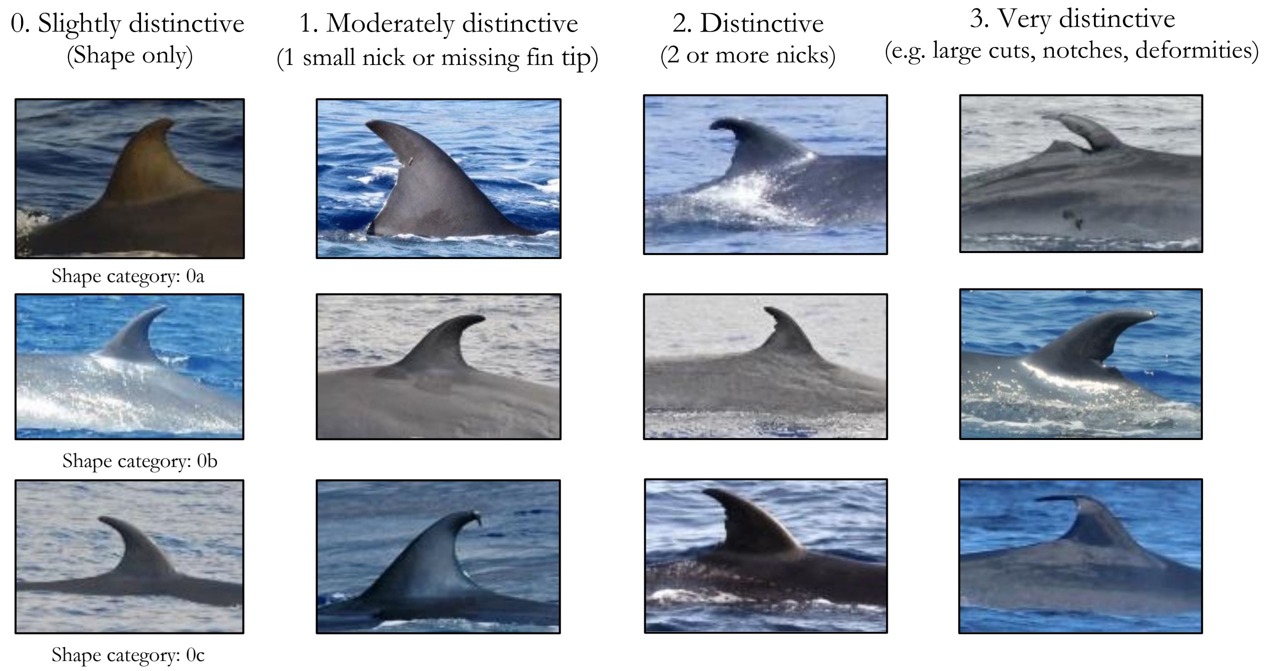
  0a – Broad (Br) Wide base, broad in the middle, does not taper (gradual narrowing) to a thin tip

  0b – Thin/Upright (T/U) Narrow base, upright (not ‘C’ shaped), narrow, pointed tip

  0c – Curved/Hooked (C/H) Typical falcate shape, curved and tapering to a point

1. Moderately distinctive - One small – medium size nick in the trailing/leading edge of the dorsal fin and/or fin missing tip;
2. Distinctive - More than one small – medium size nick in the trailing/leading edge of the dorsal fin;
3. Very Distinctive – includes fins that can be immediately recognized by large nicks, cuts, very unusual shape, disfigured fin or half/no dorsal fin;
9. Not distinctive - No distinctive features.

The definition of dorsal fin shape classes (0a – 0c) for unmarked fins facilitated the search and matching process of a new image with similarly shaped dorsal fins in the catalogue.


0. Slightly distinctive (Shape only)

1. Moderately distinctive (1 small nick or missing fin tip)

2. Distinctive (2 or more nicks)

3. Very distinctive (e.g. large cuts, notches, deformities)

Shape category: 0a

Shape category: 0b

Shape category: 0c

Figure 3.3. Examples for each of the Bryde’s whales dorsal fin distinctiveness categories: 0. slightly distinctive (shape only; no nicks in the leading or trailing edge); 1. moderately distinctive (1 small nick or missing fin tip); 2. distinctive (2 or more nicks); 3. very distinctive (e.g. large cuts, notches, very unusual shape, disfigured fin or half/no dorsal fin). For category 0 (slightly distinctive), an example is presented for each of the shape categories.

3.2.2.3 Matching process

The matching process depended on individual distinctiveness, that is, the ability to distinguish an individual animal from others and to recognize an identified animal on subsequent occasions, by comparing chosen natural markings. Therefore, the features used to identify the animals should be distinct enough to eliminate the possibility that two animals in a population are identified as the same individual – twins (Urian *et al.*, 2015). The type of marks used in the matching process (level of distinctiveness) should not only be related to the species being studied but also to the characteristics of the study, such as, the frequency of sampling periods, overall duration of the study, and if possible, the range and relative size of the population being studied (Urian *et al.*, 2015). Subtle or temporary markings may be used with small populations in a limited range and within a short time period, while only very well-marked animals should be used with large populations that range across extensive areas and/or over a long time period (Urian *et al.*, 2015). As pointed out by these authors, an important source of variation in photographic CMR (capture-mark-recapture) studies is the rescaling of estimates of the marked population to arrive at an estimate of the total population, as not all animals have reliable marks and thus are not distinguishable. Those authors recommend researchers to stratify their data sets by distinctiveness ratings and generate a series of abundance estimates to investigate the influence of including animals of varying distinctiveness.

In this study, the dorsal fins of Bryde's whales were used as the primary natural feature to identify individuals, based on their shape and permanent marks (e.g. nicks, notches, cuts) on their leading and trailing edge, identifiable from images of both the left and right side of the fin. Following the recommendation of Urian *et al.* (2015), two levels of fin distinctiveness to define a "marked" individual were explored in the analysis: WM - well-marked individuals, with distinctiveness classes 1, 2 and 3; and ALL – slightly distinctive and well-marked with distinctiveness classes 0, 1, 2 and 3 (see previous Section).

The use of poor photo quality images it is known to increase the risk of error in the matching process (Hammond, 1986; Urian *et al.*, 2015). To minimize both false positive (considering two different individuals as the same animal) and false negative (images of the same individual being recorded as different animals) matches, only pictures with quality "good" and "very good" (quality 2 and 3) were used in the analysis, although all images, regardless of image quality, were compared within the catalogue.

Besides poor quality images, there are two main reasons for misidentification errors: 1 - errors in identification as a result of changes in the natural markings over time; and 2 - misidentification as a result of the matching process (Ashe and Hammond, 2022). The first main reason was not addressed in this analysis due to time constraints, but the data were collected and will be considered for future publication. Pertaining to the second reason, there are multiple potential reasons for misidentification of animals during the matching process, among them: choosing identifying features that are less appropriate to the characteristics of the study; fatigue, especially in large catalogues that are searched and compared manually; conservative protocols that promote false rejections of true matches; animals with similar markings (Urian *et al.*, 2015; Ashe and Hammond, 2022). To facilitate the matching process the number of comparisons can be reduced by subdividing catalogues into mark types (Urian *et al.*, 2015). Software applications may also facilitate the matching process, and software Finscan (Hillman *et al.*, 2002) was tested on the Bryde's whales dataset in this study. However, it was found not to be reliable in matching bent dorsal fins (common in this species), dorsal fins at some angles to the camera, and especially slightly distinct dorsal fins (only shape).

Photo-identification mark-recapture studies have traditionally used conservative protocols for the matching process to minimize errors in assigning false positives. The consequence is an increase in false negatives (Urian *et al.*, 2015; Ashe and Hammond, 2022). As pointed out by Ashe and Hammond (2022), deciding always to call ambiguous matches a non-match (erring on the side of false negatives) is not always a precautionary approach. It will cause recapture rates to be biased low, which will cause estimates of abundance to be positively biased and estimates of survival rates to be negatively biased (Hammond, 1986, 1990; Friday *et al.*, 2008). As long as protocols require researchers to force an inherently subjective matching process into a binary (match/not-a-match) outcome, biases are likely to happen in the parameter estimates (Ashe and Hammond, 2022), for the reasons mentioned previously. As such, the level of uncertainty associated with any particular match should be quantified and incorporated into resulting population parameter estimates (Urian et al. 2015).

A catalogue of the best pictures of individuals was created, against which new pictures of dorsal fins were visually compared. To facilitate the matching process, the catalogue was organized in folders according to the dorsal fin distinctiveness classes (0a, 0b, 0c, 1, 2 and 3). If no match was found in the corresponding distinctiveness class folder, the search extended to other folders, especially for slightly distinct dorsal fins (shape only). Uncertainty was explicitly included in the matching process by assigning certainty level to each match, adapted from Ashe and Hammond (2022). Three levels of matching uncertainty were considered: 3 – certain (≥ 90% confident); 2 – likely (≥ 70% and < 90% confident); 1 – uncertain (< 70% confident). Whenever there was a match, the image was assigned to that particular individual in the catalogue and added to its respective capture history folder, otherwise it was considered a new individual, assigned a new individual code (sequential numbers, e.g. Be0033) and the image was moved to the respective new capture history folder. When available, left and right pictures of the dorsal fin were chosen for each encounter and included in the corresponding individual capture history folder and catalogue. For confirmation of a match and level of certainty, the image was compared with other images in the individual's capture history folder looking for secondary marks in those images that may increase level of certainty in the match. Finally, matches were checked and confirmed by three other researchers from the MWM with experience in photo-identification. The accepted matches were agreed by consensus among the author and the three other researchers that reviewed the original matches. An encounter history (zeros and ones) was created for each matching certainty level (certain and likely) to be used in the analysis, reflecting whether or not a putative individual was captured during a sampling occasion (sighting).

3.2.2.4 Mark-recapture analysis

Assumptions

Data used in mark-recapture analysis to estimate survival rates and abundance should meet some general assumptions, otherwise the population parameters estimates may be biased. Those assumptions about the data are (Hammond, 2018; Ashe and Hammond, 2022):

1. Marks are unique;
2. Marks cannot be lost or missed;
3. All marks are correctly recorded and reported;

Other assumptions related to the behaviour of the animals or the researcher are also made by the simplest mark-recapture models (Hammond, 2018), namely:

a. Marking does not affect future survival or catchability;
b. Animals must have an equal probability of being captured within each sampling occasion.

Data selection - datasets

In the mark-recapture analysis, eight datasets of Bryde's whales captured in Madeira archipelago were explored considering three variables: (1) confirmed (SC) or non-confirmed (SN) Bryde's whale species identification (Section 3.2.2.2); (2) level of distinctiveness, with well-marked individuals (WM) or slightly marked and well-marked individuals (ALL); and (3) matching uncertainty level, with certain matches (level 3) or probable and certain matches (levels 2 and 3) (Section 3.2.2.3). Images of calves were processed and matched in the same way as other animals, but they were not included in the mark-recapture analysis. Depending on the analysis, each dataset was filtered by year and by month to consider the seasonal presence (June to November) of the species in Madeira. Finally, a dataset including all year-round captures and recaptures of individual Bryde's whales with matching certainty level 2 and 3 in all locations of the study area was used to study the movement of the animals between those locations.

Cormack–Jolly–Seber models

Apparent survival between years (φ; incorporating any permanent emigration) and annual recapture probability (p) of non-calf Bryde's whales were estimated for each year for the period 2005-2021 for the Madeira archipelago, using Cormack-Jolly-Seber (CJS) models (Lebreton *et al.*, 1992) and treating each year as a sampling occasion. Due to the strong seasonal presence of the species in Madeira waters, sighting events from June to November were pooled to build the capture histories.

Goodness-of-fit (GOF) tests were run to test for lack of fit of the global CJS model for each of the datasets explored, prior to running the models. The GOF tests were done in R with package R2ucare (Gimenez *et al.*, 2018). All analyses in R were carried out with version 3.6.2 (R Core Team, 2019) using RStudio (version 1.2.1335, RStudio Team 2019). The GOF test includes specialized interpretable test components (e.g. Test 2.CT and Test 3.SR) to identify features of the data that indicate departure from model assumptions, such as: equal recapture probability between individuals encountered and not encountered in a given sampling occasion (Pradel, 1993), which, may indicate trap-dependence; and equal probability of recapture between newly and previously captured individuals (Pradel *et al.*, 1997), which is typically caused by a so-called transience effect, i.e. the presence of individuals seen only once (defined as transients). The global test, combining all test components, was used to assess the general goodness of fit of the CJS model for each dataset.

A set of candidate models was considered with apparent survival and recapture probabilities: constant over time (.), varying annually (t), or characterized by a linear temporal trend (T) (Lebreton *et al.*, 1992). The results of the GOF Test 3.SR (Section 3.3.4) for all datasets either justified or suggested (marginally non-significant) testing for the effect of transience on estimates of apparent survival. This was done by constructing time-since-marking models with two classes ("trans"), one where survival probability was estimated for the first annual interval after first capture (first "transient" class) and the other for all subsequent annual intervals (second "transient" class). Furthermore, to test for combinations of effects on φ and p, additive (+) and interactive (*) models were built. The variance inflation factor (ĉ, "c- hat"), as global GOF test X^2/degrees of freedom, was calculated to evaluate overdispersion in the data (Lebreton *et al.*, 1992).

The influence of different residency patterns on apparent survival probability was investigated for each dataset, considering that apparent survival is actually the product of the probability of returning to the study area and the probability of an animal surviving from one sampling occasion to the next.

Residency pattern groups were identified by categorizing individuals, using Site Fidelity Indices (Section 3.2.2.6). Separate models were run for each of those groups, with the models' parameterization allowing for survival and recapture probabilities to be constant over time (.), vary annually (t), or characterized by a linear temporal trend (T).

Robust Design models

The annual number of individuals using Madeira inshore waters was estimated for the period 2006-2021 by fitting Pollock's Robust Design (RD) models to the capture histories of non-calf Bryde's whales in the study area (Pollock, 1982; Kendall *et al.*, 1995, 1997). These models also include parameters relating to temporary emigration from, and reimmigration to, the study area between years. RD models are a combination of open population models and closed population models. They use data from primary sampling occasions to estimate survival and temporary emigration and data from secondary sampling occasions (within primary sampling occasions) to estimate abundance for the corresponding primary sampling occasion. The primary sampling occasions are assumed to be closed to gains (birth and immigration) and losses (death and emigration), and consecutive primary sampling occasions should be separated by sufficient time to allow the sampled population to change through gains and losses. The seasonal period that Bryde's whales are present in Madeira (June to November) was considered as a primary sampling occasion, leaving enough time between primary sampling occasions to allow the sampled population to change through gains and losses. The frequency and length (monthly and bimonthly) of the secondary sampling occasions varied from year to year depending on the number of captures and their distribution in the corresponding primary sampling occasion (Section 3.3.4.2). Each secondary occasion should provide a representative sample of the population to avoid introducing heterogeneity of capture probabilities. The varying secondary sampling occasion length was a compromise among (a) maximizing the number of secondary occasions while, (b) leaving a gap between them to allow mixing of animals and (c) ensuring a useable number of recaptures between them. The models were fitted to all the datasets.

Candidate models considered effects that were constant over time (.), varied over time (t), were characterized by a linear temporal trend (T), and/or had a transience effect (*trans*) on survival probabilities (φ; GOF Test 3.SR was either marginally non-significant or significant depending on the dataset; Section 3.3.4). Capture (p) and recapture (c) probabilities were assumed equal in all models (p=c) and were modelled to vary only by primary sampling occasion (s) or by both primary and secondary sampling occasion (s:t). The probability of temporary emigration/re-immigration from/to the study area between years (primary occasions) was incorporated in the models through the parameters γ' (probability of being outside the study area conditional on being outside the study area in the previous year) and γ'' (probability of being outside the study area conditional on being inside the study area in the previous year), with γ'' thus representing the annual probability of temporary emigration and 1 – γ' the annual probability of re-immigration. Temporary emigration was modelled as random (γ' = γ'') or no emigration (γ' = 1; γ'' = 0), and these parameters were modelled as either constant (.) or varying over time (t).

POPAN models

The POPAN parameterization of the Jolly-Seber (JS) model (Schwarz and Arnason, 1996) was fitted to the "Madeira" and the "Madeira – Canary Islands" datasets for the period 2006-2021 to estimate the size of the corresponding "super-populations". Super-population is defined as the total number of non-calf whales using the study area, in this case "Madeira" and "Madeira – Canary Islands", over the whole study period. The POPAN model parameters, probability of apparent survival (φ), capture (p), and recruitment into the study area from the super-population (pent), were modelled as constant (.), varying over time (t), or as a trend over time (T). The results of the GOF Test 3.SR (Section 3.3.4.2 - POPAN) either justified or suggested (marginally non-significant) testing for the effect of transience for both datasets, which included additive and interactive effects with (t) and (T).

Model Selection, adjustment for overdispersion and model-averaging

The quasi-likelihood AIC for small size samples (QAICc) was used to assess the support that candidate CJS and POPAN models had from the data. Two of the four datasets were adjusted for over dispersion using estimated ĉ, for both matching uncertainty level 2 and 3 (Section 3.3.4 and Section 3.3.4.2) and the group of datasets with matching certainty 3 (Appendix II, Table II.7-1). Neither overall model fit nor overdispersion in the data was assessed for RD models due to the unavailability of GOF tests for these models. As such, relative model fit was assessed with AICc.

The models with ΔQAICc or ΔAICc ≤10 relative to the model with the lowest QAICc or AICc, were considered to have some support from the data and were selected to obtain model-averaged estimates of the parameters of interest (Burnham and Anderson, 2002). All mark-recapture analysis was carried out in software MARK (version 9.0; Cooch and White, 2017) through R-Mark (version 2.2.7; Laake, 2013) in R.

Proportion of marked animals

The number of slightly-marked, well-marked and unmarked individuals was determined for each encounter from their distinctiveness level, according to the criteria explained in Section 3.2.2.3. These data were used to calculate the number of identified and unidentified individuals for each dataset. In the WM datasets (WM-SC, WM-SN, WM-SC.3 and WM-SN.3) the animals classified as well-marked were considered as identified individuals while the slightly-marked and the unmarked individuals were considered unidentified individuals. In the remaining datasets (ALL-SC, ALL-SN, ALL-SC.3, ALL-SN.3) the identified individuals were the slightly-marked and the well-marked individuals and the unidentified individuals were the remaining unmarked animals.

For each dataset, a binomial generalized linear model with a logit link function was fitted to the number of identified and unidentified individuals in each encounter to estimate the proportion of identifiable individuals in the population, θ, in each year (Jourdain *et al.*, 2021).

Total population size was estimated as:

$$\widehat{N}_{total} = \frac{\widehat{N}}{\widehat{\theta}}$$

where $\widehat{N}$ is number of identifiable animals estimated by capture– recapture. The uncertainty, measured by the coefficient of variation (CV) was estimated using the delta method as:

$$CV^2_{N_{total}} = CV^2_N + CV^2_\theta$$

The 95% confidence intervals (CI) were calculated assuming a log normal distribution, with:

Lower CI = $\frac{N_{total}}{c}$; Upper CI =$N_{total} * c$;   where $c = e^{1.96\sqrt{\ln{(1+CV^2_{N_{total}})}}}$

3.2.2.5 *Mother-calf association and calving rates*

As mentioned previously, animals were classified as calves when they were less than half of an adult body length and were usually accompanied by an adult, presumably the mother. The remaining animals were classified as non-calves, here referred to as adults. A female-calf pair was assumed whenever a calf was seen in a sighting closely associated with a unique adult animal (swimming very close to each other) and over a sequence of sightings, when they existed. In a few sightings, a calf was seen close to more than one adult. In those cases, the capture history of the calf was checked to find a consistent association with one particular individual, which was then considered the mother. When a calf was identified for the first time and seen in association with an unidentified adult, this sighting was considered in the time series of sightings of a female-calf pair in that year if the calf was later (in the same year) identified consistently with an identified female.

Calving (or fecundity) rates and calving intervals were estimated from direct calculations based on the individual capture histories of identifiable females, recording whether or not each female had a calf born that year. Females were not encountered every year of the study period and to deal with these incomplete capture histories, two datasets of female capture histories were considered. The first dataset (D1) included females with: continuous yearly capture histories, yearly capture histories between 4 and 6 years with only one year missing and capture histories with more than 6 years with a maximum of two years missing. The second dataset (D2) included only females with a continuous sequence of at least 5 years with captures, within their capture histories, which were used in the analysis. Furthermore, the capture histories of mothers in D1 and D2 were divided in two periods (2003-2012 and 2014-2021) as long as they followed the criteria for D1, to investigate possible changes in calving rates between the two periods. The fecundity rate and calving interval was first calculated for each female in both datasets and later averaged over all females in each dataset. The calving rate was calculated as the number of calves associated with a female divided by the period (last year seen minus first year seen) that female was captured in the study area, while the calving interval was calculated as the inverse. A Kruskal-Wallis test was used to check for significant differences ($p < 0.05$) between D1 and D2 and between 2003-2012 and 2014-2021, as the data in all datasets were not normally distributed (normality tested with a Shapiro-Wilk test).

3.2.2.6 *Site fidelity and residency*

Bryde's whale patterns of use of Madeira archipelago inshore waters for the period 2005 – 2021 were investigated using Site Fidelity Indices (SFI). Following Tschopp *et al.* (2018), composite SFI were calculated to quantify the degree of site fidelity of the population (Bryde's whales using Madeira inshore waters) to be comparable with other studies and populations. Furthermore, the framework proposed by Verborgh *et al.* (2022) was applied to identify individuals with higher site fidelity in the population and investigate their patterns of use of the local study area.

The SFI were calculated, both at the population and individual level, based on the indicators *Occurrence*, *Permanence* and *Periodicity* (Morteo *et al.*, 2012; Tschopp *et al.*, 2018; Verborgh *et al.*, 2022), with day being the sampling occasion. The indicators range from 0 to 1 can be described as follows:

- *Occurrence* (*IO*) is the number of recaptures of an individual during the study period:

  $$IO_i = \frac{\sum_{j=1}^{T} c_{ij} - 1}{T-1}$$

  where *c* is the binary value representing a capture (1) vs. an absence of capture (0) of an individual (*i*) in a sampling occasion (*j*), and *T* is the total number of sampling occasions (days in present study).

- *Permanence* (*IT*) is the proportion of time that an individual spent in the study area calculated as:

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

where F_i is the time difference (in days) between an individual's last recapture and its first capture and F is the time of the full sampling period in days.

- *Periodicity* (*It*) is an individual's re-occurrence computed by dividing the number of recaptures by the time between the first capture and last recapture:

  $$It_i = \frac{\sum_{j=1}^{T} c_{ij} - 1}{F_i}$$

  where F_i and c_{ij} are described above.

Eight indices, based on the combinations of *IO*, *IT* and *It*, were considered in the analysis, as tested by Tschopp *et al.* (2018) and Verborgh *et al.* (2022). Four of the SFI have an arithmetic mean structure (IA1-IA4) and four had a harmonic mean structure (IH1-IH4) as shown in Table 3.1. All eight SFI range from 0 (population with no site fidelity) to 1 (resident population)(Tschopp *et al.*, 2018).

Tschopp *et al.* (2018) in their analysis considered IH4 as the best composite index, among the indices tested, to quantify the site fidelity of a population and recommended it as the Standard SFI (SSFI) for its better overall performance, especially with imperfect detections and non-continuous effort. As recommended by Tschopp *et al.* (2018), the SSFI mean value was calculated for all datasets (WM-SC; WM-SN; ALL-SC; ALL-SN) with certainty 2-3 and certainty 3, using the complete datasets (including animals seen only once) to provide an estimate for the whole population of Bryde's whales using Madeira inshore waters.

Table 3.1. Site Fidelity Indices using *Occurrence* (*IO*), *Permanence* (*IT*) and *Periodicity* (*It*) (Tschopp *et al.*, 2018).

Indices with an arithmetic mean structure (IA)	Indices with a harmonic mean structure (IH)
$IA1 = \frac{1}{3}(IO + IT + It)$	$IH1 = \frac{3}{\frac{1}{IO} + \frac{1}{IT} + \frac{1}{It}}$
$IA2 = \frac{1}{2}(IO + IT)$	$IH2 = \frac{2}{\frac{1}{IO} + \frac{1}{IT}}$
$IA3 = \frac{1}{2}(IO + It)$	$IH3 = \frac{2}{\frac{1}{IO} + \frac{1}{It}}$
$IA4 = \frac{1}{2}(IT + It)$	$IH4 = \frac{2}{\frac{1}{IT} + \frac{1}{It}}$

To identify individuals with higher site fidelity in the population a standardized method (Verborgh *et al.*, 2022) was followed, consisting of two steps:

1. calculate the SFI for each individual;
2. define the population site fidelity structure from K-means clustering analysis based on the SFI values, and group individuals into different site fidelity level clusters.

The indices were calculated for each individual and those indices that had Pearson's correlation coefficients between them lower than 0.8 were selected, to be used in step 2 (K-means analysis). The K-means methodology attempts to organize observations into mutually exclusive clusters so that observations within the same cluster are as similar as possible, while observations from different clusters are as different as possible. The different clusters ideally separate individuals with lower SFI (individuals that only use the area occasionally) from those with higher SFI (individuals with high site fidelity). Individuals only seen once were not used in the clustering analysis since they have a SFI value of zero.

The K-means clustering started with the calculation of the Euclidean distance between individuals, using the selected indices values of each individual. Then the optimal number of clusters to group the individuals was selected using the average Silhouette method (package "cluster"; Maechler *et al.*, 2021), which measures how similar a point (an animal SFI) is to its own cluster (cohesion) compared to other clusters (separation). The highest average silhouette width value indicates the optimal number of clusters. This method indicated six to be the optimal number of clusters for datasets with only well-marked individuals (WM) and seven for datasets with all individuals (ALL). However, these numbers of clusters were too many to allow any meaningful biological interpretation of site fidelity structure of the population using the inshore waters of Madeira. Thus, the optimal number of clusters was chosen, after being tested for two to five clusters, according to the following rules:

1. The number of clusters below five with an average Silhouette value peaking consistently across all or most datasets;
2. When visualized as a PCA in the first two dimensions, the clusters have minimal or no overlap;

The chosen optimal number of clusters was used to separate the individuals with the K-means method and the results were visualized as a Principal Component Analysis (PCA) in the first two dimensions, using the package "factoextra" (Kassambara and Mundt, 2020).

Other clustering methodologies besides K-means were tested, namely divisive and agglomerative hierarchical clustering (results not presented). However, K-means had in general better or similar results to hierarchical clustering methods across the four datasets analysed, when the within cluster sum of squares and the average silhouette width values were compared for each of the optimal number of clusters tested. Usually, within cluster sum of squares and the average silhouette width are used to validate the clustering method (Verborgh *et al.*, 2022).

The selected SFI were compared among clusters with Kruskal-Wallis tests and *post-hoc* Dunn tests, applying the Benjamini-Hochberg correction (Benjamini and Hochberg, 1995), and using the package rstatix (Kassambara, 2021). Further details on this methodological approach are given in Verborgh *et al.* (2022). The analysis was carried out using an R script provided by the authors of the method (Supplementary Material 1) in R (version 3.6.2; R Core Team, 2019), using RStudio (version 1.2.1335, RStudio Team 2019).

3.2.3 Satellite telemetry

3.2.3.1 Tag deployment and data collection

The search for Bryde's whales to deploy satellite tags or PTTs (Platform Transmitting Terminals) covered the south and north of Madeira Island and the east and west of Desertas Islands (southeast of Madeira), especially around the two northern Islands (Figure 3.2). Most search trips had multiple purposes, such as collecting photo-identification data and skin biopsies of several species, including Bryde's whales.

Figure 3.4. Left: the rigid inflatable boat "Kogia" used to search and deploy satellite tags on Bryde's whales (photo: Luís Berimbau). Right: Preparing to implant on a Bryde's whale a SPOT 240c LIMPET satellite tag deployed from a 25-bar pressure injection rifle.

The search and satellite tag deployment were made from a 6.5 m rigid inflatable boat ("Kogia") with an elevated observation platform (height of 2 m) for two seated observers and a cruising speed of 10 knots (Figure 3.4). The minimum crew to deploy the satellite tags consisted of the boat skipper, the photo-identification person and the person to deploy the tag. Whenever there were four people on board, including an extra trained and certified person to do the biopsy sampling, attempts were made to deploy the satellite tag and immediately afterwards obtain the biopsy sample to minimize any disturbance to the animal. If there was no extra person on board to do biopsy sampling, the person deploying the tag would subsequently try to obtain the biopsy sample in a new approach to the animal. Obtaining the biopsy sample was a secondary objective in relation to the deployment of the satellite tags and thus it was only attempted if the animal did not show a strong reaction to the satellite tag implantation, as measured on a 4-pt scale (Hooker *et al.*, 2001).

Once a Bryde's whale was found and approached, a visual assessment was made of the animal's overall size, health condition (e.g. emaciation, wounds) and behaviour, to decide whether or not to try to tag the animal. Only animals assessed to be greater than 10 m length, in apparently good health condition and receptive to be approached were considered candidates to be tagged. If whales were found in a group with more than one suitable animal, the most approachable animal was chosen to maximize the chances of tagging and reducing stress on the animal(s).

Before tag deployment it was confirmed that the animal was not previously tagged by cross-checking with previously tagged animals and looking at the photo-identification images collected for marks on both sides of the dorsal fin and the surrounding dorsal area. Usually, several attempts were made before the tag was deployed. The attempts stopped whenever the animal showed signs of avoidance/disturbance or the boat had been with the animal(s) for one hour (30 minutes for females with dependent calves), whichever occurred first. The signs of avoidance/disturbance included: repeated changes in the direction of travel each time the boat approached, increased swimming speed, and increased diving time. If these signs persisted after three attempts of approaching the individual whale or group (including mother and calf pairs), the boat would stop following the animal(s) and no approach attempts were made to that individual or group again on that day. Post-tagging follow-up observations of 10-15 minutes were made to confirm tag attachment, monitor reaction and behaviour of the animal and collect more photographic information. These follow-up observations were mostly done at a distance greater than 100m to minimise disturbance and assess the animal's behaviour without influencing it. A brief closer approach was made to check the tag attachment.

The PTTs implanted on the Bryde's whales were the Wildlife Computer SPOT 240c LIMPET (Low Impact Minimally Percutaneous Electronic Transmitter) model, weighing 49g. The tag was attached to the animal's dorsal fin or surrounding area by two 6-petal titanium darts (length: 65mm; width: 24 mm; weight: 6g) screwed to the base of the tag. The darts were sterilized and kept in vacuum-sealed bags (protected by the rubber tubes provided with darts) prior to deployment.

The satellite tag with the darts was deployed mounted on a custom-made arrow, with the tag specific deployment cup, for use with a pressure injection rifle. The tag and arrow were deployed from a 25-bar pressure Dan-Inject CO2 rifle (model JM.SP.25) equipped with a 13 mm barrel.

The number of programmed transmitting hours per day was 13 h in the first 100 days (a minimum of two daily positions expected) and 6 hours (minimum of one daily position expected) thereafter, giving a life expectancy of the PTT battery greater than 160 days.

The locations of the PTTs, and associated animals, were estimated by the Argos system (a global low polar orbit satellite network for location and data collection), using the Doppler shift in the tag transmission frequency as the satellite passed overhead (Argos User's Manual, www. argos-system. org/ manual/).

3.2.3.2 *Data processing*

The messages transmitted by the PTT were processed by the Argos Centres to estimate tag location using the Kalman filtering location processing algorithm. This algorithm provides more positions and better accuracy when compared with the alternative least squares analysis. All estimated locations go through three plausibility tests before being validated (Argos User's Manual, www. argos-system. org/ manual/).

Once the locations were downloaded from Argos servers, they were plotted to check tracks, and locations with quality Z (invalid location) or very unrealistic latitude and longitude values were removed. In practice, the unrealistic locations corresponded to the initial location after deployment. The deployment location taken by GPS was also added to each of the tag tracks. Locations with quality 3 (250 m accuracy), 2 (500 m accuracy), 1(1500 m accuracy), 0 (>1500 m accuracy) and A and B (unbounded accuracy estimation) were kept for analysis.

The whales' tracks obtained by the Argos system were irregular time series of locations of varying quality. Variables such as satellite coverage of the area used by the whale, location of the PTT on the animal's body, the animals' diving behaviour and sea conditions affect the rates of successful messages' transmissions by the PTT and the rate of reception of those messages by the Argos satellites. As a result, the locations temporal irregularity and the error in the observed locations needed to be considered prior to further analysis with HMM (Hidden Markov Models). Following the workflow proposed by McClintock and Michelot (2018), the tracks were first regularized (sequence of regular locations equally spaced in time) together by fitting a continuous-time state-space model with the package FoieGras (version 0.7.6; Jonsen and Patterson, 2021) with time steps of 8 hours, taking in consideration ARGOS locations errors given by the Kalman filtering algorithm.

3.2.3.3 Data analysis

All processed animal track data were analysed together using HMMs to infer the animals' behaviour from the observed movement patterns based on second order variables such step length and turning angles. An HMM is a time series model that includes two components, an observable series (some quantification of movement) and an underlying, non-observable state sequence (Langrock *et al.*, 2012). Each bivariate (step length and turning angles) observation is assumed to be generated by one of N distributions, and the unobservable (hidden) sequence of states, S1, . . . , S*t*, modelled as a Markov chain, which determines which of the N distributions is selected at each time *t* (Langrock *et al.*, 2012). These states can be interpreted as behavioural states of the observed animals in the context of their movement (Morales *et al.*, 2004).

The analysis was carried out using the movement package momentuHMM (Version 1.5.0), with the function fitHMM selected to specify and fit the HMM using maximum likelihood methods, with a single imputation. The analysis included running two and three state sets of models, each comprising 25 models with initial parameter values randomized between plausible minimum and maximum values for both step length (and standard deviation) and turning angle (and turning angle concentration)(Michelot and Langrock, 2022). The best-fitting model for each of the model sets (2 and 3 states) was identified by comparing their likelihoods and choosing the one with the highest value (maximum likelihood). The states are expected to represent animals' behavioural states characterized by differences in step length and turning angles.

The HMMs had the step length modelled by a gamma distribution and the turning angles by a von Mises distribution (McClintock and Michelot, 2018). The final best model was selected using Akaike Information Criterion (AIC) among the two and three state models. The most likely sequence of hidden states was calculated using the Viterbi algorithm (McClintock and Michelot, 2018).

These results are expected to give ecological context to the interpretation of the results of the photo-identification/mark-recapture analyses (this Chapter) and to the results on the spatial and temporal distribution of the species (Chapter 4). Further analysis will be carried out prior to this study's submission for peer-reviewed publication considering environmental data and the use of HMMs based on multiple imputation of the position process drawn from a single-state continuous-time movement model (McClintock *et al.*, 2017; McClintock and Michelot, 2018).

3.3 RESULTS

3.3.1 Data summary

A total of 2 823 pictures of Bryde's whale dorsal fins were selected, processed and compared with each other to create a Bryde's whale dataset that included the photo-identification catalogue and the capture histories of each animal in the catalogue during the study period (2002 – 2021). In Table 3.2, the number of pictures in this dataset by type of survey and location is given. The total number of pictures processed and compared with the catalogue and the total of pictures for which an animal's ID was assigned, by type of survey, year and location, are presented in Appendix II, Tables I.2-1 and I.2-2, respectively.

Table 3.2 – The number of Bryde's whales' (species confirmed or suspected) dorsal fin images processed and compared with the catalogue, by type of survey and location of interest in the study area. NSS – non-systematic surveys for photo-identification and biopsy sampling studies; SLS – shipboard line-transect surveys; OE – Opportunistic encounters; OS – Other type of surveys (e.g. seismic prospection surveys); and WW – whale-watching trips.

Survey type	Madeira	Canaries	Azores	Algarve	Guinea-Bissau	Mauritania	Senegal	Total	%
NSS	173	85	1	2				261	9%
SLS	114	22	3					139	5%
OE	11	33	5		3			52	2%
OS						2	1	3	0.1%
WW	1977	257	125	9				2368	84%
Total	2275	397	134	11	3	2	1	2823	100%

The locations with most sampling effort and therefore images collected were the Macaronesia archipelagos of Madeira, Canary Islands and Azores, in decreasing order. For the remaining areas, there were few images because of either low sampling effort or low presence of the species (e.g. Algarve). In Madeira archipelago, the photo-identification images were obtained throughout the study period, mostly around Madeira Island (Table 3.3). In contrast, in the remaining archipelagos of Azores and Canary Islands, images were collected around multiple islands and with incomplete coverage of the study period (Table 3.3). The Bryde's whales sightings monthly distribution from which the photo-identification images were obtained is presented in Figure II.2-1 (Appendix II).

Between 2002 and 2021, there were 1 555 sightings of Bryde's whales made in 839 sampling days (unique dates) that yielded a total of 329 photo-identified animals in the overall study area with matching certainty 2 and 3 (likely and certain) and 327 with certainty 3. Madeira, with 635 sampling days, had the highest number of identified individuals, followed by the Canaries (189 sampling days) and Azores (50 days) and finally Algarve (5 sampling days), Guinea-Bissau, Mauritania and Senegal (one sampling day), reflecting the sampling effort in each area. Seventy five percent of the sightings were of one animal, 24% of two animals, 1% of three animals and 0.1% of four animals.

In Table 3.4 are presented the number of animals identified in each dorsal fin distinctiveness class in each location of the study area, the total by location and dorsal fin distinctiveness class and the overall total for the study area. The recaptures in this dataset were used to study the displacements of the species in the Central East Atlantic, including Macaronesia. The percentage of photo-identified animals in all study areas confirmed to the species level following the criteria explained in Section 3.2.2.2. were 72% overall, 71% in the Azores, 73% in the Canary Islands, and 79% in Madeira.

Table 3.3 – Number of Bryde's whales (species confirmed and suspected) pictures processed and compared with the catalogue, by archipelago/island and year.

Archipelago	Island	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	Total
Azores	offshore																	3				3
	Faial			4						2			8	3	2		32	18	2		2	73
	Pico												3		1		10	2			1	17
	São Miguel																34					34
	Terceira																5	2				7
Canary Islands	El Hierro				1	1						7		3		35	18					65
	Fuerte Ventura													3		33	3					39
	Gran Canaria	4		1			2	5		2		4			2							20
	La Gomera				2		2							2		5		9				20
	La Palma														1		47	4				52
	Lanzarote													5			10					15
	Tenerife						2			2		13	7	30	34	58	40					186
Madeira	Madeira	6	20	29	37	28	32	83	19	54	24	35	7	500	217	50	486	121	178	78	257	2261
	Porto Santo	2						6										5				13
Total		12	20	34	40	29	38	94	19	60	24	59	25	546	257	181	685	164	180	78	260	2805

Table 3.4 – Number of Bryde's whales individuals identified in each study area location for the period 2002 – 2021, by the dorsal fins' classes of distinctiveness. The total of individuals is not the sum of the individuals identified in each location because many animals were sighted in multiple locations of the study area.

Dataset	Distinctiveness class				total
	0	1	2	3	
Madeira	130	45	25	34	234
Canary Is.	61	24	9	16	110
Azores	21	6	4	4	35
Algarve	1	1	0	1	3
Mauritania	0	1	0	0	1
Guinea-Bissau	0	1	0	1	2
Senegal	0	0	0	1	1
Total	184	62	32	51	329

In Table 3.5 is given the number of identified animals in each of the four datasets explored in the mark-recapture analysis to estimate apparent survival (Section 3.2.2.4) as well as site fidelity (Section 3.2.2.6) of non-calf Bryde's whales in Madeira between 2005 and 2021.

In Table 3.6 is presented the number of identified animals in each of the four datasets explored in the mark-recapture analysis to estimate abundance of non-calf Bryde's whales in Madeira between 2006 and 2021 and the super population size (Section 3.2.2.4).

Although the number of individuals in the dataset with certainty level 2 and 3 is mostly equal to the number individuals in the dataset with certainty level 3, the number of recaptures of those individuals in those datasets are, as expected, different.

Table 3.5 – Number of Bryde's whale individuals in each dataset used in the apparent survival estimation analysis and in the site fidelity analysis for the period 2005 – 2021 in Madeira archipelago, by dorsal fins class of distinctiveness. The numbers without brackets correspond to animals identified with certainty level 2 or 3 and the numbers in brackets to animals identified with certainty level 3. Datasets used in these analyses were obtained by combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (ALL).

Dataset	Distinctiveness class				total
	0	1	2	3	
WM-SC	0 (0)	40 (40)	21 (21)	25 (25)	86 (86)
WM-SN	0 (0)	44 (44)	25 (25)	31 (31)	100 (100)
ALL-SC	103 (102)	40 (40)	21 (21)	25 (25)	189 (188)
ALL-SN	126 (125)	44 (44)	25 (25)	31 (31)	226 (225)

Table 3.6 – Number of Bryde's whales individuals in each dataset used in the abundance estimation analyses (Pollock's Robust Design and POPAN) for the period 2006 – 2021 in Madeira archipelago, by dorsal fins class of distinctiveness. The numbers without brackets correspond to animals identified with certainty level 2 or 3 and the numbers in brackets to animals identified with certainty level 3. Datasets used in these analyses were obtained by combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (ALL).

Dataset	Distinctiveness class				total
	0	1	2	3	
WM-SC	0 (0)	40 (40)	20 (20)	23 (23)	83 (83)
WM-SN	0 (0)	44 (44)	24 (24)	29 (29)	97 (97)
ALL-SC	99 (98)	40 (40)	20 (20)	23 (23)	182 (181)
ALL-SN	122 (121)	44 (44)	24 (24)	29 (29)	219 (218)

In Madeira archipelago, 76 animals (33%) were seen in two or more years over the study period, while 158 animals (67%) were only seen in one year (Figure 3.5).

In Figure 3.6 is given the number of animals identified in each year for the first time in Madeira archipelago, the animals captured in each year but identified in previous years and the cumulative discovery curve for the study period. The number of individuals identified for the first time in each year outnumbered the number of individuals previously identified in Madeira archipelago, in more than two-thirds of the years; the exceptions were 2009, 2011, 2013, 2018 and 2020. From 2014 onwards the total number of identified animals increased considerably when compared with the previous years, except for 2016 and 2020.

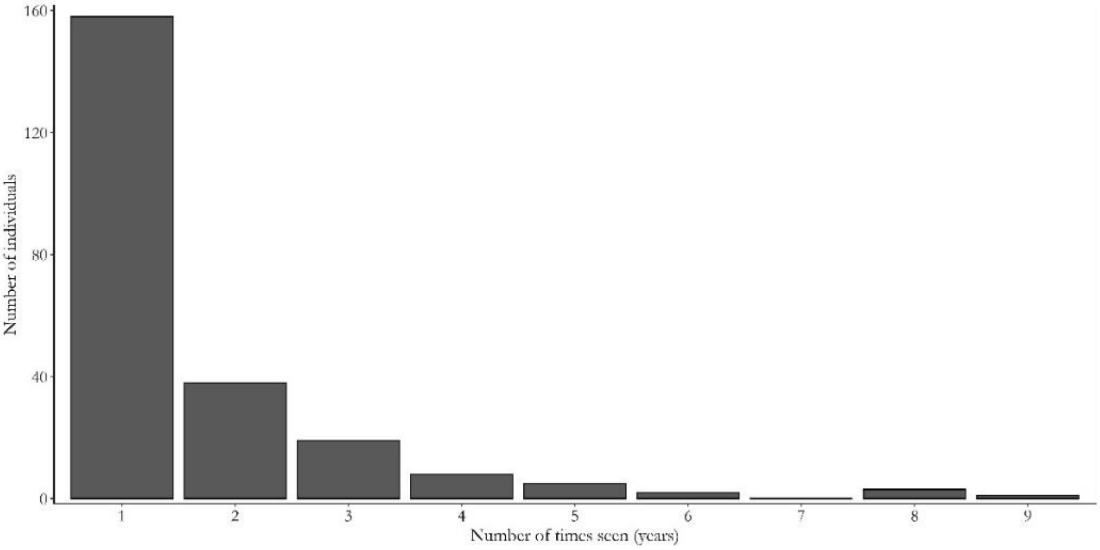


Figure 3.5. Frequency of captures (number of years seen) of the 234 animals identified in Madeira archipelago between 2002 and 2021.

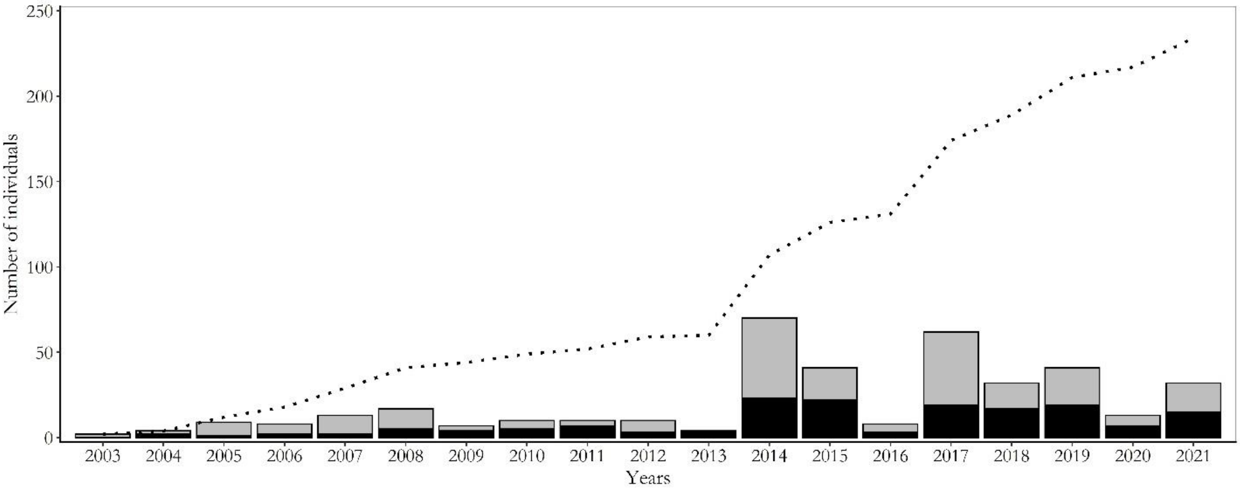


Figure 3.6. The number of Bryde's whales' photo-identified for the first time (grey) and photo-identified previously (black) by year, and the cumulative discovery curve of new individuals from 2002 – 2021 in Madeira archipelago.

The cumulative discovery curve for Madeira increased moderately in the first years and started to level off towards 2013, increasing considerably again from 2014 onwards without reaching a plateau by the end of the study period. The cumulative discovery curve for the overall study area for the same period (not presented) had a similar pattern to the Madeira cumulative discovery curve, also driven by the Madeira data.

Figure 3.7 shows the proportion of animals only seen in one year, transients, relative to the total number of individuals identified in the corresponding year. The year 2017 had the highest proportion (55%) of transients, followed by 2019 (54%), 2021 (53%), 2004, 2014 and 2015 (all with 50%). The average percentage of transients in the first (2003 – 2012) and second (2013 - 2021) halves of the study period was 25% (SD = 18%) and 40% (SD = 17%), respectively. In spite of the two animals sampled in 2002 being well marked and identified, the images did not reach the chosen quality threshold and thus were not considered in Figure 3.6 and Figure 3.7. Nevertheless, these two matches confirm the presence of the species in Madeira archipelago waters in 2002, one year before it was previously referenced (Freitas *et al.*, 2012).

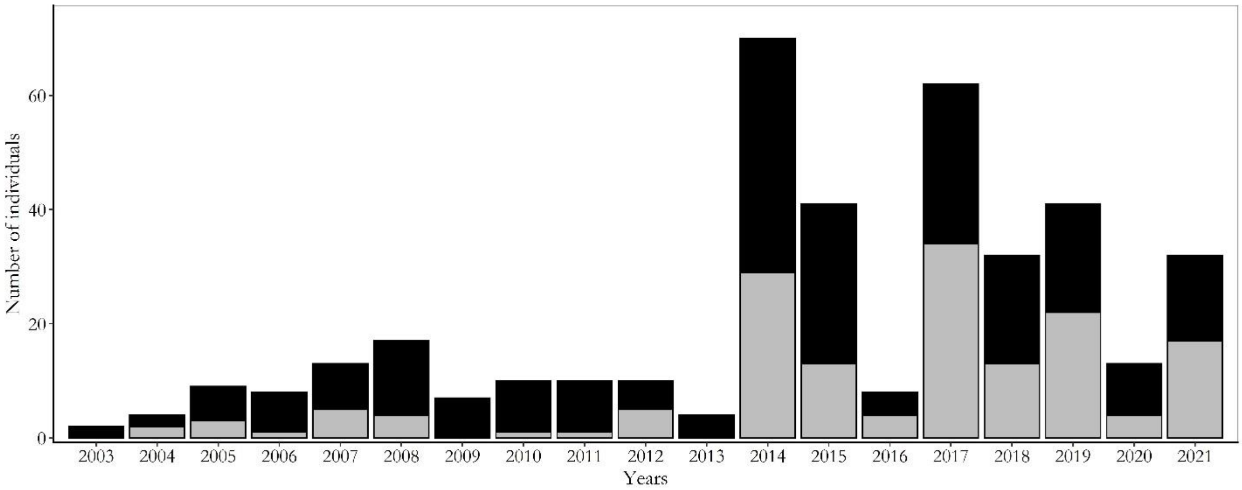


Figure 3.7. The number of individuals seen in only one year (transients, grey) in comparison with the total number of photo-identified individuals (black and grey combined) by year in Madeira archipelago.

More well-marked animals (68%; distinctiveness classes 1-3) than slightly marked animals (distinctiveness class 0) were captured in the first half of the study period (2005 – 2013). In the second half of the study period (2014 – 2021) this pattern reversed, with only 47% of the animals captured being well-marked. Furthermore, 58% of well-marked animals and 32% of the slightly marked animals were identified as females in the first half of the study against 36% and 24% in the second half, respectively. Additionally, 80% of the females captured in the first half of the study were well-marked compared to only 57% in the second half.

Six satellite LIMPET tags were deployed in Madeira inshore waters over the course of three years (2018 – 2020) to further understand the ecology of Bryde's whales in the Central East Atlantic. Table 3.7 shows the date of deployment, number of days and positions transmitted of each animal tagged.

Table 3.7 – Summary table of the satellite tags deployed in Bryde's whales in Madeira inshore waters. The table includes the date of deployment, number of days transmitting and positions transmitted, animals tagged and sex inferred from animals seen associated with calves.

Tags	Deployment date	Days transmitting	Positions transmitted	Animal tagged	Sex
MBM_S6_01	02/09/2018	22	261	Be0107	Unknown
MBM_S6_02	25/07/2019	5	6	Be0288	Unknown
MBM_S6_03	26/10/2018	55	400	Be0194	Unknown
MBM_S6_04	19/08/2019	2	17	Be0306	Unknown
MBM_S6_05	09/08/2019	0	0	Be0308	Unknown
MBM_S6_06	09/08/2020	21	157	Be0024	Female

Three out of the six tags transmitted between three weeks and two months, while the remaining tags never transmitted or transmitted a few days. In one case (MBM_S6_02), the low position of the tag on the body explained the short transmission period and, in general, the low quality of the positions (Figure 3.8).

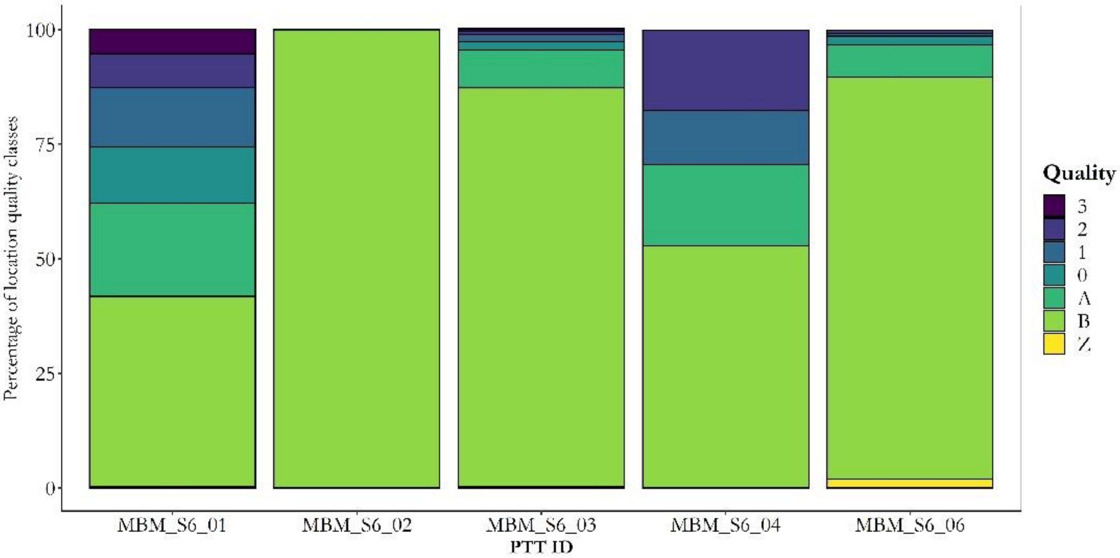


Figure 3.8. Percentage of location quality classes for all the deployed satellite tags (PTT) in Bryde's whales in Madeira that transmitted positions.

3.3.2 Movements

3.3.2.1 Photo-identification

From the 329 animals' photo-identified in the study area, 53 were seen in two or more areas, 81 were only seen in one location in two or more sampling periods (2 months) and 195 were seen in one location in only one sampling period (Table 3.8). Madeira had the highest number of captured animals (234), followed by the Canary Islands (110), the Azores (35), the Algarve (2), Guinea-Bissau (2), Mauritania and Senegal (1), reflecting partially the sampling effort in each area.

When the type of capture history (shown in Table 3.8) is considered in relative terms, 40% of animals captured in the Canary Islands were seen in two or more areas, followed by the Azores (34%) and Madeira (23%); however, animals seen in two or more areas were all seen in Madeira (Table 3.10). Conversely, the percentage of animals captured in multiple sampling periods in only one location was highest in Madeira (30%) followed by the Azores and the Canary Islands, each with 6%. The Azores had the highest percentage of animals seen in only one sampling period (60%), followed by the Canary Islands (54%) and Madeira (47%).

Table 3.9 gives a summary of the number of animals captured or recaptured in only one location and the number of animals recaptured among two or more locations. The same data are presented in Table 3.10, but giving a more detailed chronological account of the captures by animal and area, while Figure 3.9 presents the data in a geographical context, making it easier to visualize the animals' displacements between locations.

Table 3.8 – The number of photo-identified animals in each location of the study area by uncertainty level (number of likely and certain matches presented without brackets; number of certain matches presented in brackets) and by type of capture history, i.e., animals seen in two or more locations, animals seen only in one location in two or more sampling periods (2 months), and animals only seen one location in one sampling period.

	Number of animals "captured" by area							
Capture history	Madeira	Canaries	Azores	Algarve	Mauritania	Guinea-Bissau	Senegal	Total
Animals seen in 2 or > locations	53 (44)	44 (37)	12 (9)	0 (0)	1 (1)	0 (0)	0 (0)	53 (44)
Animals seen only in one location, 2 or > sampling periods	71 (68)	7 (6)	2 (2)	1(1)	0 (0)	0 (0)	0 (0)	81 (77)
Animals only seen in one location in one sampling period	110 (120)	59 (60)	21 (21)	2 (2)	0 (0)	2 (2)	1 (1)	195 (206)
Total	234 (226)	110 (103)	35 (31)	2 (2)	1 (1)	2 (2)	1 (1)	329 (327)

Table 3.9 – Summary table of number of animals captured in each location of the study area by certainty level (number of likely and certain matches presented without brackets; number of certain matches presented in brackets), including animals seen only in one location (underlined; e.g. 181 (188) animals only seen in Madeira) and between locations (e.g. 40 (34) animals seen both in Madeira and the Canary Islands). The number of animals seen in three locations (Madeira, Azores and the Canary Islands) is marked with an asterisk.

	Madeira	Canaries	Azores	Algarve	Mauritania	Guinea-Bissau	Senegal
Madeira	181 (188)	40 (34)	8 (6)	0 (0)	1 (1)	0 (0)	0 (0)
Canaries		66 (66)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Azores		4 (3)*	23 (23)	0 (0)	0 (0)	0 (0)	0 (0)
Algarve				3 (3)	0 (0)	0 (0)	0 (0)
Mauritania					0 (0)	0 (0)	0 (0)
Guinea-Bissau						2 (2)	0 (0)
Senegal							1 (1)

Madeira and the Canary Islands had the highest number of animals recaptured between them (40), followed by Madeira and the Azores (8), and the Canary Islands and the Azores (4). There was also an important match between Madeira and Mauritania, confirming the displacement of Bryde's whales along the West African coast. No matches were found between Madeira, or any of the other Macaronesia archipelagos, and Algarve, Guinea-Bissau or Senegal, possibly due to the low sampling effort in those areas.

The captures of animals photo-identified in more than one location (e.g. Be0004, Be0016, Be0019, Be0058, Be0065, Be 0072, Be0084, Be0102, Be0148) for the years 2014 and 2017 (with more sampling effort in the Macaronesia archipelagos), suggest an overall seasonal sequence of displacement South-North-South, with animals being seen in the Canary Islands, followed by Madeira, Azores, Madeira and finally the Canary Islands (Table 3.10). Although the full sequence is not seen for any particular animal, the recaptures were usually in the first periods of the year in the Canary Islands, in the middle of the year Madeira and Azores, and at the end of the year in Madeira and Canary Islands. It is important to note that the Azores, contrary to Madeira and the Canary Islands, had the sampling effort concentrated between June and October (Figure II.2-1, Appendix II).

In Appendix II.4 are shown the tables representing captures over time of animals seen in multiple occasions in any location of the study area (Tables II.3.1-2) and animals seen only once in any location of the study area (Tables II.4.1-4).

Table 3.10 – Table showing the “captures” of photo-identified animals seen in multiple sampling locations of the study area over time. The animals’ identification, dorsal fin distinctiveness (CL) and site fidelity to Madeira (SF; 1–regular visitors, 2–occasional visitors, 3–rare visitors, 0–transients) are given on the left side of the table, as well as, the number of times animals were photo-identified in total and in each location, identified by letters and colours (M – Madeira, green; C – Canary Is., blue; A – Azores, yellow; GU – Guinea, grey; MA – Mauritania, violet). The captures between 2002 and 2021, by year and sampling period, are presented on the right side of the table, also identified with letters and colours. The sampling unit was 2 months (J – January-February; M – March-April; M – May-June, J – July-August, S – September-October, N – November-December), i.e., an animal seen at least once in a location in a sampling period was considered present in that location and counted as one capture in that sampling period. In some years (2014, 2017 and 2021), several animals were captured in two locations within the same sampling period (shown in the table).

Ind	CL	SF	M	C	A	AL	MA	GU	SE	total
Be0004	1	1	6	2						8
Be0005	1	1	8	1						9
Be0008	1	0	1		1					1
Be0016	1	1	15		1					15
Be0018	1	2	3	1						4
Be0019	1	1	8	3						11
Be0023	1	0	1	1						2
Be0026	1	1	11	3						14
Be0046	1	1	12		1					12
Be0055	1	0	1	1						2
Be0058	1	2	2		4					2
Be0062	1	0	1	1						2
Be0065	1	1	9	5						14
Be0069	1	2	1	2						3
Be0070	1	0	1	1						2
Be0072	1	2	1	3						4
Be0075	1	0	1	1						2
Be0084	1	2	3	1						4
Be0087	1	1	5	1						6
Be0089	1	0	1	1	1					2
Be0099	1	1	7	1						8
Be0101	1	1	4	1						5
Be0102	1	0	1	1	1					2
Be0103	1	3	1	1						2
Be0108	1	3	1	1						2
Be0115	0	0	1				1			1
Be0118	1	3	2	2						4
Be0124	1	2	3	1						4
Be0126	1	0	1	1						2
Be0128	1	0	2	1						3
Be0131	1	2	3	2	1					5
Be0135	1	0	1	1						2
Be0142	1	0	1	1						2
Be0143	1	0	1	1	1					2
Be0148	1	0	1	1						2
Be0153	1	0	1	1						2
Be0154	1	0	1	1						2
Be0156	1	0	1	1						2
Be0171	1	0	1		1					1
Be0178	1	2	1		1					1
Be0189	1	2	2	2						4
Be0218	1	2	4	1						5
Be0220	1	2	2		1					2
Be0224	1	0	1	1						2
Be0233	1	2	2	1						3
Be0236	1	1	2	1						3
Be0299	1	2	3	1						4
Be0356	0	0	1	1						2
Be0380	1	0	1	1						2
Be0383	1	0	1	1						2
Be0385	0	2	2	1						3
Be0388	1	0	1	1						2
Be0390	1	0	1		1					1

Ind	2002						2003						2004						2005						2006					
	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N
Be0004														C																
Be0005																												M		
Be0008																A														
Be0016																													M	
Be0018																						M								
Be0019																														
Be0023																														
Be0026																												M		
Be0046																														
Be0055																														
Be0058																														
Be0062																														
Be0065																					M		M					M		
Be0069																														
Be0070																														
Be0072																														
Be0075																														
Be0084																														
Be0087																														
Be0089																														
Be0099																														
Be0101																														
Be0102																														
Be0103																														
Be0108																														
Be0115																														
Be0118																														
Be0124																														
Be0126																														
Be0128																														
Be0131																														
Be0135																														
Be0142																														
Be0143																														
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Be0156																														
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Be0178																														
Be0189																														
Be0218																														
Be0220																														
Be0224																														
Be0233																														
Be0236																														
Be0299																														
Be0356																														
Be0380																														
Be0383																							C							
Be0385																														
Be0388																														
Be0390																														

Ind	2007						2008						2009						2010						2011					
	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N
Be0004																														
Be0005																											M	M		
Be0008				M																										
Be0016										M																		M		
Be0018										M	M																			
Be0019				M			M			M																		M		
Be0023																														
Be0026				M			M				M						M			C							M			
Be0046										M	M				M						M									
Be0055																						C								
Be0058																						A								
Be0062																														
Be0065				C			C																					M		
Be0069																														
Be0070																														
Be0072																														
Be0075																														
Be0084	M																													
Be0087																						M								
Be0089																														
Be0099																														
Be0101																	M													
Be0102																														
Be0103																														
Be0108																														
Be0115																														
Be0118																														
Be0124																														
Be0126																														
Be0128																														
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Be0171																														
Be0178																														
Be0189																														
Be0218																														
Be0220																														
Be0224																														
Be0233																														
Be0236					M																									
Be0299																														
Be0356																														
Be0380																														
Be0383																														
Be0385																														
Be0388																														
Be0390																														

Ind	2012						2013						2014						2015						2016					
	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N
Be0004			M												C	M	M	M				M								
Be0005																M	M					M					C			
Be0008																														
Be0016																	M	M	M			M		M	M			M		
Be0018																											C			
Be0019															C			M	M			M	M			C				
Be0023																														
Be0026																M C							C							
Be0046				M											M	M						M								
Be0055																														
Be0058										A	A											M								
Be0062																														
Be0065														C		M	M			C										
Be0069			C													M								C						
Be0070			C													M														
Be0072			C																											
Be0075			M																										C	
Be0084															C	M														
Be0087															M							M							M	
Be0089															M													C		
Be0099																M	M					M								C
Be0101																														
Be0102																A M											C			
Be0103																M														
Be0108																M														C
Be0115																														
Be0118																				C						C				
Be0124																	M	M				M								C
Be0126																							C							
Be0128																									M					
Be0131																	M			C		M				C				
Be0135																													M	
Be0142																													C	
Be0143																														
Be0148																													M	C
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Be0171																														
Be0178																														
Be0189																											C		C	
Be0218																														
Be0220																	M													
Be0224																								C						
Be0233																														
Be0236																														C
Be0299																													C	
Be0356																						M						C		
Be0380																												C		
Be0383																													M	
Be0385																	M						C							
Be0388																											C			
Be0390																														

Ind	2017						2018						2019						2020						2021					
	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N
Be0004										M																				
Be0005					M												M													
Be0008																														
Be0016				A	M					M	M																M			
Be0018																														
Be0019		C																												
Be0023			C						M																					
Be0026				M	M											M	M													
Be0046										M																	M	M A		M
Be0055					M																									
Be0058				A	M																									
Be0062			C						M																					
Be0065		C			M	M											M													
Be0069																														
Be0070																														
Be0072				C	M	C																								
Be0075																														
Be0084																						M								
Be0087			C						M																					
Be0089				A																										
Be0099					M	M																M	M							
Be0101			C		M	M					M																			
Be0102																														
Be0103		C																												
Be0108																														
Be0115				M									MA																	
Be0118																											M	M		
Be0124																														
Be0126																							M							
Be0128					M			C																						
Be0131				A											M															
Be0135					C																									
Be0142										M																				
Be0143				A	M				C																					
Be0148																														
Be0153			C																											
Be0154																													M	
Be0156	C																											M		
Be0171				A	M																									
Be0178				A	M																									
Be0189				M																								M		
Be0218			C			M			M	M					M															
Be0220					M					A																				
Be0224					M																									
Be0233	C				M																							M		
Be0236					M																									
Be0299					M										M							M								
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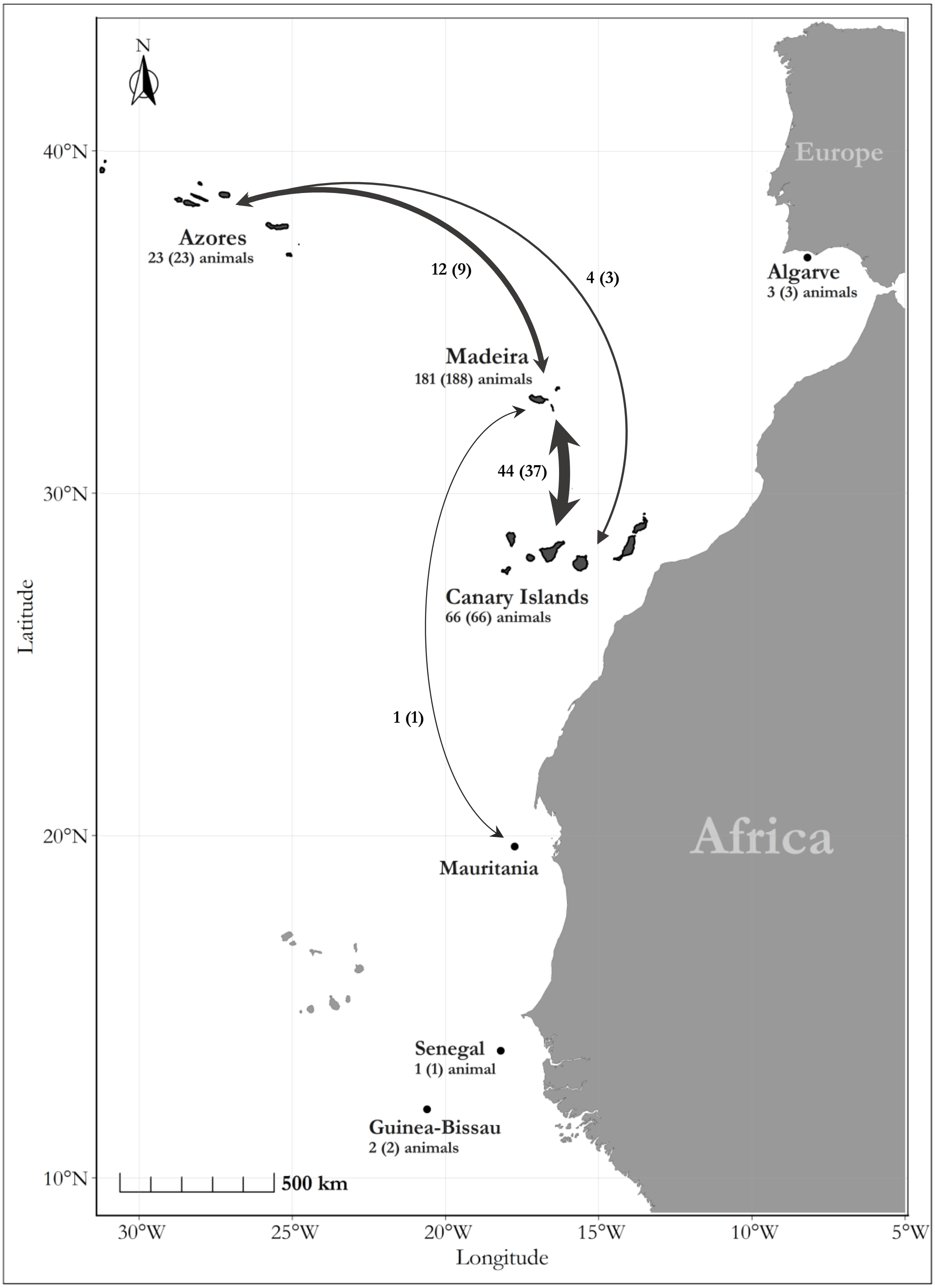

Figure 3.9. Map showing the general movements of animals in the overall study area, reflected by the recaptures of animals between sampling locations by level of certainty in the matches (number of likely and certain matches presented without brackets; number of certain matches presented in brackets). The thickness of the arrows is proportional to the number of animals recaptured between two locations (numbers next to arrow). The number of animals captured exclusively in each location is given below the name of the location.

3.3.2.2 Satellite telemetry

The total distance travelled by Bryde's whale Be0107, Be0194 and Be0024 while tagged were 1 647 km, 2 295 km and 1 078 km, respectively, with average swimming speeds between 1.75 and 3.16 km/h (Table 3.11). The first animal was tracked for 22 days, the second for 55 days and the third for 21 days. Table 3.11 also shows the minimum and maximum speeds of each animal the average speed standard deviation, as well as the mean track steps length and respective statistics.

Table 3.11 – Summary statistics of the estimated tracks of the three Bryde's whales with sufficient positions data from the satellite tags for analysis. The table includes the date of deployment, number of days transmitting; mean travelling speed (km/h), and respective standard deviation, minimum and maximum speeds, and total linear travel distance, mean distance of each track step and respective standard deviation, minimum and maximum distance of the track steps.

Tags	Animal tagged	Deployment date	Days transmitting	Travelling speed (km/h)				Linear travel distance (km) - steps				
				Mean	Std. Dev	Min	Max	Total	mean	Std. Dev	Min	Max
MBM_S6_01	Be0107	02/09/2018	22	3.16	1.89	0.28	9.28	1647	25.73	15.46	2.21	74.27
MBM_S6_03	Be0194	26/10/2018	55	1.75	1.54	0.03	10.16	2295	13.99	12.30	0.22	81.27
MBM_S6_06	Be0024	09/08/2020	21	2.25	2.71	0.19	15.04	1078	17.96	21.70	1.52	120.32

Animal Be0107 went 156 km southwest of Madeira (tagging location), turned northeast passing by Madeira and reaching a maximum distance of 350 km away from island, going through the seamounts north of Madeira (Godzilla, Lion and Dragon) (Figure 3.10, tag MBM_S6_01). Then it returned south, passing west of Madeira, and continuing southwards until the tag stopped transmitting, not far from the southernmost position it had reached previously. The animals Be0194 and Be0024 travelled away from Madeira, with the first animal going southeast towards the banks north of the Canary Islands, including Dacia and Concépcion, followed by the waters north of Lanzarote island, reaching a maximum distance from Madeira of 555 km and 150 km from the Moroccan coast (Figure 3.10, tag MBM_S6_03). The second animal travelled north towards Porto Santo Island, and then transited through open ocean passing between seamounts Seine, Unicorn and Ampère, west of Gorringe, until it reached the deep waters of the Tagus abyssal plain. The final position was recorded off the coast of Portugal mainland, at a distance of 1 082 km from Madeira and 257 km west of Sines (Figure 3.10, tag MBM_S6_06).

The best HMM identified three states, based on step length and turning angles, from which Bryde's whales' behaviour can be inferred. State 1 can be described as area-restricted search (ARS) pattern that may be associated with search for prey and foraging, with a mean step length of 12.05 km (SD: 7.71 km) and mean turning angle of 0° (radian; concentration: 0.73)(Figure 3.11, Table II.5.1, Appendix II).

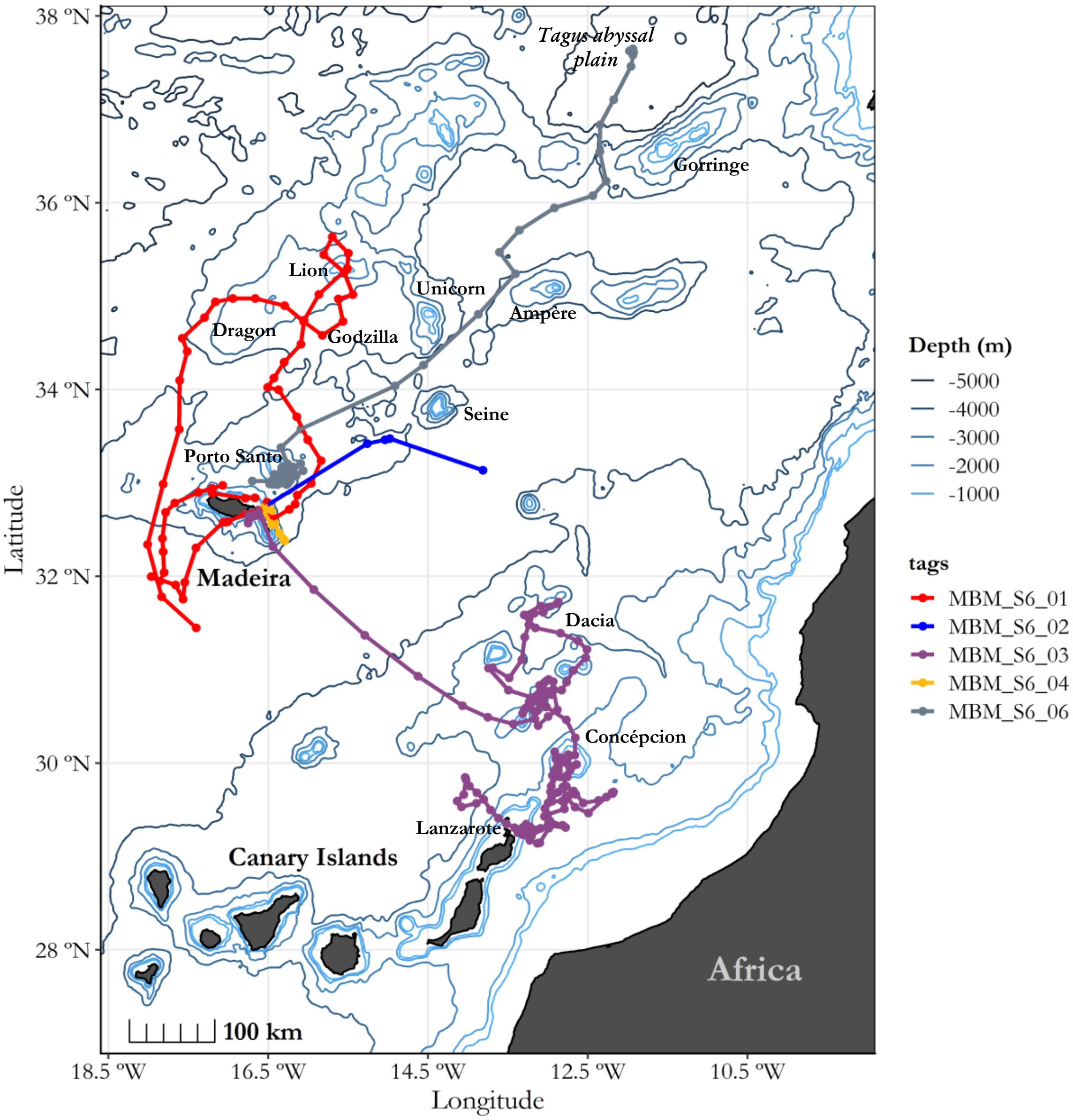

Figure 3.10. Map showing the sequential geographic positions (dots), and likely path (line), of five Bryde's whales tagged in Madeira Island and followed by satellite telemetry. The tags were deployed in the following animals, by sequential order of the tags: Be0107, Be0288, Be0194, Be0306, Be0308 and Be0024.

State 2 can be associated with transit behaviour, with a mean step length of 79.59 km (SD: 23.27 km) and mean turning angle of 0° (concentration: 13.42), while State 3 may be interpreted as exploratory behaviour, with a mean step length of 32.75 km (SD: 10.18 km) and mean turning angle of 0° (concentration: 1.8). In Appendix II, Table II.5.1 also gives the transition probabilities between the three States, while Figure.II.5.2 to Figure.II.5.4 present those transition probabilities visually over the sequence of track positions. In the same Appendix, are also presented the diagnostic plots of the selected HMM, including the auto-correlation function plots of the variables used in the model (step length and turning angle) (Figure II.5.5 and Figure II.5.6).

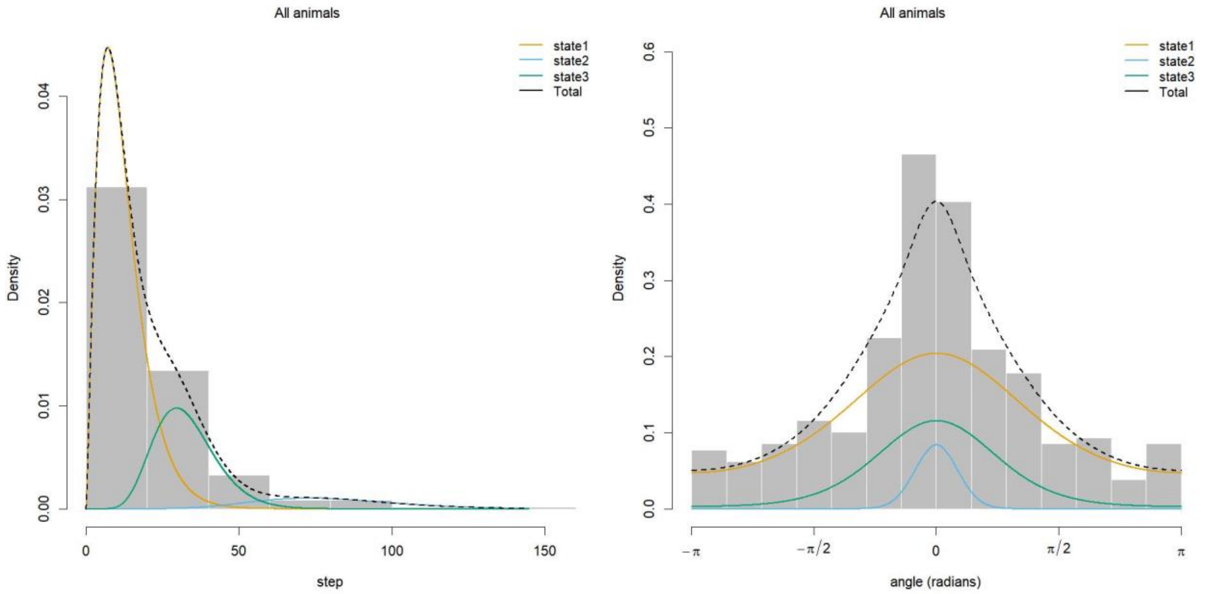

Figure 3.11. Left: Frequency distribution histogram of step length values of all tracks analysed (MBM_S6_01, MBM_S6_03 and MBM_S6_06) and the corresponding distribution curves by state (1-3) and total. Right: Frequency distribution histogram of turning values of the same tracks and the corresponding distribution curves by state (1-3) and total.

Table 3.12 – Summary of the inferred behavioural states (State 1 – Area Restricted Search, probably associated with prey searching and feeding; State 2 – Transiting; State 3 – Exploring), described by the number of days, hours, percentage of time, mean speed and speed standard deviation (SD) each animal displayed while being tracked.

Tag /animal	State	1	2	3	All states
MBM_S6_01 Be0107	days	5.67	1.67	14.00	21.33
	hours	136	40	336	512
	% hours	**27%**	**8%**	**66%**	100%
	mean speed	1.90	7.51	3.18	1.97
	speed SD	1.55	1.86	0.98	1.89
MBM_S6_03 Be0194	days	47.33	1.67	6.00	55.00
	hours	1136	40	144	1320
	% hours	**86%**	**3%**	**11%**	100%
	mean speed	1.39	6.97	3.14	1.75
	speed SD	0.78	3.99	1.65	1.54
MBM_S6_06 Be0024	days	14.33	2.00	4.00	20.33
	hours	344	48	96	488
	% hours	**70%**	**10%**	**20%**	100%
	mean speed	0.99	7.57	4.24	2.25
	speed SD	0.69	4.44	1.92	2.71

The animals' tracks total temporal length went from 20.33 days (488 hours) to 55 days (1320 hours) (Table 3.12). Animal Be0107 spent most of its time in exploratory activity (State 3; 66%) followed by ARS (State 1; 27%), while animals Be0194 and Be0024 invested most of their time on ARS (86% and 70%, respectively) followed by exploratory activity (11% and 20%, respectively) (Table 3.12).

Consistently, all animals had very similar speeds for each state, with State 1 showing the lower speeds (0.99 – 1.90 km/h), followed by State 3 (3.18 – 4.24 km/h) and State 2 (6.97 – 7.57 km/h), which is in line with the speeds one would expect from the activities of prey searching and feeding, exploring and transiting, respectively.

Spatial representation of the behavioural states of Be0194, Be0024 and Be0107 are presented in Figure 3.14, Figure 3.12 and Figure 3.13, respectively. Animals were mostly in State 1 (ARS) around inshore waters of Madeira archipelago and Lanzarote Island and over seamounts. The animals were in State 2 (transit) when travelling in open ocean between features (e.g. islands and seamounts) and switched to State 3 (exploratory activity) when approaching the islands and seamounts or when travelling between nearby islands or seamounts.

Curiously, animal Be0024 that was tagged in August (middle of the seasonal presence of Bryde's whales in this area of the Atlantic) was tracked northwards, while the animals tagged in September (Be0107) and October (Be0194) were tracked and lost when moving southwards.

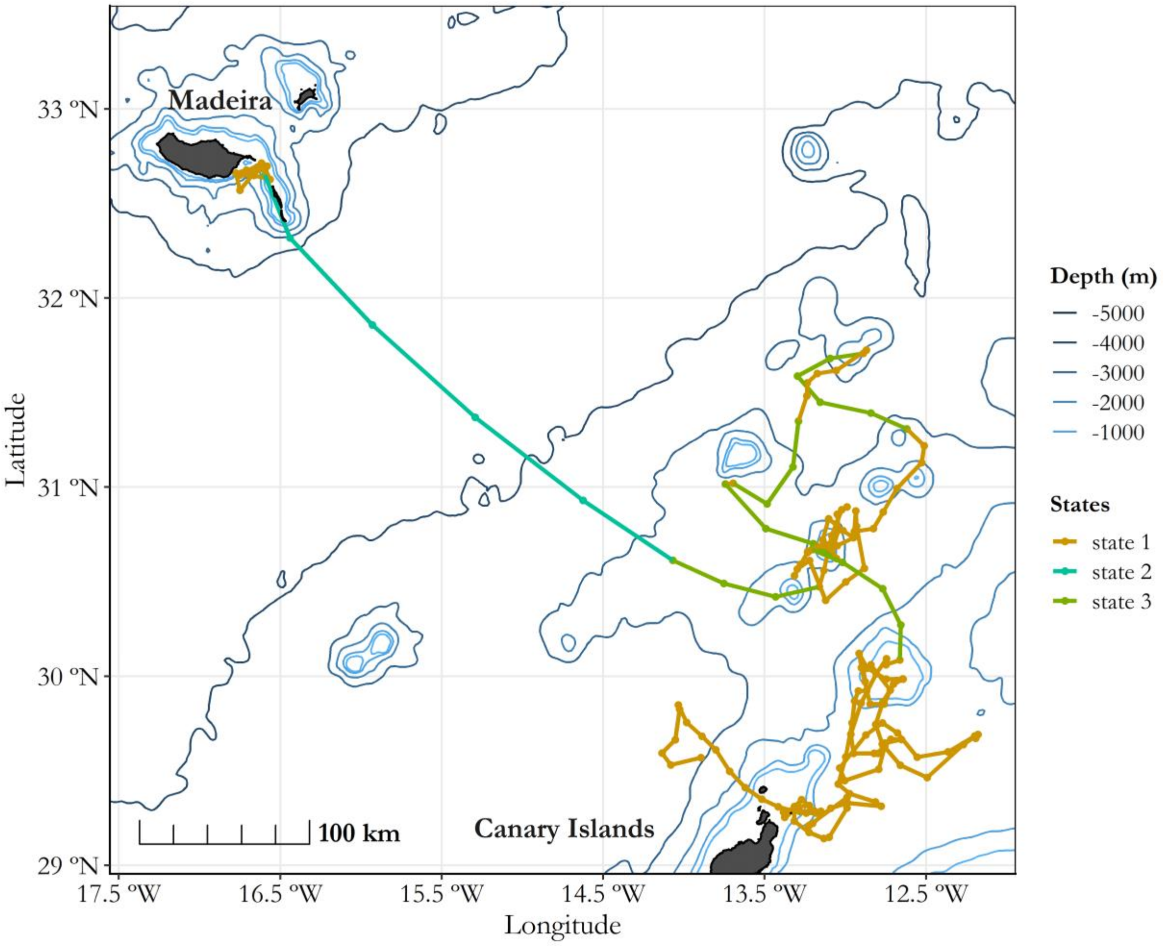

Figure 3.12. Track of Bryde's whale Be0194 (MBM_S6_03), tagged in October of 2018, with the identification of each of the states identified by the selected Hidden Markov Model.

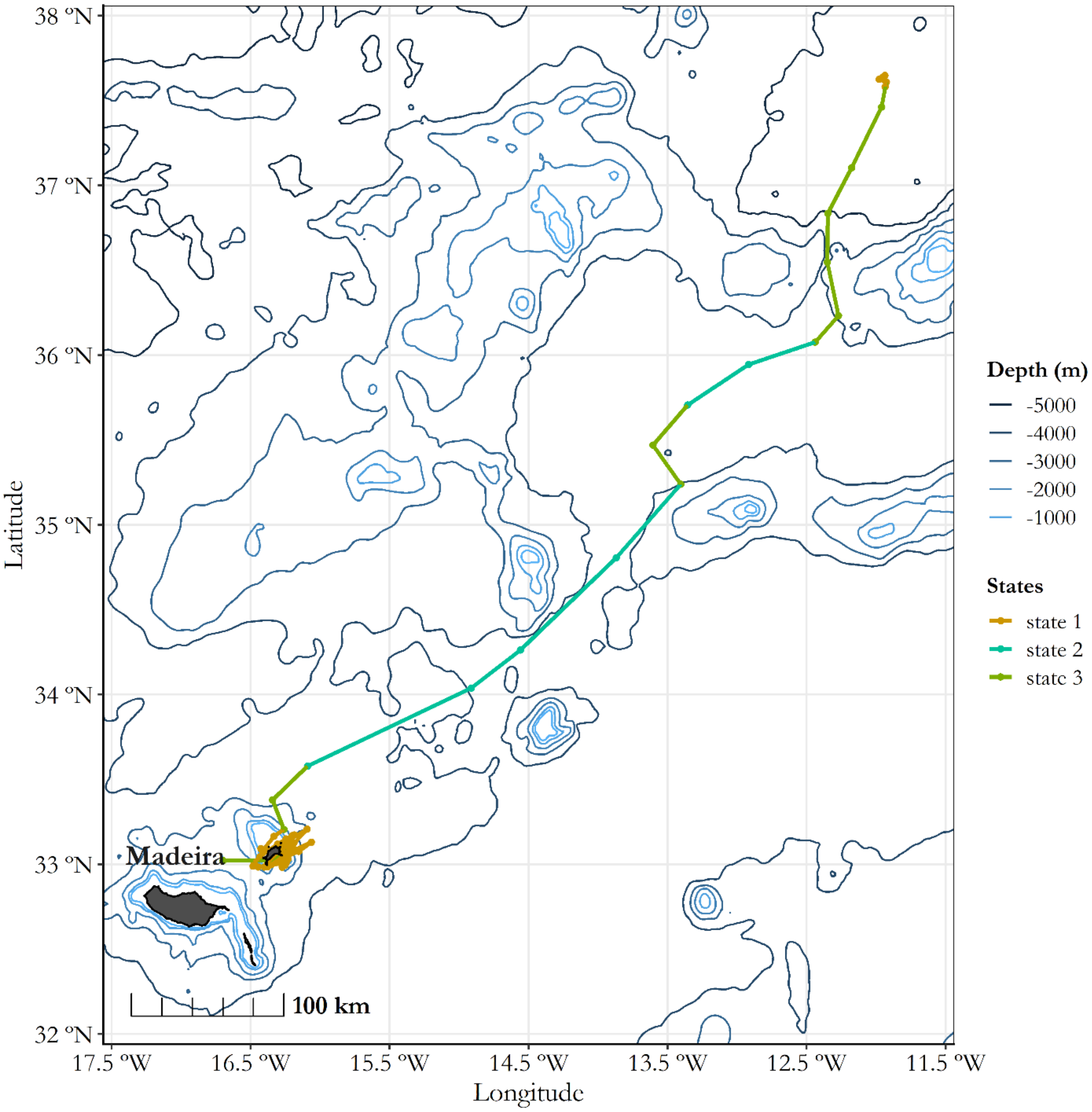

Figure 3.13. Track of Bryde's whale Be0024 (MBM_S6_06), tagged in Agosto of 2020, with the identification of each of the states identified by the selected Hidden Markov Model.

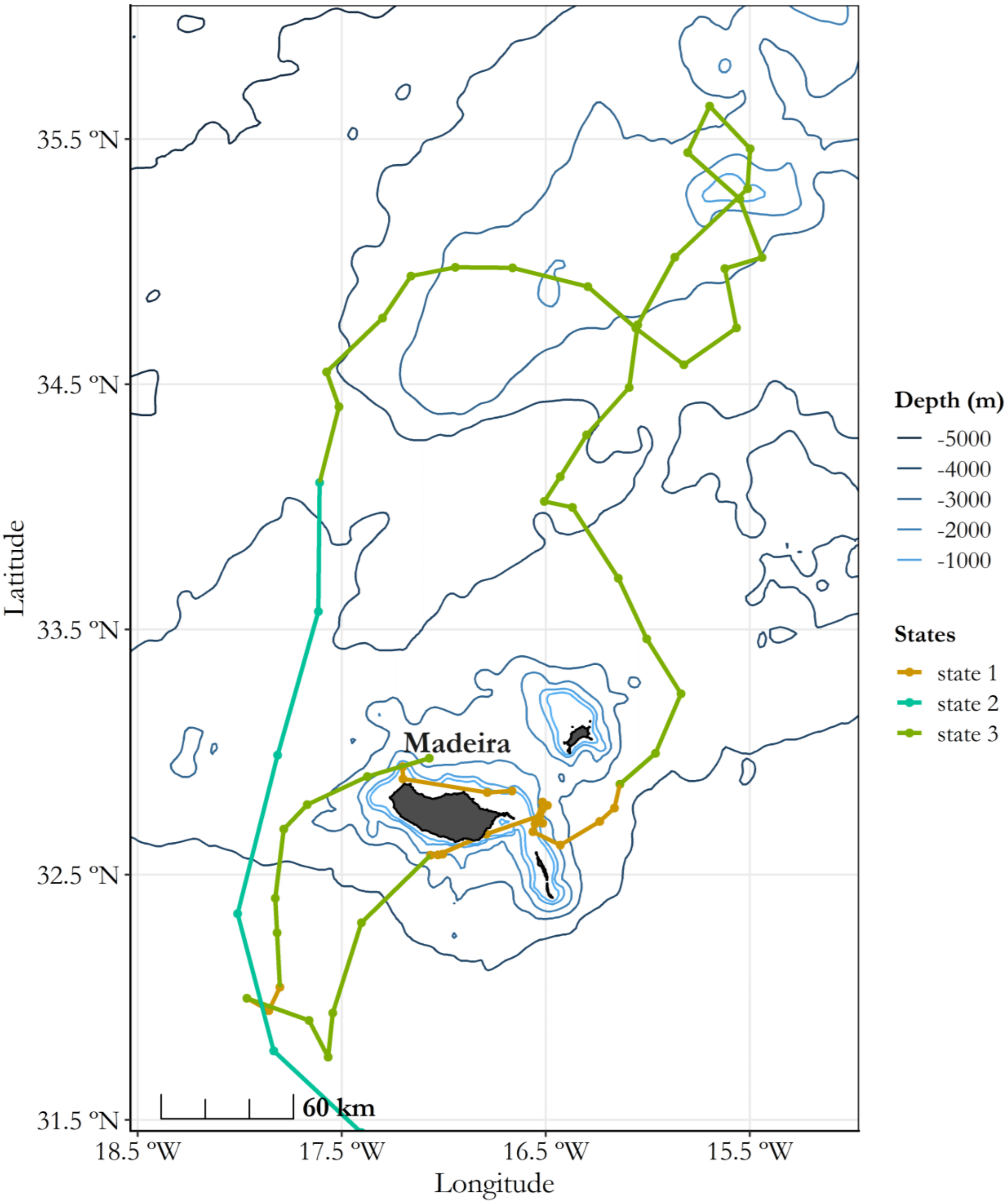

Figure 3.14. Track of Bryde's whale Be0107 (MBM_S6_01), tagged in September of 2018, with the identification of each of the states identified by the selected Hidden Markov Model.

3.3.3 Site fidelity to Madeira archipelago

3.3.3.1 Site fidelity indices

The SSFI (IH4) for the Bryde's whale population using Madeira inshore waters for the period 2005-2021, calculated for each of the four datasets (certainty level 2 and 3), are presented in Table 3.13. Although the number of animals varies considerably among datasets, the SSFI, and the respective standard deviation (SD) and the confidence intervals (CI), are very similar, indicating consistency in the site fidelity levels across the datasets.

The indices "IA1","IA2","IA3","IH2","IH3" and "IH4" were not strongly correlated (Pearson's correlation coefficients <0.8) in the four datasets and were thus selected to identify the site fidelity structure of the population.

The optimal number of clusters chosen was three, applying the rules specified in Section 3.2.2.6. In Figure II.6.1 and Figure II.6.2 of Appendix II, are presented the graphics with the results from the Silhouette method and the clusters configuration represented on the two first dimensions of Principal Component Analysis, for the four datasets.

Table 3.13 – The standard site fidelity index (SSFI) of the Bryde's whale population using Madeira inshore waters, calculated for each of the datasets (WM-SC, WM-SN, ALL-SC, ALL-SN) using the IH4 index (Tschopp *et al.*, 2018). Datasets were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (ALL)

Dataset	n	SSFI	SD	95% CI
WM-SC	86	0.0037	0.0046	0.0000 - 0.0127
WM-SN	100	0.0033	0.0045	0.0000 - 0.0121
ALL-SC	188	0.0033	0.0054	0.0000 - 0.0139
ALL-SN	225	0.0034	0.0046	0.0000 - 0.0123

Table 3.14 – Total number of animals, number of transients (seen only once) and non-transient animals (seen more than once) in each dataset (WM-SC, WM-SN, ALL-SC, ALL-SN), with the non-transient animals grouped in one of three selected clusters according to their individual site fidelity index (ISF). Also shown is the number of females (inferred from animals associated with calves) and animals of unknown sex in each cluster and transients for the dataset ALL-SN. Datasets were obtained by combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well-marked (distinctiveness classes 1-3; WM) and all identified animals, including well-marked and with distinctive shaped dorsal fins (ALL).

Dataset	Number of non-transient animals				transient animals	total of animals
	Cluster 1	Cluster 2	Cluster 3	Total clusters		
WM-SC	18	29	8	55	31	86
WM-SN	18	32	8	58	42	100
ALL-SC	29	64	8	101	87	188
ALL-SN	28	70	8	106	119	225
unknown sex	*11*	*56*	*5*	*72*	*107*	*179*
Female (%)	*17 (61%)*	*14 (20%)*	*3 (38%)*	*34 (32%)*	*12 (11%)*	*46 (20%)*

Table 3.14 shows the total number of non-transient animals (seen more than once) for which the individual SFI was calculated as well as the number of animals grouped in each of the three clusters. The common animals among datasets are consistently allocated to the same clusters across the datasets (e.g. cluster 3 with the same 8 animals in all datasets), with an increase in the number of animals in clusters 2 and 4 as the number of animals increases in the datasets, especially when comparing WM datasets with ALL datasets.

The SSFI (IH4) values of each cluster for the four datasets are presented in Figure 3.15 and Table II.6.1 of Appendix II. Although the Kruskal-Wallis χ^2 tests were significant or very significant for the SSFI among clusters for all datasets ($p < 0.005$ or $p < 0.001$), according to the *post-hoc* pairwise comparisons (Dunn test) the SSFI values were significantly different between cluster 1 and 3 and clusters 2 and 3, but not between clusters 1 and 2, for all datasets.

For the remaining SFI (IA1, IA2, IA3, IH2 and IH3), the Kruskal-Wallis χ^2 tests were also either significant or highly significant among clusters for all datasets ($p < 0.005$ or $p < 0.001$). Although the Dunn tests were also significant or very significant ($p <0.005$ or $p < 0.001$, respectively) for most SFI post-hoc pairwise comparisons in the four datasets, there were in most SFI (except IH2 with all clusters significantly or very significantly different) a pair of clusters that was not significantly different across the datasets (Table II.6.3, Appendix II). The absence of significant differences can be broadly visualised in the graphs of the indices presented in Figure 3.16 for datasets WM-SN and ALL-SN and in Figure 1.6.3 (Appendix II) for datasets WM-SC and ALL-SC. These results justify the combined use of non-correlated SFI to determine and characterize the site fidelity structure of the Bryde's whales using Madeira inshore waters.

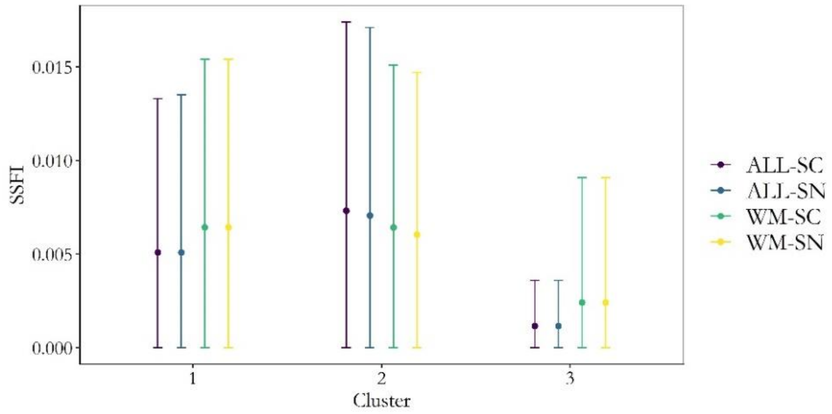

Figure 3.15. The estimated SSFI (IH4 index) values for each cluster, and the respective lower and upper 95% confidence intervals, by dataset. Datasets were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well-marked (distinctiveness classes 1-3; WM) and all identified animals, including well-marked and with distinctive shaped dorsal fins (ALL).

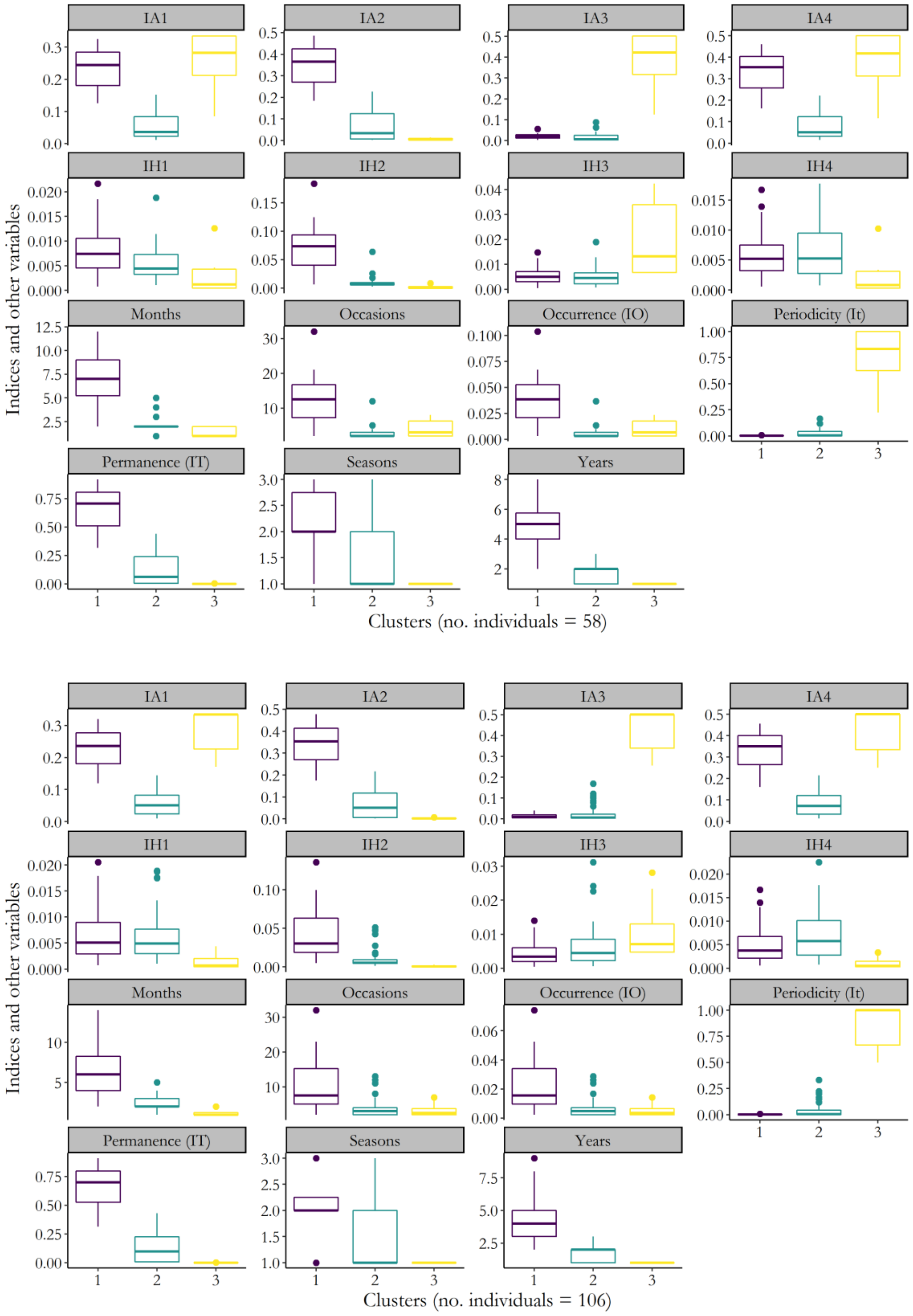

Figure 3.16. Results of the parameters characterizing each site fidelity clusters, based on K-means, for Bryde's whales' population using Madeira inshore waters. The top graphs were based on the WM-SN dataset (58 animals) and the bottom graphs on the ALL-SN dataset (106 animals). WM-SN – well-marked individuals (distinctiveness classes 1-3), confirmed or suspected as Bryde's whales; ALL – all identified animals, including well-marked and with distinctive shaped dorsal fins (ALL), confirmed or suspected as Bryde's whales.

The site fidelity structure was very similar across the datasets analysed, with identical results between the two WM datasets and between the two ALL datasets. All datasets share the same pattern of differences and similarities in the parameters amongst clusters (Figure 3.16), albeit with some differences in the absolute values. As such, the results of the dataset ALL-SN (the dataset with most animals) is here used to describe the site fidelity structure of the Bryde's whales using Madeira inshore waters (Figure 3.16, bottom).

Although cluster 1 and 2 had similar SSFI, they had differences in occurrence and permanence, but not periodicity. The differences are clearly reflected in the indices IA2 and IH3 (Figure 3.16). Cluster 1, with 28 animals, had the highest Occurrence and Permanence means (OI=0.023; IT=0.658) and medians (OI=0.016; IT=0.658), indicating that these animals visited the study area on average more times and stayed longer during the study period than animals from the other clusters. These animals, which we can name as "regular visitors", visited Madeira inshore waters on average four years out of the 17 years of the study, although some individuals were seen up to nine years. They were usually seen in Madeira in two seasons, some animals in three seasons, and over six different months (maximum 14 months) during the study period. Cluster 2, which we can name as "occasional visitors", had lower Occurrence and Permanence mean (OI = 0.006; IT = 0.123) and median (OI = 0.005; IT = 0.097) values, indicating that they were not as regular Madeira visitors as cluster 1 and stayed less time in the study area during the study period. This pattern is reflected by the number of years (mean = 1.75; median = 2; max = 3), seasons (mean = 1.5; median = 1; max = 3) and months (mean = 2.4, median = 2; max = 5) during the study period these animals were seen in Madeira. Finally, cluster 3, which we can name as "rare visitors", had the lowest Occurrence and Permanence mean (OI = 0.006; IT = 0.0006) and median (OI = 0.0036; IT = 0.0003) values, indicating that they stayed overall little time in the study area. The animals of cluster 3 were captured in the study area in only one year, one season and one month during the study period. However, the animals of this cluster had high values of periodicity, indicating that they were captured in few but consecutive occasions, resulting in high values of IA1, IA3 and IA4. The rare visitors, unlike the transients (captured once in the study area) were capture two or more times during the short visit to the study area.

The proportion of females in the "regular visitors" classification (61%) is much higher than in the "occasional visitors" (20%), "rare visitors" (38%) or transients (11%) classifications (Table 3.14). However, when a one sample two tailed z-test for proportions is applied to the data, the null hypothesis that the proportion of females was equal to 50% could not be rejected for any of the clusters, including transients, as expected in a population with a balanced sex ratio and with females randomly mixed amongst clusters.

In Appendix II, Table II.6-4, are presented the results of a pair-wise comparison of the proportion of females between clusters, including transients, using a two-sample two-tailed z-test for proportions. All pair-wise comparisons of clusters showed significantly different proportions of females, except cluster 3 ("rare visitors") with cluster 1 ("regular visitors") and cluster 2 ("occasional visitors").

For the period 2005 – 2012, the combined average percentage of regular and occasional visitors was 71% of all animals captured in that period, while the remaining 29% were rare visitors and transients. For the period 2014 – 2021 those values were 56% for regular and occasional visitors and 44% for rare visitors and transients (Figure 3.17).

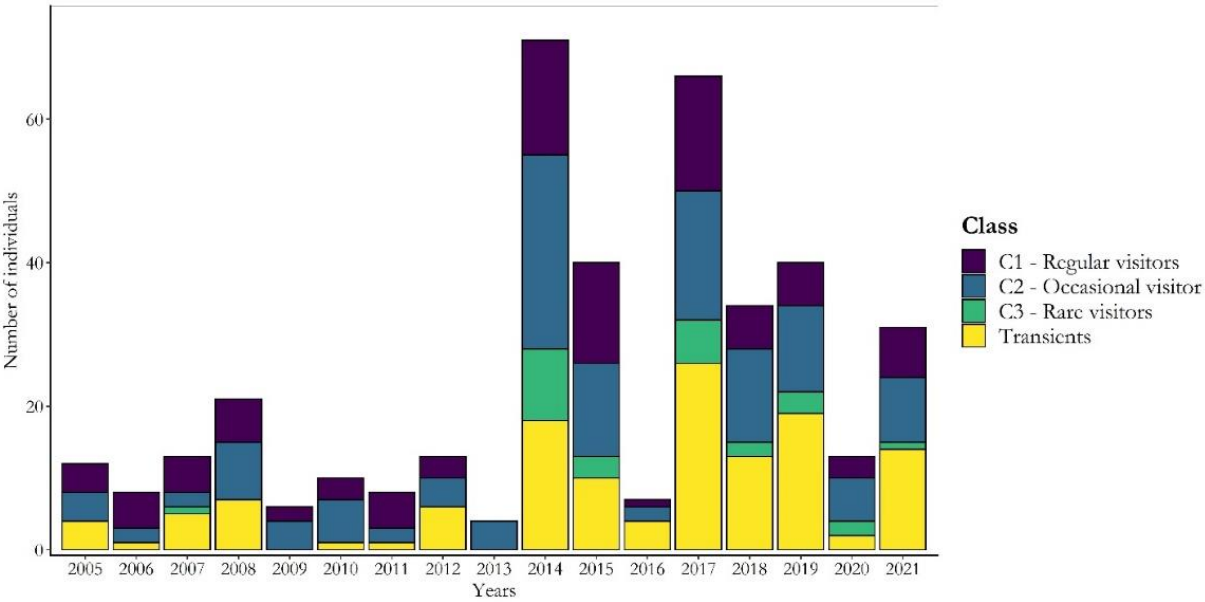

Figure 3.17. Distribution of the number of "captured" animals in dataset ALL-SN (all identified animals, including well-marked and with distinctive shaped dorsal fins (ALL), confirmed or suspected as Bryde's whales) by year, site fidelity class (clusters 1,2 and 3) and transients.

Table 3.15 – Percentage of females and animals of unknown sex by classes of higher site fidelity (regular and occasional visitors) and lower site fidelity (rare visitors and transients) for 2005 – 2012 and 2014 – 2021.

	Regular and occasional visitors		Rare visitors and transients		ALL	
	Females	unknown sex	Females	unknown sex	Females	unknown sex
2005-2012	63%	37%	10%	90%	46%	54%
2014-2021	38%	62%	11%	89%	28%	72%

The percentage of identified females and animals of unknown sex also changed between 2005 – 2012 and 2014 – 2021, mostly for regular and occasional visitors and all site fidelity classes combined (Table 3.15). In the first period most of the regular and occasional visitors were females while rare visitors and transients were of unknown sex, while in the second period animals of both combined site fidelity classes were mostly of unknown sex.

From all the animals tagged with satellite transmitters, two were allocated to the cluster of "regular visitors" (Be0024 and Be0194), two to the cluster of "occasional visitors" (Be107 and Be0288) and two were transients (Be0306 and Be0308). In Table 3.16 are given the average number of days each satellite tagged animal spent in the Madeira inshore waters (photo-identification study area) and the respective site fidelity class based on SFI.

Table 3.16 – Mean number of days each satellite tagged animal spend in Madeira photo-identification study area (Madeira inshore waters), the identification of the animals and respective tag ID, date of deployment and site fidelity class, based on SFI (Site fidelity indices).

Tags	Deployment date	total nº days after tagging		Proportion time inside study area	Animal tagged	Site fidelity class	Obs.
		inside study area	outside study area				
MBM_S6_01	02/09/2018	6.00	14.33	30%	Be0107	Occasional visitors	
MBM_S6_02	25/07/2019	<1	~4	~20%	Be0288	Occasional visitors	Short transmission period
MBM_S6_03	26/10/2018	3.67	51.00	7%	Be0194	Regular visitors	Tagged end of season
MBM_S6_04	19/08/2019	1.17	0.00	100%	Be0306	Transients	Short transmission period
MBM_S6_05	09/08/2019	-	-	-	Be0308	Transients	
MBM_S6_06	09/08/2020	13.33	6.67	67%	Be0024	Regular visitors	Female with calf

3.3.4 Demographic parameters of Bryde's using Madeira archipelago

3.3.4.1 Apparent Survival from 2005 to 2021

The CJS models included the effect of transience on the apparent survival probability to address the lack of fit indicated by the GOF test 3.SR for two of the four datasets with matching uncertainty 2-3 analysed (Table 3.17). The models with most support (QAICc weight) were two candidate models in the case of the dataset WM-SC and one candidate model in the remaining datasets (Table 3.18).

The model with most support for all datasets included the effect of transience in survival and recapture probabilities varying annually. In the case of the dataset with two candidate models (WM-SC), the second candidate model had survival constant and recapture probability varying over time (years). Among the models with lowest AIC scores, and similar QAICc weights, were those with additive or interactive effect between a liner trend, T, and transience in survival. However, there were contradictory effects, with $\varphi(T + trans)$ having a downwards effect (negative slope) on survival and $\varphi(T * trans)$ an upwards effect (positive slope). This contradiction let to these models not being considered in the final selected models; the effects of these models in model averaging would in any case cancel each other out.

Table 3.17 – Results of four components of the goodness-of-fit tests (GOF), the global combined test of overall CJS model fit and the variance inflation factor (ĉ), calculated as the χ^2/degrees of freedom. Datasets for which survival estimates were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (ALL).

Dataset	Global test	2.CT	3.SR	2.CL	3.SM	ĉ
WM-SC	$\chi^2 = 35.401$ df= 50 p= 0.941	χ^2= 6.965 f= 14 p= 0.936	χ^2= 18.267 df= 12 p= 0.108	χ^2= 7.710 df= 14 p= 0.904	χ^2= 2.459 df= 10 p= 0.991	0.708
WM-SN	$\chi^2 = 38.707$ df = 51 p = 0.897	$\chi^2 = 6.242$ df = 14 p = 0.960	$\chi^2 = 20.352$ df = 13 p = 0.087	$\chi^2 = 9.523$ df = 14 p = 0.796	$\chi^2 = 2.590$ df = 10 p = 0.989	0.759
ALL-SC	$\chi^2 = 60.062$ df = 56 p = 0.331	$\chi^2 = 7.056$ df = 14 p = 0.933	$\chi^2 = 32.557$ df = 13 p = **0.002**	$\chi^2 = 12.950$ df = 16 p = 0.676	$\chi^2 = 7.499$ df = 13 p = 0.875	1.073
ALL-SN	$\chi^2 = 69.241$ df = 56 p = 0.11	$\chi^2 = 6.382$ df = 14 p = 0.956	$\chi^2 = 41.054$ df = 13 p = **0.000**	$\chi^2 = 14.000$ df = 16 p = 0.598	$\chi^2 = 7.797$ df = 13 p = 0.857	1.236

Table 3.18 – The best-supported candidate CJS models (≤10 ΔQAICc) for the period 2005-2021 for each dataset with matching certainty 2-3, with probability of apparent survival (φ) constant (.) or accounting for transience (*trans*) and probability of recapture changing over time (*t*). Datasets for which survival estimates were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (ALL).

Dataset	Model	QAICc	ΔQAICc	QAIC weight	Deviance	Number of parameters
WM-SC	$\varphi(trans)\ p(t)$	469.973	0.000	0.942	280.647	18
	$\varphi(.)\ p(t)$	475.562	5.589	0.058	288.777	17
WM-SN	$\varphi(trans)\ p(t)$	501.949	0*	1	279.80884	18
ALL-SC	$\varphi(trans)\ p(t)$	765.697	0**	1	367.491	18
ALL-SN	$\varphi(trans)\ p(t)$	711.486	0***	1	319.384	18

* - The next model had a ΔQAICc of 10.409

** - The next model had a ΔQAICc of 13.525

*** - The next model had a ΔQAICc of 15.281

The equivalent datasets but with matching certainty 3 (WM-SC.3, WM-SN.3; ALL-SC.3 and ALL-SN.3) were also analysed and had similar results. The candidate models with most support from the data were the same candidate models selected for the corresponding datasets with matching certainty 2-3, with the exception of dataset ALL-SN.3 with one more model, which included the effect of transience on survival and constant recapture probability over time (Appendix II, Table II.7-2).

The apparent survival estimate for non-transient animals was estimated to be greater than 0.98 for all datasets, ranging from 0.986 in WM-SC to 1 in ALL-SN (Table 3.19). As expected, the apparent survival estimates for transients was considerably lower than for non-transients, with a minimum of 0.58 in ALL-SN and a maximum of 0.74 in WM-SC, reflecting not only true survival of the animals but also permanent emigration.

Table 3.19 – Apparent survival estimates for the period 2005-2021 for each dataset with matching certainty 2-3, and the respective standard error and 95% confidence intervals. Datasets for which survival estimates were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (ALL).

Dataset	Parameter	Estimate	Standard error	95% CI
WM-SC	non-transients	0.986	0.016	0.886 - 0.998
	transients	0.737	0.105	0.493 - 0.890
WM-SN	non-transients	0.988	0.015	0.874 - 0.999
	transients	0.658	0.084	0.481 - 0.800
ALL-SC	non-transients	0.996	0.013	0.405 - 1.000
	transients	0.637	0.066	0.500 - 0.754
ALL-SN	non-transients	The parameter estimation hit the upper bound and was fixed at 1		
	transients	0.581	0.067	0.446 - 0.705

The equivalent datasets with matching certainty 3 (WM-SC.3, WM-SN.3, ALL-SC.3 and ALL-SN.3), had a similar pattern in the apparent survival estimates as the datasets which included matches with certainty 2-3, but with slightly lower estimated values especially for transients (Appendix II, Table II.7-3).

The recapture probabilities estimated for each year (2005-2021) by the candidate models of each dataset with matching certainty 2-3 are presented in Figure 3.18. The recapture probabilities reached the highest values in 2014 (>0.5), followed by 2015 and 2006. The lowest recapture probabilities were estimated for 2013, 2016 and 2020. The remaining years had varying recapture probabilities around 0.25 but, depending on the year and dataset, reaching higher or lower values. The datasets with matching uncertainty 3 had, in general, similar estimates of recapture probability as the datasets with matching uncertainty 2-3 (Appendix II, Figure II.7-1).

The apparent survival probability was also estimated for animals with different site fidelity indices, as defined in Section 3.3.3. The apparent survival of animals with a regular presence in the study area (Cluster 1) was estimated as 1 across the four datasets, although it was only possible to fit simpler models due to the limited data (Table 3.20). The animals defined as occasional visitors had apparent survival probabilities following a downwards trend over the years, with estimates ranging from 0.84 to 0.96 across years and datasets (Figure 3.19). No estimates were calculated for cluster 3 (non-transient animals with a rare presence in Madeira inshore waters) due to the lack of data to fit models.

Results of the four components of the goodness-of-fit tests (GOF) and the global combined test of overall CJS model fit for the datasets used in this analysis are given in Appendix II, Table II.7-4, as well as the recapture probabilities estimated by the models for regular animals and occasional animals for each dataset.

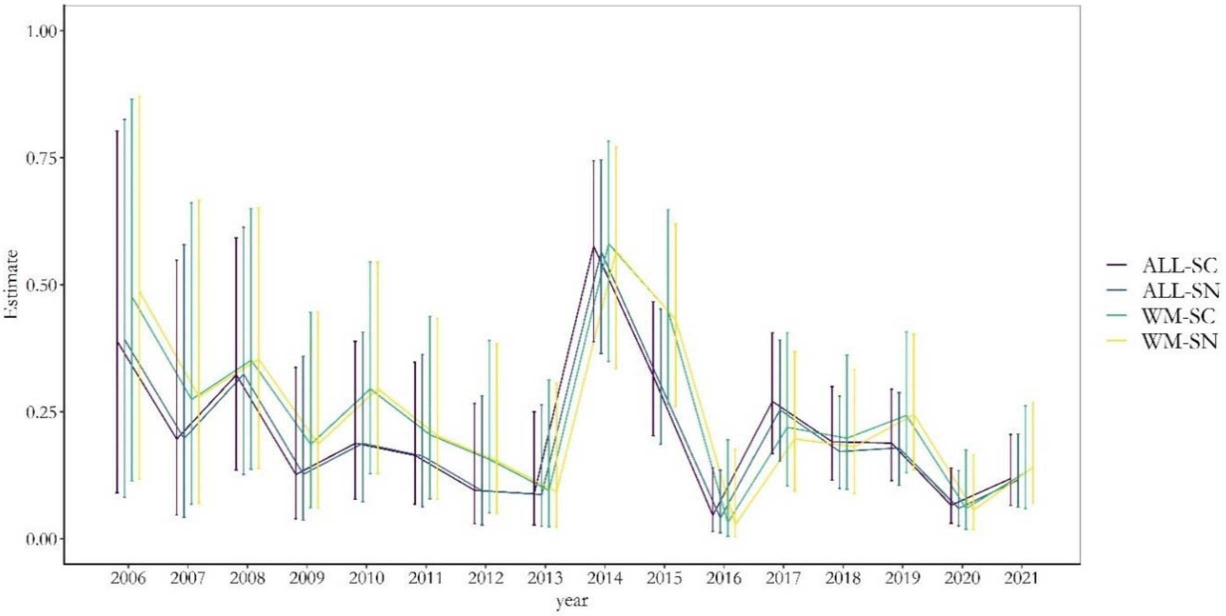

Figure 3.18. Yearly recapture probability estimates of non-calf Bryde's whales for the period 2005-2021 for each of the datasets with match uncertainty 2-3, and the respective 95% confidence intervals. Datasets the were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (ALL).

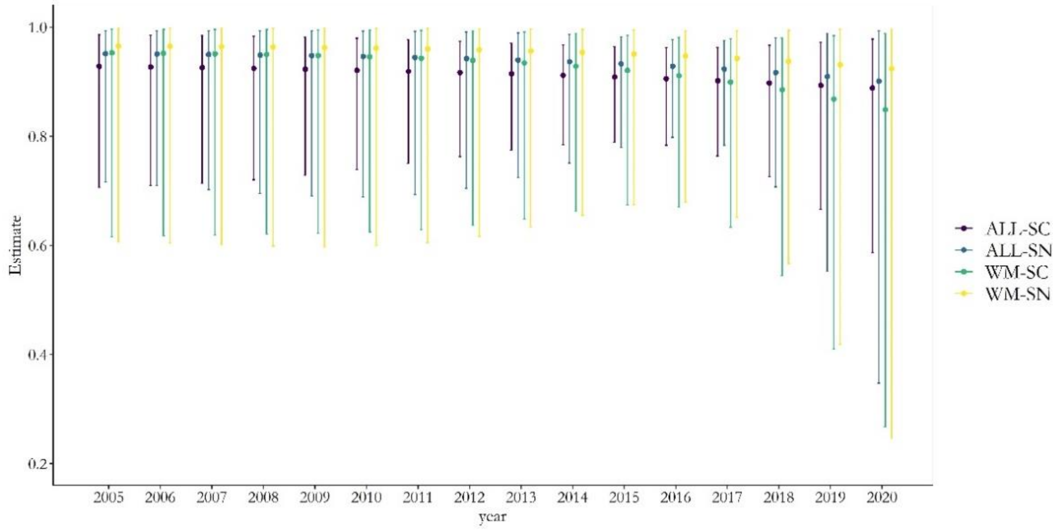

Figure 3.19. Yearly apparent survival probability estimates of non-calf Bryde's whales classified as occasional visitors of Madeira inshore waters (cluster 2) for the period 2005-2021 for each of the datasets with match certainty 2-3, and the respective 95% confidence intervals. Datasets were obtained combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (ALL).

Table 3.20 – The best-supported candidate CJS models (≤10 ΔQAICc) for the period 2005-2021 for clusters of animals with different site fidelity patterns (Regular and Occasional), for each dataset of matching uncertainty 2-3. The selected models had apparent survival probability (ϕ) constant (.) or with a trend (*T*) and probability of recapture (p) either constant (.) or changing over time (*t*). Datasets for which survival estimates were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (ALL).

Dataset	Site Fidelity	Model	AICc	ΔAICc	AIC weight	Deviance	Number of parameters
WM-SC	Regular	*φ(.) p(.)*	284.407	0*	1.000	246.614	2
	Occasional	*φ(.) p(.)*	127.786	0.000	0.605	77.314	2
		φ(T) p(.)	128.637	0.851	0.395	75.879	3
WM-SN	Regular	*φ(.) p(.)*	284.407	0*	1.000	246.614	2
	Occasional	*φ(.) p(.)*	146.042	0.000	0.706	78.282	2
		φ(T) p(.)	147.797	1.755	0.294	77.782	3
ALL-SC	Regular	*φ(.) p(t)*	410.791	0**	1.000	287.216	17
	Occasional	*φ(.) p(.)*	286.537	0.000	0.697	111.222	2
		φ(T) p(.)	288.203	1.666	0.303	110.771	3
ALL-SN	Regular	*φ(.) p(t)*	404.095	0***	1.000	286.126	17
	Occasional	*φ(.) p(.)*	320.839	0.000	0.679	119.030	2
		φ(T) p(.)	322.337	1.498	0.321	118.420	3

* - The next model had a ΔQAICc of 37.168

** - The next model had a ΔQAICc of 19.048

*** - The next model had a ΔQAICc of 29.993

3.3.4.2 Abundance from 2006 to 2021

Abundance over the study period (2006 – 2021) was estimated for Madeira archipelago inshore waters using Robust Design (RD) models. The super population (total number of animals using the study area during the study period) was estimated for both Madeira archipelago and the Madeira – Canary Islands using POPAN.

Robust Design

RD models demand a considerable amount of data to be able to estimate all the parameters, especially the more complex models. The datasets considered in this analysis (WM-SC, WM-SC.3, WM-SN, WM-SN.3, ALL-SC, ALL-SC.3, ALL-SN, ALL-SN.3), although with 14 primary sampling occasions (2006-2012, 2014-15, 2017-2021), had a limited number of secondary occasions in some years and few captures in some of those sampling occasions (Table 3.21; Appendix II, Table II.8-1). Even for the dataset with less strict distinctiveness and matching criteria (ALL-SN, animals with dorsal fin distinctiveness classes 0-3 and matching uncertainty 2 and 3), and thus with more captures, it was not possible to estimate all the parameters of more complex RD models that were initially considered, including heterogeneity in capture probabilities. Thus, none of the models including heterogeneity of capture probabilities were considered further and results from them are not presented. The years 2013 and 2016 were not included in the analysis due to the very small number of captures in each of those years.

As in the CJS models to estimate survival (Section 3.3.4), in this analysis the models with additive or interactive effect between T and transience in survival were among the models with lowest AIC scores, and similar AIC weights. However, they had the same contradictory effects as in the CJS models and were thus not considered in the final RD selected models for the same reasons given in Section 3.3.4.

Sub-datasets of the original datasets considered for the analysis were also explored, namely, selecting sequences of years with more captures (e.g. time series 2014-2015, 2017-2021 and time series 2014-2015, 2017-2019). Nevertheless, the results were similar to the full time series, with only simpler models being fitted. It was not possible in the same model to estimate survival considering both transience and temporary emigration/immigration. It was only possible to estimate the latter parameter whenever survival was modelled as constant. However, these models had much worst AICc scores (ΔAICc >10), indicating no support for them. Their estimated survival rate was lower than expected (≤ 0.90), probably driven by transience (not considered in the models), and the estimated temporary emigration/immigration rate was close to zero or very low (≤ 0.12, with wide SE).

Table 3.21 – Table showing the structure of the data used in the RD analysis of the datasets with matching uncertainty 2-3 (likely and certain): top table - number of captures for datasets of well-marked individuals (WM-SC, WM-SN) for each secondary occasion within primary occasion (year); bottom table – number of captures for datasets of all individuals (ALL-SC, ALL-SN) for each secondary occasion within primary occasion (year). In each cell, the digit on the left corresponds to the number of captures in the datasets SC (WM or ALL) and the digit on the right to the number of captures in the datasets SN (WM or ALL), for a particular secondary occasion. The tables also show the number and length of secondary occasions for each primary sampling occasion. SC – animals confirmed as Bryde's whale; SN – animals suspected to be Bryde's whales but not confirmed; WM - well-marked animals (distinctiveness classes 1-3); ALL – all identified animals, including well marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3).

Primary occasion (Year)	**Secondary occasion length**	**Number of secondary occasions by primary occasion**					
		1	**2**	**3**	**4**	**5**	**6**
2006	month	1, 1	2, 2	3, 3	1, 1		
2007	month	5, 5	3, 4				
2008	bimonth	7, 7	6, 6				
2009	bimonth	1, 1	3, 3				
2010	bimonth	7, 7	1, 2	1, 1			
2011	bimonth	2, 3	2, 2				
2012	month	5, 5	1, 1	0, 1			
2013	-	-	-	-	-	-	-
2014	month	4, 5	16, 18	17, 18	9, 10	5, 5	3, 3
2015	month	2, 2	11, 11	8, 10	2, 2		
2016	-	-	-	-	-	-	-
2017	month	1, 1	2, 4	11, 11	10, 10	4, 4	
2018	month	9, 9	2, 2	3, 3	2, 2	1, 2	
2019	month	8, 8	1, 1	6, 7	6, 6	1, 1	
2020	month	2, 2	2, 2	4, 4	2, 2		
2021	month	3, 3	6, 8	5, 5	2, 2		

Primary occasion (Year)	**Secondary occasion length**	**Number of secondary occasions by primary occasion**					
		1	**2**	**3**	**4**	**5**	**6**
2006	month	1, 1	3, 3	3, 3	2, 2		
2007	month/bimonth	7, 12	5, 1	1, 0			
2008	bimonth	8, 8	12, 12				
2009	bimonth	2, 2	4, 4				
2010	trimester	8, 8	2, 3	1, 1			
2011	bimonth	3, 4	4, 4				
2012	bimonth	8, 8	1, 1	0, 1			
2013	-	-	-	-	-	-	-
2014	month	7, 8	22, 26	30, 36	19, 22	14, 14	6, 6
2015	month	2, 2	17, 19	19, 23	3, 3	1, 1	2, 2
2016	-	-	-	-	-	-	-
2017	month	2, 2	6, 8	24, 24	32, 37	17, 18	
2018	month	15, 15	5, 5	5, 6	3, 3	4, 5	
2019	month	18, 18	3, 3	10, 12	7, 8	1, 1	
2020	month	2, 2	4, 4	6, 6	3, 3		
2021	month	12, 15	14, 16	1, 1			

One final model was selected for each dataset based on the model selection criteria, incorporating the effect of transience in the estimation of survival and no temporary emigration. The exception was dataset WM-SC which also had a second model where survival was modelled as constant (Table 3.22). The same models were also selected for the equivalent datasets with only matching uncertainty 3 (Appendix II, Table II.8-2).

Table 3.22 – The best-supported candidate RD models (ΔAICc ≤ 10) for the study period (2006-2012, 2014-2015, 2017-2021) and study area (Madeira inshore waters), for each of the datasets with matching uncertainty 2 – 3 analysed. The models included the probability of survival (*S*) as constant (.) or accounting for transience (*trans*), with no temporary emigration ($\gamma''(.)=\gamma'(.)=0$) and probability of capture and recapture changing by primary sampling occasion (*s*) or by primary and secondary sampling occasion (*s:t*), The probability of capture and recapture were assumed to be equal in all models (p(s)=c(s)). Datasets for which abundance was estimated, combined animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (ALL).

Dataset	Model	AICc	ΔAICc	AIC weight	Deviance	Number of parameters
WM-SC	$S(trans)\ \gamma''(.)=\gamma'(.)=0\ \ p(s)=c(s)$	657.731	0.00	0.99	496.94	30
	$S(.)\ \gamma''(.)=\gamma'(.)=0\ \ p(s)=c(s)$	666.387	8.66	0.01	508.28	29
WM-SN	$S(trans)\ \gamma''(.)=\gamma'(.)=0\ \ p(s)=c(s)$	661.894	0	1	455.70	30
ALL-SC	$S(trans)\ \gamma''(.)=\gamma'(.)=0\ \ p(s{:}t)=c(s{:}t)$	591.137	0	1	377.17	67
ALL-SN	$S(trans)\ \gamma''(.)=\gamma'(.)=0\ \ p(s{:}t)=c(s{:}t)$	473.971	0	1	242.25	68

The models selected for the datasets with only well-marked animals (WM-SC and WM-SN) included the probability of capture changing by primary sampling occasion (year, s) while the models selected for datasets with slightly marked and well-marked animals (ALL-SC and ALL-SN) included capture probability also changing by secondary sampling occasion (*s:t*).

The abundance estimates of the datasets with matching uncertainty 2-3, corrected for proportion of unmarked animals, and the respective 95% confidence intervals, are presented in Figure 3.20 and compared with datasets of matching uncertainty 3 in Figure II.8-1, Appendix II. These estimates, their respective standard error, CV and 95% confidence intervals are presented from Table II.8-3 to Table II.8-6, Appendix II, and the corresponding proportions of marked individuals from Table II.8-7 to Table II.8-8, Appendix II. The abundance estimates have an overall upwards trend from 2006 to 2021. The years 2012 and 2017-2021 have the highest uncertainty in the abundance estimates. For the datasets of well-marked individuals with matching uncertainty 2-3 (WM-SC and WM-SN), models estimate 18 (95%CI: 8 – 41) animals in 2006, increasing to a peak in 2017 between 163 (95%CI: 126 – 209; WM-SC) and 184 (95%CI: 144 – 236; WM-SN) animals. For the remaining datasets with the same matching uncertainty level (ALL-SC and ALL-SN), models estimated 25 (95%CI: 10 – 63) animals in 2006, and between 185 (95%CI: 137 – 251; ALL-SC) in 2019 and 213 (95%CI: 147 – 310; ALL-SN) animals in 2021.

Temporary emigration and heterogeneity in capture probabilities are usually two important aspects to model in known open populations. The impossibility of modelling these two parameters, together with transience in survival, due to the limited size of this study's datasets may potentially generate biases in estimation of parameters such as survival, abundance and capture probabilities. The possibility and implications of those biases are addressed in the discussion.

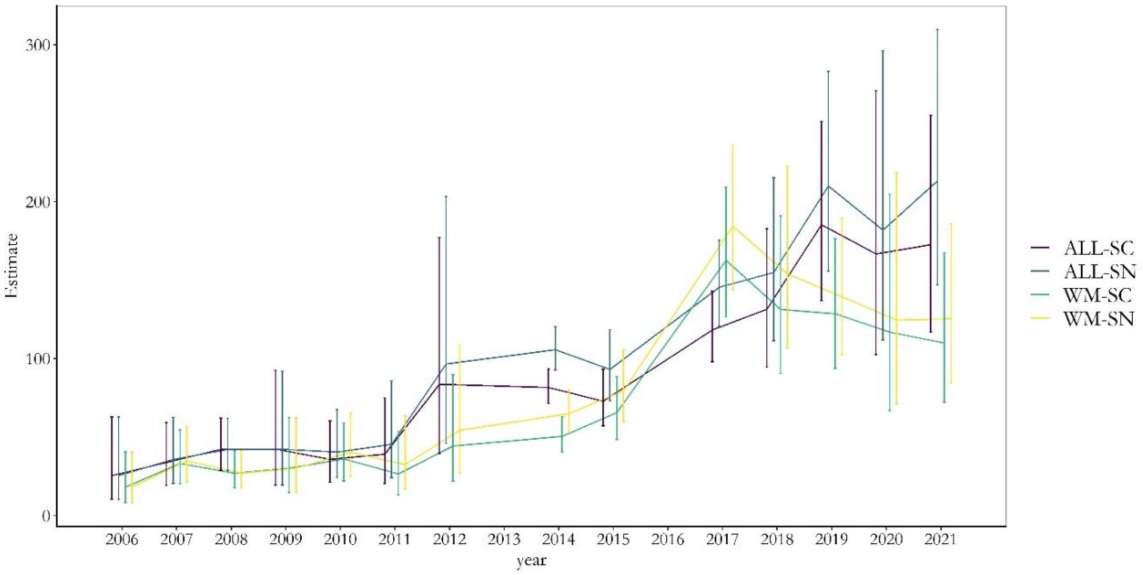

Figure 3.20. Robust-design yearly abundance estimates for Madeira inshore waters for the study period (2006-2012, 2014-2015, 2017-2021), corrected for the proportion of unmarked animals and based on datasets with likely or certain matches (uncertainty 2-3). WM-SC – well-marked individuals (distinctiveness classes 1-3) confirmed as Bryde's whales; WM-SN – well-marked individuals (distinctiveness classes 1-3) confirmed or suspected to be Bryde's whales; ALL-SC – all identified individuals, including well-marked individuals and individuals with distinctive shape dorsal fins (distinctiveness classes 0-3) confirmed as Bryde's whales; ALL-SN – all identified individuals, including well-marked and individuals with distinctive shape dorsal fins (distinctiveness classes 0-3), confirmed or suspected to be Bryde's whales

POPAN

The GOF tests carried out on the datasets of "Madeira" and "Madeira – Canary Islands", both the ones with matching uncertainty 2 -3 and matching uncertainty 3, gave an indication of transience in some of those datasets, namely the lack of fit in the test 3.SR (Table 3.23 and Table 3.24; Appendix II, Table II.9-1 and Table II.9-2). As such, the POPAN models for all datasets included the effect of transience on apparent survival probability regardless of the matching uncertainty level considered.

The POPAN models with the lowest QAICc values fitted to the "Madeira" datasets had a temporal trend (T) in the recruitment from the super-population into the study area (parameter pent). In the datasets with matching uncertainty 2-3, these models received between 78% and 99% of the QAICc weights (Table 3.25), while in the datasets with matching uncertainty 3, the QAICc weight values were between 86% and 100% (Appendix II, Table II.9-3). The remaining models with support from the data had a constant pent and carried low or no weight (between 0% and 22% of the QAICc weight; Table 3.25 and Appendix II, Table II.9-3), regardless of the matching uncertainty level.

Table 3.23 – Results of four the components of the goodness-of-fit tests (GOF), the global combined test of overall CJS model fit and the variance inflation factor ($\hat{c}$), calculated as the χ^2/degrees of freedom, applied to the "Madeira" datasets with matching uncertainty 2 and 3 used in the POPAN analysis (2006 – 2021). Datasets for which survival estimates were obtained, combining: SC – animals confirmed as Bryde's whale; SN – animals suspected to be Bryde's whales but not confirmed; WM - animals well marked (distinctiveness classes 1-3); ALL: all identified animals, including well marked and with distinctive shaped dorsal fins.

Dataset	Global test	2.CT	3.SR	2.CL	3.SM	$\hat{c}$
WM-SC	χ^2 = 33.035 df=46 p=0.924	χ^2=7.096 df=13 p=0.897	χ^2=15.978 df=11 p=0.142	χ^2=7.271 df=13 p=0.888	χ^2=2.690 df=9 p=0.975	0.718
WM-SN	χ^2 = 36.290 df = 47 p = 0.871	χ^2 = 6.373 df = 13 p = 0.932	χ^2 = 18.376 df = 12 p = 0.105	χ^2 = 9.084 df = 13 p = 0.767	χ^2 = 2.457 df = 9 p = 0.982	0.772
ALL-SC	χ^2 = 64.699 df = 52 p = 0.111	χ^2 = 6.723 df = 13 p = 0.916	χ^2 = 34.036 df = 12 p = **0.001**	χ^2 = 16.566 df = 15 p = 0.345	χ^2 = 7.374 df = 12 p = 0.832	1.244
ALL-SN	χ^2 = 73.605 df = 52 p = **0.026**	χ^2 = 6.049 df = 13 p = 0.944	χ^2 = 42.469 df = 12 p = **0.000**	χ^2 = 17.624 df = 15 p = 0.283	χ^2 = 7.463 df = 12 p = 0.826	1.415

Table 3.24 – Results of four the components of the goodness-of-fit tests (GOF), the global combined test of overall CJS model fit and the variance inflation factor ($\hat{c}$), calculated as the χ^2/degrees of freedom, applied to the "Madeira –Canary Islands" datasets used in the POPAN analysis (2006 – 2021). Datasets for which survival estimates were obtained, combining: SC – animals confirmed as Bryde's whale; SN – animals suspected to be Bryde's whales but not confirmed; WM - animals well marked (distinctiveness classes 1-3); ALL: all identified animals, including well marked and with distinctive shaped dorsal fins.

Dataset	Global test	2.CT	3.SR	2.CL	3.SM	$\hat{c}$
WM-SC	χ^2 = 51.917 df = 46 p= 0.254	χ^2 = 14.569 df = 13 p = 0.335	χ^2 = 14.290 df = 10 p = 0.160	χ^2 = 14.868 df = 13 p = 0.316	χ^2 = 8.19 df = 10 p = 0.610	1.129
WM-SN	χ^2 = 62.827 df = 46 p = 0.05	χ^2 = 16.790 df = 13 p = 0.209	χ^2 = 16.991 df = 11 p = 0.108	χ^2 = 20.389 df = 12 p = 0.060	χ^2 = 8.657 df = 10 p = 0.565	1.366
ALL-SC	χ^2 = 63.751 df = 56 p = 0.223	χ^2 = 14.082 df = 13 p = 0.368	χ^2 = 17.517 df = 12 p = 0.131	χ^2 = 16.689 df = 16 p = 0.406	χ^2 = 15.463 df = 15 p = 0.419	1.138
ALL-SN	χ^2 = 80.503 df = 55 p = 0.014	χ^2 = 15.863 df = 13 p = 0.257	χ^2 = 29.312 df = 12 **p = 0.004**	χ^2 = 18.591 df = 15 p = 0.233	χ^2 = 16.737 df = 15 p = 0.335	1.464

Table 3.25 – The best-supported candidate POPAN models (≤10 ΔQAICc) for the period 2006-2021 for each "Madeira" dataset with matching uncertainty 2 - 3, with probability of apparent survival (ϕ) constant (.) or accounting for transience (*trans*), probability of recapture changing over time (*t*) and probability of recruitment from the super-population into the study area (pent) with a trend over time (T). Datasets for which survival estimates were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (ALL).

Dataset	Model	QAICc	ΔQAICc	QAIC weight	Deviance	Number of parameters
WM-SC	$\varphi(.)\ p(t)\ pent(T)$	520.571	0.000	0.753	-87.033	20
	$\varphi(trans)\ p(t)\ pent(T)$	522.871	2.300	0.238	-87.352	21
	$\varphi(.)\ p(t)\ pent(.)$	529.521	8.950	0.009	-75.500	19
WM-SN	$\varphi(.)\ p(t)\ pent(T)$	561.277	0.000	0.726	-149.307	20
	$\varphi(trans)\ p(t)\ pent(T)$	563.784	2.507	0.207	-149.351	21
	$\varphi(.)\ p(t)\ pent(.)$	566.554	5.277	0.052	-141.511	19
	$\varphi(trans)\ p(t)\ pent(.)$	568.991	7.714	0.015	-141.594	20
ALL-SC	$\varphi(.)\ p(t)\ pent(T)$	890.618	0.000	0.699	-431.954	20
	$\varphi(trans)\ p(t)\ pent(T)$	892.746	2.128	0.241	-432.114	21
	$\varphi(.)\ p(t)\ pent(.)$	896.128	5.510	0.044	-424.170	19
	$\varphi(trans)\ p(t)\ pent(.)$	898.269	7.652	0.015	-424.302	20
ALL-SN	$\varphi(.)\ p(t)\ pent(T)$	686.216	0.000	0.577	-409.661	20
	$\varphi(trans)\ p(t)\ pent(T)$	688.295	2.079	0.204	-409.835	21
	$\varphi(.)\ p(t)\ pent(.)$	688.766	2.549	0.161	-404.872	19
	$\varphi(trans)\ p(t)\ pent(.)$	690.842	4.625	0.057	-405.036	20

For each of the "Madeira – Canary Islands" datasets, the model with the lowest QAICc value had consistently a temporal trend (T) in the parameter pent, regardless of the matching uncertainty level (Table 3.26; Appendix II, Table II.9-4). Although the second model with the lowest QAICc in most of these datasets included the parameter pent constant, the parameter pent with a temporal trend received 54% to 89% and 71% to 100% of the QAICc weights among the selected models with matching certainty 2-3 and 3, respectively. The remaining models with support from the data had a constant pent and carried lower weight (between 0% and 46% of the QAICc weight; Table 3.25 and Appendix II, Table II.9-3), regardless of the matching uncertainty level.

All selected models for both super-populations had capture probability varying between sampling occasions (years) and the apparent survival probability, regardless of certainty level, was either constant or accounted for the effect of transience.

Table 3.26 – The best-supported candidate POPAN models (≤10 ΔQAICc) for the period 2006-2021 for each "Madeira – Canary Islands" dataset with matching uncertainty 2 - 3, with probability of apparent survival (ϕ) constant (.) or accounting for transience (*trans*), probability of recapture changing over time (*t*) and probability of recruitment from the super-population into the study area (pent) with a trend over time (T). Datasets for which survival estimates were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (ALL).

Dataset	Model	QAICc	ΔQAICc	QAIC weight	Deviance	Number of parameters
WM-SC	*φ(.) p(t) pent(T)*	601.337	0.000	0.552	-75.376	20
	φ(trans) p(t) pent(T)	602.328	0.991	0.336	-76.850	21
	φ(.) p(t) pent(.)	605.565	4.227	0.067	-68.709	19
	φ(trans) p(t) pent(.)	606.314	4.976	0.046	-70.399	20
WM-SN	*φ(.) p(t) pent(T)*	556.115	0.000	0.507	-130.751	20
	φ(.) p(t) pent(.)	557.860	1.745	0.212	-126.627	19
	φ(trans) p(t) pent(T)	558.018	1.903	0.196	-131.248	21
	φ(trans) p(t) pent(.)	559.694	3.580	0.085	-127.171	20
ALL-SC	*φ(.) p(t) pent(T)*	1001.241	0.000	0.487	-454.524	20
	φ(.) p(t) pent(.)	1002.453	1.212	0.265	-451.094	19
	φ(trans) p(t) pent(T)	1003.461	2.220	0.160	-454.532	21
	φ(trans) p(t) pent(.)	1004.665	3.425	0.088	-451.099	20
ALL-SN	*φ(.) p(t) pent(T)*	876.585	0.000	0.536	-545.336	20
	φ(.) p(t) pent(.)	876.875	0.290	0.464	-542.867	19

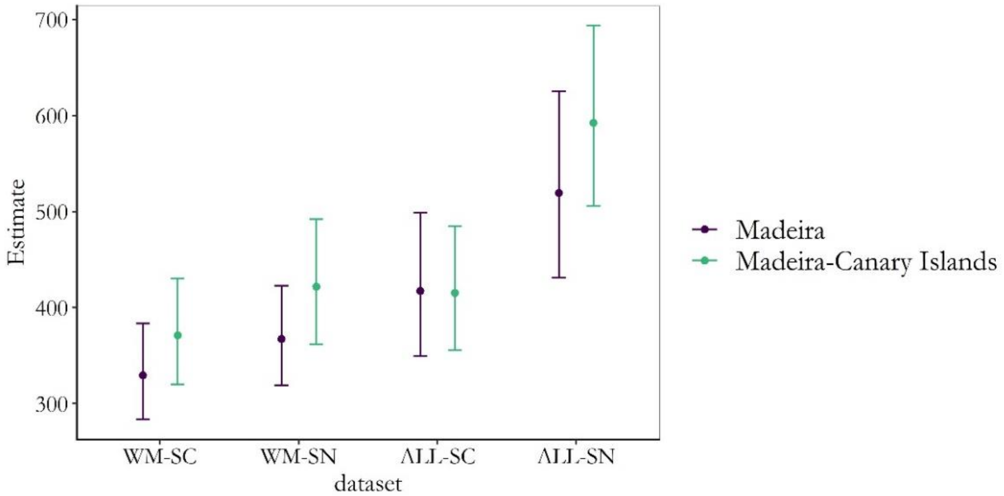

Figure 3.21 – The POPAN abundance estimates, corrected for the proportion of unmarked animals, of "Madeira" and "Madeira-Canary Islands" super-populations based on datasets with likely or certain matches (certainty 2-3). WM-SC – well-marked individuals (distinctiveness classes 1-3) confirmed as Bryde's whales; WM-SN – well-marked individuals (distinctiveness classes 1-3) confirmed or suspected to be Bryde's whales; ALL-SC – well-marked and slightly marked individuals (distinctiveness classes 0-3) confirmed as Bryde's whales; ALL-SN – well-marked and slightly marked individuals (distinctiveness classes 0-3) confirmed or suspected to be Bryde's whales.

In Figure 3.21 and Table II.9-5 (Appendix II) are presented the POPAN abundance estimates, corrected for the proportion of unmarked animals, for the super-population of "Madeira" and "Madeira-Canary Islands", based on datasets with likely and certain matches (certainty 2-3). As expected, the estimates for the "Madeira" super-population are lower than for the "Madeira-Canary Islands" super-population, except for the dataset ALL-SC that has similar values.

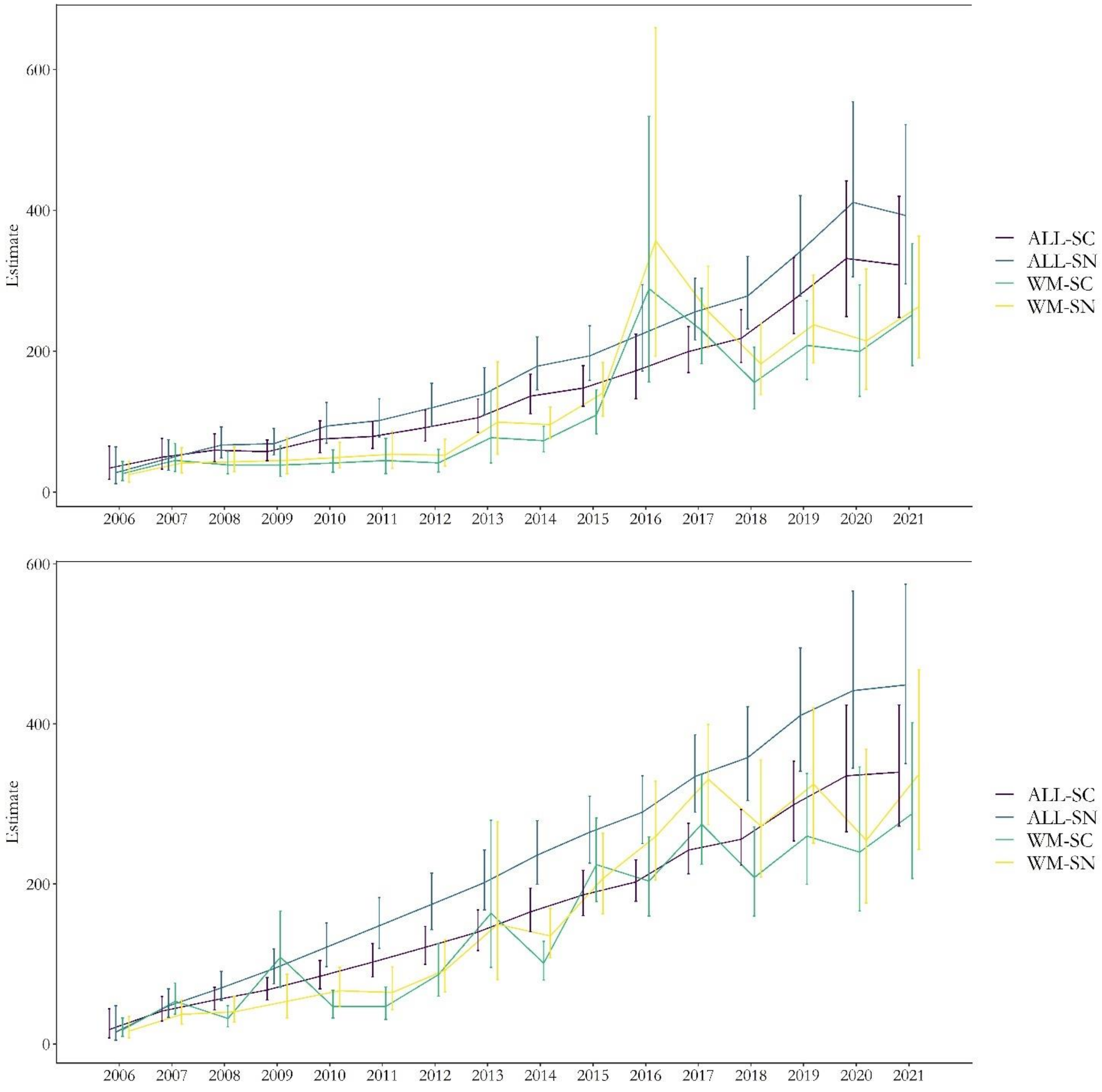

Figure 3.22 – POPAN yearly abundance estimates, corrected for the proportion of unmarked animals, of "Madeira" (top) and "Madeira-Canary Islands" (bottom) super-populations based on datasets with likely or certain matches (certainty 2-3). WM-SC – well-marked individuals (distinctiveness classes 1-3) confirmed as Bryde's whales; WM-SN – well-marked individuals (distinctiveness classes 1-3) confirmed or suspected to be Bryde's whales; ALL-SC – all identified individuals, including well-marked individuals and individuals with distinctive shape dorsal fins (distinctiveness classes 0-3) confirmed as Bryde's whales; ALL-SN – all identified individuals, including well-marked and individuals with distinctive shape dorsal fins (distinctiveness classes 0-3), confirmed or suspected to be Bryde's whales.

The abundance estimates based on the datasets with only certain matches (certainty 3) (Appendix II, Table II.9-6; Figure II.9-1), were consistently higher than the equivalent estimates based on datasets with likely and certain matches (certainty 2-3). The abundance estimates were corrected for the proportion of unmarked animals using the values given in Table II.9-7 to Table II.9-10, Appendix II.

The abundance estimates closest to the real number of Bryde's whales for both super-populations are probably the ones obtained based on the dataset ALL-SN, that includes captures based on likely and certain matches of confirmed and suspected Bryde's whales. Those estimates are of 519 whales (SE=75; 95%CI=431 – 625, CV=16%) and 592 whales (SE=73; 95%CI=506 – 694, CV=13%) using "Madeira" and "Madeira-Canary Islands" waters during the study period, respectively.

The POPAN yearly abundance estimates show an increasing trend in number of whales using both "Madeira" and "Madeira-Canary Islands", across all datasets (Figure 3.22; Appendix II, Figure II.9-2 and Figure II.9-3). In both cases, the selected POPAN models indicate that such an increase is, mostly, driven by recruitment of animals from the super-populations to the study areas. The corrected POPAN yearly abundance estimates, for the "Madeira" super-population have a similar pattern to the corresponding Robust Design abundance estimates (Figure 3.20), albeit being in general higher than the latter, across years and datasets.

3.3.5 Mother-calf association and calving rates

Bryde's whales' mother-calf pairs are frequently sighed in the Macaronesia archipelagos. Females do not only seasonally immigrate with their newborn calves to Macaronesia archipelagos but may also give birth in these waters, as is suggested by the stranding of a newborn calf (< 4 m length) on 6 August 2004 in the Southeast of Madeira Island (Freitas *et al.*, 2012; unpublished data from the MWM). Mother-calf pairs were, on average, 12.5% of all sightings recorded between 2002 and 2021, with the lowest percentage in the Azores and the highest in the Canary Islands (Table 3.27).

Although most animals migrate away from these archipelagos in late autumn until early spring, in relative terms, more females with calves stayed around Madeira and the Canary Islands through winter than the remaining animals. In January, 35.7% and 66.7% of the sightings were of mother-calf pairs in Madeira and the Canary Islands, respectively, while in the remaining of the year those percentages were on average 11.8% and 15.5%, respectively (Table 3.27).

Table 3.27 – Number of sightings, and respective percentages, of mother-calf pairs and of the remaining animals for the study period (2002 – 2021) for Madeira, Canary Islands, Azores and all archipelagos combined. Also presented for these areas are the number of sightings, and respective percentages, for January and the remaining months combined to show the higher tendency, in relative terms, of mother-calf pairs to stay over winter in Macaronesia, rather than migrate as the remaining animals.

		Female - Calf Pairs		Remaining animals	
		n	%	n	%
Jan - Dec	All archipelagos	199	12.5%	1392	87.5%
	Madeira	154	12.0%	1125	88.0%
	Canary Islands	41	16.5%	207	83.5%
	Azores	5	6.7%	70	93.3%
Feb - Dec	All archipelagos	190	12.1%	1375	87.9%
	Madeira	149	11.8%	1116	88.2%
	Canary Islands	37	15.5%	201	84.5%
	Azores	5	6.7%	70	93.3%
Jan	All archipelagos	7	41.2%	10	58.8%
	Madeira	5	35.7%	9	64.3%
	Canary Islands	2	66.7%	1	33.3%
	Azores	0	-	0	-

Table 3.28 shows the yearly capture histories of females with multiple calves, calves seen in association with their mother in two consecutive years and/or used to calculate the calving rates. The yearly capture histories of all females with calves are given in Table II.10-3 (Appendix II). Fifty-six females were identified with calves in the three archipelagos over the study period. Most females had short capture histories (≤ 3 years) with only one calf being recorded (n= 35), while the remainder had longer recapture histories and/or gave birth to multiple calves over the study period (n=21) (Appendix II, Table II.10-3).

Six calves were seen with their mothers in the year after their birth, allowing a rough calculation of the maximum time (in months) a calf may stay with its mother before weaning and the association ended (Table 3.29). The average number of days between the first and last time the mother-calf pair was captured was 414 days (13.6 months). However, one should bear in mind that calves may separate from their mothers earlier or later and go unnoticed, because they or the female were not captured alone after the separation or in association with each other, respectively.

Table 3.28 – Time series of years that Bryde's whales, identified as females (accompanied by a calf), were observed in Madeira, Azores or the Canary Islands with or without a calf between 2003 and 2021, with multiple calves, calves seen in association with their mother in two years and/or used to calculate the calving rates. A – Animal considered adult at a particular year based on size; C – animal considered a calf at a particular year based on size; 1? – it was not possible to confirm that the calf with the adult was the same from one year to the next. The numbers indicate the sequence of identified calves a female had throughout the period the animal was captured. Also shown is the site fidelity of animals to Madeira (based the Site Fidelity Index, see previous Section) as well as the animals used to calculate the calving rates, according to the two criteria established. The field dataset indicates the animals part of dataset D1 and dataset D2 used to calculate calving rates.

Female	Site Fidelity	Dataset	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	Total calves
Be0003	Regular	D1,D2	A	A	1	1	2	A	A	3												**3**
Be0016	Regular	D2				A		A			A			A	1	1	A	A			A	**1**
Be0017	-	-			1			A														**1**
Be0021	Occasional	-			1									A		A		2				**2**
Be0023	-	-															1	1?				**1**
Be0026	Regular	D1,D2				A	1	1	2	A	A			3	A		A		4			**4**
Be0030	Occasional	-						1		A	2				A							**2**
Be0031	-	-					C										1					**1**
Be0046	Regular	D1						1	2	A		A		3	A			4			A	**4**
Be0052	Regular							A						A			1				2	**2**
Be0056	-	-						A						1		A	2					**2**
Be0057	Regular	-							1	A				2							3	**3**
Be0059	Regular	-								C							1	A				**1**
Be0065	Regular	D1,D2		A	1	A	A	A			A			A	A		2		3			**3**
Be0084	Occasional	-					1							A						2		**2**
Be0087	Regular	D2								A				A	A	A	1	1				**1**
Be0099	Regular	D1												A	A	1	1			2		**2**
Be0118	Rare	-													1	1					A	**1**
Be0122	Occasional	D1		A											A		1	A	A			**1**
Be0128	-	-														1	A	2				**2**
Be0131	Occasional	D1												A	1	1	A		A			**1**
Be0195	Occasional	D1															A		A	1		**1**
Be0321	Occasional	D1																A		1	A	**1**

Table 3.29 – Number of days (and months) between the mother-calf pair first and last time captured in Madeira, Azores or the Canary Islands, for females seen with the same calf in consecutive years.

Female ID	Calf ID	First seen	Location	Last seen	Location	First and last seen		Female in the year after
						Days	Months	
Be0003	Be0015	2005	MAD	2006	MAD	378	12.4	with new calf
Be0016	Be0125	2015	MAD	2016	MAD	374	12.3	alone
Be0087	Be0218	2017	CEH	2018	MAD	426	14.0	not captured
Be0099	Be0152	2016	CTN	2017	MAD	458	15.1	not captured
Be0118	Be0117	2015	CTN	2016	CTN	416	13.7	not captured
Be0131	Be0132	2015	CTN	2016	CTN	434	14.3	Alone
					Mean	414	13.6	

Only two females were seen with two different calves from one year to the next, with the first calf being sighted with its mother in the previous two consecutive years (Be0003 and Be0026). The remaining females were either not seen the following year, after being one or two years with the same calf, or were seen without a calf ((Appendix II, Table II.10-3). No calf was seen in the third year with their mother although one calf (Be0020) was seen as an adult (9 years after birth) in a single sighting together with its mother (Be0065) (Appendix II, Table II.10-2).

A total of 75 calves were recorded in mother-calf pairs, of which 62 were given a new individual code. Some of the identified calves were recaptured within the birth year or the year after, both by matching the dorsal fin and secondary markings and by the close association with their mother. Furthermore, some of these calves had distinctive features (well-marked or distinctive dorsal fin shapes) since the birth year and were recaptured several years later as adults (7 animals), two of which were seen in two subsequent years (Appendix II, Table II.10-2). Calves Be0059 and Be0031 were seen with their calves 7 and 10 years later, respectively (Appendix II, Table II.10-1).

Data from nine (D1) and five (D2) identified females were used to estimate calving rates based on the individual capture histories for the period 2003 – 2021. A total of 20 calves and 12 calves were identified with females in D1 and D2, respectively. The same animals capture histories were divided in two periods (2003-2012 and 2014-2021). Estimated calving rates and calving intervals are given in Table 3.30. The results of Kruskal-Wallis tests showed no statistical differences between D1 and D2 and between periods.

Table 3.30 – Calving rate (calves per year) and calving interval (number of years between calves), and respective statistics, of Bryde's whales in Macaronesia (Madeira, Azores and the Canary Islands), directly calculated from identified females individual capture histories for the period 2003 – 2021. Two datasets (D1 and D2) were used to calculate the overall calving rate and calving interval and two datasets to calculate the same parameters for two periods, 2003-2012 and 2014-2021 (Section 3.2.2.5).

Dataset	Calving rate		Calving interval		Calving rate		Calving interval	
	D1	D2	D1	D2	2003-2012	2014-2021	2003-2012	2014-2021
n	9	5	9	5	4	9	4	9
Min	0.17	0.20	2.67	2.67	0.20	0.17	2.50	3.00
Average	0.25	0.26	4.17	4.13	0.33	0.24	3.29	4.39
Max	0.38	0.38	6.00	5.00	0.40	0.33	5.00	6.00
SD	0.06	0.09	1.06	1.19	0.09	0.05	1.16	0.93
SE	0.02	0.04	0.35	0.53	0.04	0.02	0.58	0.31
L95% CI	0.21	0.19	3.47	3.09	0.24	0.20	2.16	3.78
U95% CI	0.30	0.34	4.86	5.18	0.41	0.27	4.43	5.00

3.4 DISCUSSION

To contribute to the understanding of the ecological importance of open ocean islands to cetaceans and address the thesis overarching questions (Section 1.3), the movements and migration patterns of Bryde's whales in Madeira archipelago and surrounding ocean basin were investigated, together with the site fidelity patterns and population parameters (apparent survival, abundance and calving rates) of the animals using Madeira archipelago's waters. Photo-identification and mark-recapture analysis were the main methodology used in the study, complemented by satellite telemetry.

3.4.1 Validation of method assumptions

The presence of both Bryde's whales and sei whales in most of the study locations (Madeira, Azores and the Canary Islands) and the difficulty to distinguish between them at sea can result in biases in the estimation of demographic parameters. The removal of animals with unconfirmed species status reduces the amount of data to run the analyses and will result in the underestimation of population size if some or all of those removed animals are in fact Bryde's whales. Conversely, the inclusion of those individuals in the dataset will result in an overestimation of population size if they are not Bryde's whales. As such, to minimize bias in the abundance estimates, as many animals as possible were confirmed to be Bryde's whales (Section 3.2.2.2). The assumption that all individuals in a group were Bryde's whales when at least one animal was confirmed as a Bryde's whale probably holds true because no encounters with both species were identified in the dataset, although that cannot be totally ruled out. Even if this assumption was violated in a minority of sightings, the relatively small percentage of groups observed (~25%) and the much smaller encounter rates of sei whales when compared with Bryde's whales in Madeira (Section 4.3) and the Canary Islands (e.g. Carrillo *et al.*, 2010; Brederlau *et al.*, 2011; Martín *et al.*, 2011), minimizes this possible bias. As such, the datasets including animals with both confirmed and non-confirmed species (WM-SN and ALL-SN) will probably generate estimates that are at worst slightly positively biased as a result of species misidentification. Nevertheless, datasets with only confirmed Bryde's whales (SC) and both confirmed and non-confirmed Bryde's whales (SN) were explored in the analyses, to understand their impact in parameters estimation (discussed further ahead).

To minimize the risk of violation of the mark-recapture assumptions related with the correct identification of individuals (assumptions 1, 2 and 3, Section 3.2.2.4 - Assumptions) several requirements were included in this study's data organization, processing and matching process (Section 3.2.2.2 and Section 3.2.2.3), implementing as far as possible the best practices recommended by Urian *et al.*, (2015). Among them were the definition of a photo quality threshold to be used in mark-recapture analysis, the selection of adequate individual features to identify the animals (leading and trailing edge of dorsal fin), the photo-identification work being carried out by the same experienced analyst, minimizing inconsistencies during cataloguing and scoring of images, and minimizing misidentification by having the matches confirmed by multiple researchers. Furthermore, different levels of distinctiveness in animals and matching uncertainty (Section 3.2.2.3), were explicitly considered in the matching process and explored in the analysis, thus acknowledging that these assumptions may not always hold true.

The present study was based on the photo-identification technique, taking advantage of the natural markings and shapes of the dorsal fins, which is unlikely to affect the survival or catchability of animals (assumption a; Section 3.2.2.4 - Assumptions). Nevertheless, this study uses images collected by multiple contributors in diverse types of operations (commercial whale-watching, scientific surveys with different purposes and opportunistic sightings) that could potentially affect the behaviour of the animals towards the boats ("trap-shy" or "trap-happy"), thus affecting their catchability. However, GOF Test 2.CT failed to detect any departure from the model assumptions that would indicated trap dependence in the datasets used in the analysis to estimate apparent survival (CJS models) and superpopulation size (POPAN models).

The failure to assume that all animals have an equal chance of being captured in every sampling occasion (assumption b; Section 3.2.2.4 – Assumptions), also known as heterogeneity of capture probabilities, can cause bias in the estimation of parameters, especially abundance (Hammond, 2018; Hammond *et al.*, 2021). Although eliminating heterogeneity of capture probabilities is impossible, it was addressed in this study, as much as possible, during data collection (especially in Madeira archipelago), data selection and in the analysis. In Madeira archipelago, the photo-identification sampling was done year-round in all years of the study by multiple whale-watching boats, covering overlapping or adjacent areas (Table 3.3; Table II.2-1, Appendix II). The MWM scientific surveys actively collected photo-identification images of the species throughout the study period and sampled the waters around Madeira and Porto Santo Islands not covered by the whale-watching boats, although with less effort than those boats. Moreover, the movement of animals within the local study area, confirmed through satellite telemetry and the recapture of animals in short periods of time (hours to days) by whale-watching boats operating across the south of Madeira Island, suggest that these animals move around and mix, thus minimizing heterogeneity of capture probability.

In the Canary Islands, the study included Bryde's whales' photo-identification images from many contributors from several islands. It was expected with this approach to increase temporal and spatial coverage and maximize average capture probability. Although the local capture data covered most of study period, there was still an heterogenous distribution of captures across years and islands. I was only possible to run acceptable POPAN models for "Madeira – Canary Islands", producing estimates of the number of non-calf whales using both archipelagos over the whole study period (2006 – 2021). Those estimates may be, however, an underestimate of the real superpopulation size especially due to the very uneven spatial and temporal coverage in the Canary Islands (Table 3.3), which may have contributed to heterogeneity in capture probabilities. The captures of Bryde's whales in the remaining locations were too few to attempt any statistical analysis and were used only to investigate movement of animals among locations.

Recognizing that heterogeneity in capture probabilities could still be a feature of the data, especially in open populations of migratory species such as the Bryde's whales, it was addressed in the analysis both by exploring different datasets (e.g. estimating apparent survival of animals with different residency patterns) and different models that included the effect of transience (Section 3.2.2.4). The significant results of the GOF test 3.SR across datasets also supported this approach.

The assumptions under the RD are mostly a combination of assumptions of closed-population methods and open-population methods, namely the CJS model. The possible violation of open population model assumptions was investigated prior to analysis, addressed in the analysis and discussed previously. The assumptions of the closed population models were not investigated prior to data analysis and possible violations are discussed next. As pointed out by Kendall (1999), the existing tests to check the closure assumption suffer from lack of power or are insensitive to temporary emigration or behavioural responses.

The assumption of demographic closure, i.e. no births and deaths, within a primary sampling occasion may have been violated but with expected minor impact on the estimates, if we consider the short period of the primary sampling occasions in comparison with longevity and calving intervals of Bryde's whales and the very high survival rates estimated across datasets, periods and animals with different site fidelities (Sections 3.3.4 and 3.3.5). The assumption of geographic closure, i.e. no immigration and emigration, within a primary sampling occasion was probably not met, because we are dealing with an open population of highly mobile animals. The movement data, both recaptures of animals between different Macaronesia archipelagos in short periods of time (< 2 months) and satellite telemetry tracks, confirmed that animals moved in and out of the study area during primary sampling occasions (Table 3.10., Table 3.11 and Figure 3.10).

Kendall (1999) evaluated several types of violations to the closure assumption and concluded that when movement in and out of a study area was completely random, the estimators from closed-population methods were not biased, although less precise. However, for other cases of non-random movement, the author showed that closed population estimators were biased when movement was Markovian (dependent on the presence/absence of the animal in the previous time period), when an animal had one entry to and one exit from the study area, or when there was trap response or heterogeneity among animals in capture probability.

The limited number of captures across all datasets used in the RD analysis did not allow modelling both transience and temporary emigration together. Transience was shown to be a very important aspect to consider in the models, affecting considerably the estimation of survival (Section 3.3.4). Even when temporary emigration was possible to model in analysis of sub datasets comprising years with more captures (e.g. 2014-2017) and survival was considered constant (results not presented), these models had much higher AIC values and very small or zero weights when compared with models which incorporated transience in survival but not temporary emigration. The fact that RD models with transience had far more support on the data (lower AIC) indicates that this was a more important effect to take in consideration than temporary emigration.

The inability to model the expected temporary emigration and to identify its nature (random vs non-random) and extent, makes it difficult to understand and minimize possible biases in the parameter estimates. However, according to Schaub *et al.* (2004) Markovian temporary emigration can be detected with the GOF 2.CT and the power to detect it is reasonable even when on-site recapture probabilities are low, provided that survival and temporary emigration probabilities are high. In the present study the apparent survival estimates were high and the p-values of the 2.CT test were non-significant and high across all datasets (Table 3.17 and Table II.7-1, Appendix II). These results indicate the absence of both trap response behaviour and Markovian temporary emigration, assuming for the latter that temporary emigration probabilities are high. As such if the temporary emigration of Bryde's whales is completely random, then estimators from closed-population methods are not biased, although less precise (Kendall, 1999). However, it may be possible that temporary emigration is different (random or non-random) depending on the site fidelity of the animals (Section 3.4.2). Furthermore, the animals of different site fidelity classes may have different capture probabilities in the study area within a primary sampling occasion, which will result in the underestimation of abundance.

Another implicit assumption in the RD is that survival probability is not affected by the emigration status. There is no evidence that animals moving away from the study area are subject to higher mortality than animals staying in the study area. The very high apparent survival, estimated from CJS models across years, reflect a true high survival and fidelity to the study area for many animals, indicating that mortality is very low regardless of where the animals are.

3.4.2 Apparent survival

The GOF tests did not show a lack of fit of the global CJS model for any of the datasets explored, although the effect of transience was identified in most of the datasets, especially the ones that included slightly marked individuals (ALL), regardless of matching uncertainty level. The best models for all datasets estimated a constant high apparent survival for non-transient non-calf Bryde's whales in Madeira archipelago throughout the study period. The slight differences in the apparent survival estimates of these animals among datasets were well within the respective confidence intervals for all datasets.

The apparent survival of animals using Madeira archipelago inshore waters for 2005 – 2021 (> 0.98) were on the upper range of reported estimates for baleen whales (e.g. Zeh *et al.*, 2002; Larsen and Hammond, 2004; Bradford *et al.*, 2006; Ramp *et al.*, 2006; Schleimer *et al.*, 2019a), suggesting there are no major mortality issues affecting the non-calf segment of the population. The apparent survival reported for Bryde's whales in the Plettenberg Bay for South Africa inshore population was 0.93 (95%Cl = 0.852 -1.0) (Penry, 2010), while in the Hauraki Gulf (New Zealand) was 0.878 (95% CI = 0.811−0.923) (Tezanos-Pinto *et al.*, 2017), both lower than Madeira.

When looking at the estimates of apparent survival by site fidelity level, the regular visitors (cluster 1) had a constant survival of the upper bound of 1, indicating no mortality or permanent emigration of these animals from the study area during the study period. The limited number of animals in the cluster did not allow to fit more complex models to their capture histories to estimate the apparent survival and recapture probabilities. Whilst survival probability cannot truly be 1, a very high apparent survival estimate is not necessarily unrealistic considering that the study period (17 years) is much shorter than the expected longevity of these long-lived animals, and that they are regular visitors of the study area, thus with very low or no permanent emigration. Although there is no information on longevity of Bryde's whales, baleen whales and other large cetaceans such as right whales, bowhead whale, blue whale, fin whale and the sperm whale are thought to live for many decades, well over 100 years in some species (e.g. Sears and Perrin, 2009; Aguilar and García-Vernet, 2018; George *et al.*, 2018; Kenney, 2018; Whitehead, 2018).

It was possible, however, to fit more complex models to the datasets of occasional visitors (Cluster 2). The selected models were the same across the datasets tested showing consistency in the results, regardless of level of distinctiveness and species confirmation status (Table 3.20). The apparent survival of these animals throughout the study period was lower than for the regular visitors, with a downwards trend over the years. There are no obvious reasons for the true survival of occasional visitors to be different from regular visitors, assuming they are part of the same population using the same overall distribution area and thus susceptible to the same causes of mortality. Furthermore, the apparent downwards trend in survival of occasional visitors conflicts with the upwards trend in abundance (Section 3.3.4.2) over the same period. The downward trend could be an artifact caused by terminal bias (Langtimm, 2009). Alternatively, the influx of animals into the study area could have a lower survival rate but this seems unrealistic and there is no evidence to support it. Perhaps a more likely explanation is that the lower estimated survival and the negative trend may be driven by temporary emigration of animals from the study area, reflected in the animals' capture histories as permanent migration when the animals with occasional presence in Madeira did not return to the study area within the last years of the study period (Jourdain *et al.*, 2021). According to Peñaloza *et al.* (2014), long-lived species with high adult survival and highly variable non-random (Markovian) temporary emigration have terminal bias in survival estimates, because of the uncertainty about the fate of individuals that are undetected toward the end of the time series. No plausible reason was found for the stronger negative trend in apparent survival of the well-marked confirmed Bryde's whales (WM-SC) when compared with the remaining datasets of occasional animals (Cluster 2) (Figure 3.19), other than a particular structure of the data as a result of the smaller number of animals in the dataset and/or a slightly lower apparent survival of well-marked occasional visitors. It is expected that in general well-marked individuals may be older than less marked animals (marks are acquired over time), and thus more likely to die. It may also be that older animals are more likely to permanently emigrate from Madeira. These results are in line with RD and POPAN abundance estimates trends of well-marked animals for Madeira (Figure 3.20 and Figure 3.22, top) but are, however, contradicted by the relatively constant apparent survival estimates of WM-SN occasional visitors (Figure 3.19).

3.4.3 Mother-calf association and calving rates

The Macaronesia archipelagos, especially Madeira and the Canary Islands, seem to be important for mother-calf pairs, not only to immigrating pairs but possibly to pregnant mothers giving birth. For example, the stranded calf in Madeira island in 2004 was most probably a local newborn due to its very small size, less than 4 m, comparable to the maximum estimated size at birth of 3.96 m for this species (Freitas and Penry, 2021).

The highest percentage of mother-calf pairs seen in the Canary Islands (16.5%) and in Madeira (12%) when compared with the Azores (6.7%), is an indication of the importance of the two former archipelagos for lactating females as feeding areas. The percentage of mother-calf pairs in Madeira and the Canary Islands was also higher than the 10.6% reported by Tershy *et al.* (1990) for the period 1983 to 1986 in the Gulf of California. In spite not being the general pattern, a small percentage of Bryde's whales are still seen around Madeira archipelago and the Canary Islands in winter, especially mother-calf pairs that do not migrate elsewhere as expected. This is suggested by the much higher percentage of mother-calf pairs relative to other animals in January in Madeira (35.7%) and the Canary Islands (66.7%) when compared with the other months of the year (11.8% and 15.5%, respectively) (Table 3.27). They may be taking advantage of local resources with far less competition, avoiding energy expenditure with longer displacements and/or staying at these higher latitudes to exploit early on the prey availability resulting from the spring bloom. This could be particularly important for females with calves in years in which they were not particularly successful in foraging, forcing them to extend the lactation period. These choices might be driven by the lactation costs that, for example, in fin whales can be double those of total gestation and foetal development and are in excess of gestation for blue, sei and minke whales (Lockyer, 1984). Furthermore, the waters at the Bryde's whale summer grounds in the Northeast Atlantic (including the Macaronesia archipelagos) are far more thermally benign in winter to mothers and calves than the summer grounds of other baleen whales in polar regions, thus possibly not having the same energetic costs and challenges, specially to calves, that would incentivise migration southwards.

At least 75 mother-calf pairs used Madeira, Azores and the Canary Islands inshore waters during the study period (Table II.10-3, Appendix II). Most of these calves, if not all, were probably recruited to the archipelago's superpopulation, as suggested by identified calves that were resighted in the study area years later as adult females with calves (Be0031 and Be0059, Table 3.28). Among the mother-calf pairs with complete enough capture histories (a continuous sequence of three or more years where the mother was identified with and without a particular calf), five were of mother-calf pairs seen in two consecutive years (Be0003, Be0016, Be0026, Be0087, Be0131) and only one mother-calf pair (Be0065) seen together in one year (Table 3.28). The latter mother-calf pair, in spite having a complete enough capture history, was only seen once in the year, rendering impossible to calculate a minimum time they were together. The remaining calves were seen with their mothers for 13.6 months (414 days) on average (minimum = 12.3 months; maximum = 15.1 months; Table 3.29). The lactation period of Bryde's whales is believed to be between 6 and 12 months (Kato and Perrin, 2018; Freitas and Penry, 2021). However, these results indicate that most calves, if not all, stayed with their mothers for longer periods before weaning, and are in line with the report of two female whales caught together in South Africa, one larger still lactating and a one smaller (8.5 m long and approximately 2 years old) with milk in its stomach (Best, 1977). Although this is not hard evidence it does give support to the suggestion made by Freitas and Penry (2021) that lactation periods in Bryde's whales are longer than previously thought and could extend to two years.

The observation of three females (Be0003, Be0026 and Be0046) with two different calves in consecutive years may indicate that they were pregnant while lactating (Table 3.28), considering that the gestation period is 11-12 months (Kato and Perrin, 2018). Although unusual in baleen whales, considering the energetic costs and hormonal limitations, it is possible for a female to be pregnant while lactating (Lockyer, 1984). However, the observation of a female with two calves in consecutive years may also happen because that female had a calf from another female temporarily with her or because she lost her offspring early the year before.

Additionally, observations showed that female Be0003 had one resting year (no gestation or lactation) in 2008 and one gestation year in 2009 without calves, while female Be0128 was not accompanied by a calf during the gestation year. The differences in calving rates between animals may be due to lack of mating opportunities but may also be for energetic reasons. Gestation and, mostly lactation, are energetically demanding processes and having them happen simultaneously would be energetically challenging for females. Females may compensate the energetic effort by delaying pregnancies (resting years to reduce energetic expenditure) to allow the replenishment of energetic reserves (Lockyer, 2007). Conversely, the females might be able to have a lactating calf and carry simultaneously a pregnancy to term because they have enough prey available for consumption to compensate in the short term for the energetic expenditure of lactation and pregnancy. The first strategy is expected to happen if Bryde's whales are capital breeders and the second if they are income breeders. It is not clear from the data which might be the case.

Curiously, calves Be0031 and Be0059 seen in Madeira were only recaptured 10 and 7 years later, respectively, accompanied by their own calves (Table 3.28). The age of sexual maturity of Be0031 (9 years) is within what was estimated by Best (1977), while the age of sexual maturity of Be0059 is considerably lower (6 years), assuming that both animals were one year old when first captured and that these were their first calves. Best (1977) estimated the age of sexual maturity by counting the animals' ear plug layers and assuming that an ear plug layer corresponded to a year.

The average calving rate and calving interval for the period 2003-2021, calculated from two datasets of capture histories of reproducing females, were very similar (Table 3.30). The consistency of the results between the two datasets (calving rate: D1 = 0.25 calves/year, D2 = 0.26 calves/year; calving interval: D1 =4.7 years, D2=4.13 years) shows that the differences in sample size and capture history completeness among the datasets did not affect too much the results. The incomplete capture history of females with calves and the small sample size, only allowed the calculation of the minimum calving rates and calving intervals of Bryde's whales using the study area, because these animals could have had calves that were not captured with the mother or years where both mother-calf pair were in the study area but were missed. The calving interval estimates may be biased low (calving rates biased high) because of the short capture histories in D2, which did not allow for longer birth intervals to be observed. Additionally, the incomplete capture histories (function of the probability of capturing individuals) in D1 may have allowed for births to be missed in the reproductive histories of individual females, resulting in the overestimation of calving intervals (underestimation of calving rates) (Civil *et al.*, 2017). However, the similar estimates between D1 and D2, suggest the biases are minimal.

As far as the author knows, there are no calving rates and calving intervals estimated for Bryde's whales. However, these results are almost double of the calving intervals reported for humpback whales in the Gulf of Maine (mean = 2.35 years, SD = 0.7) (Clapham and Mayo, 1990) and for the Northern British Columbia (mean = 2.57, SD = 0.45) (Wray and Keen, 2020). The calving intervals calculated for Bryde's whales in Madeira are more similar to other income breeders like the killer whale (Kuningas *et al.*, 2014; Esteban *et al.*, 2016) or the long-finned pilot whales (Verborgh *et al.*, 2016). The results also show that Bryde's whales females using Madeira archipelago have longer calving intervals than the classical two years of the reproductive cycle of baleen whales (Kato and Perrin, 2018), probably as a consequence of the energetic costs of reproduction, dependent on mating opportunities and possibly following a breeding strategy more similar to income breeders.

3.4.4 Site fidelity

Site fidelity is an animal's tendency to return to a previously used area, and it is part of the behaviour that helps understand movement patterns and aspects of the animal's life history (Tschopp *et al.*, 2018). SFI were used to identify and understand individual Bryde's whales' patterns of use of Madeira archipelago inshore waters and group them in clusters with similar patterns of site fidelity, reflecting their occurrence, permanence and periodicity in the study area (Section 3.2.2.6).

Apart from the transients (animals captured only once), three site fidelity clusters or classes were identified, including regular visitors (cluster 1), occasional visitors (cluster 2) and rare visitors (cluster 3). The rare visitors, like the transients, were captured in one year, one season and one month of the study period, however, they were captured more than once during the short visit to the study area (high periodicity) (Figure 3.16, bottom). This difference is probably the result of higher probability of capture of rare visitors when compared with transients because of their behaviour (e.g. more approachable by boats), their higher distinctiveness or their differentiated use of the study area, i.e. staying longer in the most sampled area (south of Madeira Island). Actually, all eight individuals of cluster 3 are well-marked and thus more likely to be matched and recaptured than slightly distinctive animals, many of them classified as transients (Table 3.14).

The indicator periodicity separated the rare visitors from the other two classes, while the indicators occurrence and permanence, especially the latter, discriminated regular visitors from occasional visitors. The values of permanence were much higher than the values of occurrence (Figure 3.16), thus bearing more impact in the SFI used to define the site fidelity classes. The indicators occurrence and permanence can be influenced by the time animals enter the superpopulation and start using the study area during the study period. Animals recruited (born or immigrated) in later years of the study period will have naturally lower number of possible captures and a shorter possible time between first and last recapture, when compared to animals using the area from the beginning of the study, especially if they have a similar pattern of use of the area. It is possible that some animals entering late in the superpopulation and classified as occasional visitors could be classified as regular visitor if the study extended for a longer period, allowing those animals to be further captured and for longer periods. Nevertheless, animals of all site fidelity classes, except rare visitors and transients in a few years, were identified in all years of the study period (Figure 3.17), indicating that these site fidelity classes reflect real patterns and not the result of animals entering the superpopulation late in study period. Furthermore, the definition of site fidelity classes were based on multiple SFI and benefited from the information brought by the three indicators (occurrence, periodicity and permanence) used to estimate them (Verborgh *et al.*, 2022), possibly minimizing biases such as the one mentioned previously.

In spite of the increase in the number of animals using the study area over the study period (Figure 3.17), the percentage of regular and occasional visitors diminished (71% to 56%) between 2005 – 2012 and 2014 – 2021, while the percentage of rare visitors and transients increased (29% to 44%). These results suggest that Madeira archipelago may have reached its capacity to sustain animals regularly using the area, for example, to feed.

Moreover, in the first period (2005 – 2012) most animals classified as regular and occasional visitors were confirmed females (63%), while they were only 10% among rare visitors and transients (Table 3.15). Overall, for the first period there were less confirmed females (46%) than unknown sex animals (54%) using the study area. The low number of confirmed females among rare visitors and transients is expected because animals would be only identified as females if they were with a calf in the single year they visited Madeira inshore waters. However, many of those animals could be immature females or females in reproductive resting years when they were captured. In contrast, a higher percentage of animals are more likely to be identified as females among regular and occasional visitors as they return to the study area in several years during the study period, accompanied by a calf in one or more of those years. For the second period (2014 – 2021) it is harder to make inferences because a higher percentage of new animals coming into the area were rare visitors or transients, and thus less likely to be identified as females, or, being regular or occasional visitors, there were less years available to capture them with a calf when compared with females that used the area over the whole study period. At least in the first period, most animals using Madeira archipelago inshore waters were females, probably taking advantages of the local resources. It would not be surprising if that was the case in the second period.

The SSFI (HI4) discriminated the animals with higher site fidelity (regular and occasional visitors) from those of low site fidelity (rare visitors), with values that were significantly different, regardless of the dataset. However, the SSFI failed to separate the higher site fidelity animals between regular and occasional visitors. The HI4 only incorporates information about permanence and periodicity, thus leaving out occurrence which is also important to differentiate regular from occasional visitors. These differences were mostly evidenced by SFI that included both occurrence and permanence, such as, IH1, IA2 and IH2. The combination of several SFI proposed by Verborgh *et al.* (2022) was demonstrated to be a good approach to show patterns in site fidelity that were captured by different SFI.

The small number of satellite tags deployed with success (three) does not allow any robust conclusion to be reached about the pattern of use of Madeira archipelago inshore versus offshore waters by Bryde's whales with different site fidelity patterns. Nevertheless, during tracking one tagged regular visitor (Be0024) spent a higher proportion of time (67%) inside the study area, while the tagged occasional visitor (Be0107) spent most of the time (70%) outside the study area (Table 3.16). These results are in line with what would be expected from animals with different site fidelity patterns. The other regular visitor (Be0194) only spent 7% of the track time inside the study area because it was tagged close to the end of the Bryde's whale season in Madeira, with the animal starting a migration southward towards the Canary Islands (Figure 3.10).

3.4.5 Abundance

The best RD model selected for all datasets, regardless of matching uncertainty level, included transience and no immigration/emigration. The non-calf Bryde's whales had an overall upwards trend in abundance during the study period for all datasets analysed (Figure 3.20 and Figure II.8-1, Appendix II). The estimates were also very similar across datasets, regardless of species identification and matching uncertainty level. The exceptions were between datasets with different distinctiveness levels (WM and ALL). The datasets with WM individuals reached a highest abundance estimate in 2017 and had a downwards trend afterwards. The datasets with ALL individuals reached the highest abundance estimates only at the end of the time series (2019 and 2021). These different estimated abundance trends may reflect the underlaying selected models for the two types of datasets (WM animals with probability of capture varying by primary sampling occasion and ALL animals with probability of capture varying by primary and secondary sampling occasion; Table 3.22), possibility limited by the smaller WM datasets size. However, they may also reflect an increase in the number of younger animals (expected in general to be less marked than older animals) using Madeira in the last years of the study, replacing well-marked individuals, i.e., in general older animals, that use the study area less. If this is the case, then use of only well-marked individuals to estimate abundance would tell an incomplete story about the evolution of abundance of Bryde's whales in Madeira archipelago. As pointed out by Urian *et al.* (2015), most researchers assume that the behaviour of the marked animals they capture in photographic images is representative of the population and that distinctive individuals are representative of the entire population. That may not always be the case.

The estimates of the POPAN models across all datasets also showed a clear positive trend in the abundance of Bryde's whales, both for the Madeira and the Madeira-Canary Islands superpopulations. As expected POPAN estimates of abundance were in general higher for the datasets with matching uncertainty level 3 (certain matches) (Figure II.9-1, Appendix II). In these datasets there is likely to be an increase in false negatives which would result in a positive bias in abundance estimates (Urian *et al.*, 2015; Ashe and Hammond, 2022).

In spite of the correction for unmarked individuals (Section 3.2.2.4 - Proportion of marked animals) the estimates of abundance were not similar for all datasets with the same level of matching uncertainty. These differences were expected between datasets that include animals with confirmed Bryde's whales (SC) and datasets that included both confirmed and suspected Bryde's whales (SN), because of the smaller number of animals and captures of the former datasets. It was less expected between equivalent datasets of only well-marked animals (WM) and of slightly distinctive and well-marked animals (ALL), considering they were corrected for the proportion of unmarked animals. As pointed out by Urian *et al.* (2015), variation and bias can arise from the way in which the proportion of marked animals is estimated and used to scale the estimate of abundance to include unmarked animals. Usually, the proportion of well-marked animals for cetacean species is calculated or estimated in an assumed representative sample of groups, where all animals were captured with good quality images (Urian *et al.*, 2015). However, in the case of Bryde's whales that was not possible because most animals were sighted alone.

The dataset ALL-SN probably generated the abundance estimates closest to reality, i.e. least biased, both in RD and POPAN. Besides being the largest dataset explored, both in number of animals and captures, it also eliminated the bias from the exclusion of animals with unconfirmed species status and the positive bias of the datasets with only certain matches (e.g. ALL-SN.3, Appendix II). In contrast, the confidence intervals of the estimates widened with the increase in animals captured and the decrease in recaptures and capture probabilities caused by including animals with unconfirmed species status and the likelihood of missed matches occurring from the inclusion of slightly distinctive animals.

Between 2006 and 2012, the estimated number of Bryde's whales using Madeira inshore waters went from 25 to 97 animals, most of them well-marked animals (68%) and females. From 2014 onwards, the estimated number of whales per year were always above one hundred, except in 2015, reaching a maximum of 213 in 2021. In this second period the number of well-marked animals reduced to 47%, possibly as a result of older more well-marked individuals being replaced or outnumbered by younger less marked animals. The estimated super-population of Madeira-Canary Islands was 592 animals, only 73 more than the estimated superpopulation of Madeira. These results, together with the evidence of considerable movements of whales between Madeira and the Canary Islands (discussed next) suggest that most animals are shared between both archipelagos, with a small proportion added to the super-population of Madeira-Canary Islands. These abundance number are of the same magnitude of populations with more localized distribution (e.g. Kochi, East China Sea, Gulf of California, Gulf of Thailand or South African inshore), but far smaller than open ocean populations (Freitas and Penry, 2021).

The very small abundance estimates (low tens) at the beginning of the study period (2006) and the upwards trend in abundance in the following years gives strength to the possibility of a recent arrival of Bryde's whales to Macaronesia. The back-projection of the population growth trend to years previous to the study period would reach zero not many years in the past. The recent first records of the species in all Macaronesia archipelagos (1997, Canary Islands) give strength to this hypothesis. Furthermore, it seems unlikely that the Bryde's whale (even if misidentified as sei whale) would go unnoticed in the Canary Islands but specially in Madeira archipelago, where artisanal coastal whaling took place for 40 years (1941-81), considering the present local inshore sighting frequency of the species. There are no records of sei or Bryde's whales in the catch reports of Madeira coastal whaling (Records of the "EBAM - Empresa Baleeira do Arquipélago da Madeira", Madeira Whale Museum).

3.4.6 Movements

The photo-identification recaptures show, for the first time, that Bryde's whales move among all Macaronesia archipelagos, sometimes in very short periods of time (e.g. 8 days between recaptures in Madeira and the Canary Islands (Tenerife) and 18 days between recaptures in the Azores (Faial) and Madeira) (Table 3.10), covering linear distances greater than 1 200 km. The photo-identification recaptures also showed that animals of all classes of site fidelity (regular visitors, occasional visitors, rare visitors and transients) to Madeira inshore waters also used the other archipelagos' marine habitats, as expected. Other photo-identification studies have documented Bryde's whales displacements of a few hundred kilometres in relatively short periods of time, such as an animal resighted between Ecuador and Peru (Castro *et al.*, 2017), 294 km and seven months apart, or another animal that was recaptured between the Canary Islands and Madeira 43 days later and ~500 km apart (Ferreira *et al.*, 2021). However, the displacements documented in this study both through photo-identification (above) and satellite telemetry show larger movements in shorter periods of time, attesting for the high mobility of these animals in Macaronesia. The tracks of animals followed by satellite telemetry showed, for example, segments (in transit) of 355 km travelled in 40 hours (Be0107), 279 km in 32 hours (Be0194) or 281 km in 24 hours (Be0024). The latter animal, accompanied by a calf, covered 702 km in 5 days, alternating between transit and exploratory behaviour (Figure 3.13). Overall, two animals travelled > 1 000 km in 3 weeks and one animal ~2 300 km in two months (Table 3.11). Such large movements of Bryde's whales have previously only been documented in the Pacific with one tagged animal travelling ~920 km in 13 days and another ~2 650 km in 20 days (Murase *et al.*, 2016).

Movements between Madeira and the Canary Islands were confirmed previously for a small number of animals (7) (Ferreira *et al.*, 2021), however, in the present study it is shown that far more animals (53) move between these two archipelagos, not only over the years but easily within a year (Table 3.10). The same happened for movements recorded between Madeira and the Azores but for fewer animals, possibly reflecting, at least in part, differences in sampling effort between the Azores and Canary Islands. Nevertheless, it is expected that there are fewer animals moving between Madeira and the Azores than between Madeira and the Canary Islands, considering the far greater presence of the species in these archipelagos when compared with the Azores, where they are more rarely seen (Freitas and Penry, 2021). In some cases, back and forth movement between two archipelagos were also recorded in the same year (Be0016, Be0046 and Be0072; Table 3.10). No animals were captured in the same year in the three archipelagos or between Azores and the Canary Islands, probably reflecting more the differences in sampling effort among locations than the ability of animals to travel such distances, as demonstrated by recaptures between archipelagos and displacements made by tagged animals (Figure 3.10).

Bryde's whales not only travelled between archipelagos but also used offshore waters as shown by satellite telemetry data (Figure 3.10). The predicted track of animal Be0107 (Figure 3.14) showed inshore-offshore-inshore movements, including the seamounts north of Madeira. The use of offshore waters, was also confirmed by the predicted tracks of animals Be0194 (Figure 3.12) and Be0024 (Figure 3.13), the former mostly associated with seamounts north of the Canary Islands, and the latter mostly associated with deeper waters between seamounts while traveling north.

Three behavioural states (ARS, transit and exploratory) were identified from the analysis of satellite track data of three animals, using HMM. The preferential association of ARS behaviour (which is usually associated with foraging) of these animals to fixed predictable locations like islands and seamounts (Figure 3.12 – Figure 3.14), suggests that Bryde's whales were taking advantage of the usually higher productivity around these physiographic features (Doty and Oguri, 1956; Caldeira *et al.*, 2002; Palacios, 2002) and of their prey aggregating effect (Morato *et al.*, 2008; Fiedler, 2009), when compared with surrounding more oligotrophic deep open ocean waters. This strategy should help these Bryde's whales to increase their energetic acquisition by easier access to prey when compared with the energetic cost to search for, find and capture more scattered prey in the much larger open ocean, especially for lactating females like the animal Be0024 with higher energetic needs (Lockyer, 2007; Srinivasan *et al.*, 2018). The transit behaviour was consistently observed over deep waters while the animals moved from one fixed physiographic feature to another, usually changing to exploratory behaviour in their vicinity. One exception was the whale Be0107 that switched to ARS behaviour southwest of Madeira, in an area where temporary oceanic anticyclonic eddies with higher primary productivity are known to form in the wake of the island (Caldeira *et al.*, 2002, 2014). The same whale also stayed in exploratory mode during the movement between Madeira and the seamounts north of the island, even though it crossed deep sea waters. The other exception was female Be0024, accompanied by a calf, that changed to exploratory mode and afterwards to ARS behaviour in deep waters over Tagus abyssal plain. This change in behaviour may have been triggered by the availability of prey as a result of summer higher primary productivity and/or local oceanographic processes (Mann and Lazier, 1991; Nolasco *et al.*, 2013). In general contrast with these findings, in the Northwest Pacific two tagged Bryde's whales used exclusively deep open ocean waters (no apparent association with islands or seamounts) while travelling during summer southwards between the subarctic-subtropical transition area to the subtropical area. Additionally, in the Hawaiian Islands, Bryde's whales did not show a particular attraction to inshore waters of the archipelago, being mostly seen in offshore waters (Barlow, 2006; Bradford *et al.*, 2017).

The movements of Bryde's whales among islands and seamounts identified by photo-identification and satellite telemetry within a year, shows that probably each of these small habitats on its own is not enough to fulfil these animals' energetic needs (limited prey biomass available) (Table 3.10 and Figure 3.12 – Figure 3.14). The strong seasonal presence of Bryde's whales in the Macaronesia region, especially in the Canary Islands and Madeira, is an indication that these oligotrophic waters may not provide the necessary prey to sustain year-round the population using the area in spring and summer. The photo-identification (Section 3.3) and satellite telemetry (Section 3.3.2.2) data suggests some degree of south-north-south seasonal movement of animals in the central northeast Atlantic, although probably not the same for all animals (e.g. some animals, especially females with calves, are seen in Madeira and the

Canary Islands in winter; Section 3.3.5). Furthermore, the few captures of Bryde's whales in locations further south (e.g. off Mauritania and Guinea-Bissau) happened at either the beginning or the end of the year (winter) (Figure 3.9), while the recaptures in Algarve happened during summer and the beginning of Autumn. These latitudinal seasonal movements along west Africa offshore waters may be justified by animals taking advantage of higher productivity at lower latitudes in winter months resulting from a seasonal upwelling in the Mauritania-Senegalese upwelling zone (12-19ºN) that fades during summer months and a permanent strong upwelling zone between 21-26ºN (Cropper *et al.*, 2014). In spring and summer animals may benefit from a greater seasonal productivity at higher latitudes both from an increase in sunlight available for photosynthesis, both in continental waters and open ocean waters of Macaronesia, and from an increase in upwelling strength during summer months between 26º-35ºN in the West African coast (Cropper *et al.*, 2014).

The possible recent arrival of Bryde's whales to Macaronesia and their increase in abundance over recent years is an indication of the expansion of the species distribution, probably from lower latitudes along the west coast of Africa. There may be several non-mutually exclusive reasons for such an expansion, among them, population growth with distributional expansion (e.g. Andriolo *et al.*, 2010; Ví-kingsson *et al.*, 2015), shift in distribution or expansion as a result of less food availability in the original area of distribution because of overfishing and/or climate change, and an increase in productivity around Madeira archipelago. There is no evidence to confirm a population expansion except the population growth in Madeira archipelago and its very high apparent survival. The fish stocks in West Africa have been over recent decades under great fishing pressure and are overexploited (Palomares and Pauly, 2004; Lam *et al.*, 2012), which may have contributed directly or indirectly to less prey available for Bryde's whales. Morissette *et al.* (2010) showed a reasonable overlap between preys consumed by Bryde's whales and some of the fisheries taking place in Northwest Africa. Furthermore, the results from simulations with software Ecosim suggest that those ecosystems are currently heavily exploited and cannot sustain more fishing effort without collapsing (Morissette *et al.*, 2010). According to Belhabib *et al.* (2016), climate change and over-exploitation have altered species composition of fisheries catches in West Africa, while model projections show that climate change may lead to substantial reduction in marine fish production in this region by the 2050s (Lam *et al.,* 2012). Conversely, in the last two decades there was an increase in the primary productivity in the wider open ocean surrounding Madeira archipelago (Siemer *et al.*, 2021), including an increase in chlorophyll-a concentration, an increase in the number of productive days (up to 22 days during the last 21 years), and an expansion of the productive area (+7 %).

A similar northward expansion has been recorded in the Southern California Bight (Kerosky *et al.*, 2012). According to the authors there was a significant increase in the presence of calling Bryde's whales in the area from summer to early winter between 2000 and 2010, indicating a seasonal poleward range expansion. No significant correlation was found between Bryde's whale presence and local sea surface temperature, with their occurrence most likely driven by prey availability within the California Current ecosystem, which is affected by seasonal and inter-annual changes in climate and oceanographic conditions.

In conclusion, the results from this study support the hypothesis of a recent arrival of Bryde's whales to Macaronesia. This study also showed that Bryde's whales move easily among Macaronesia archipelagos and nearby seamounts, sometimes in a matter of days or weeks. Nevertheless, animals showed different degrees of site fidelity in the use of Madeira archipelago inshore waters. Furthermore, the Macaronesia archipelagos, especially Madeira and the Canary Islands, seem to be important for mother-calf pairs.

Bryde's whales in Macaronesia feed preferentially around islands and seamounts, probably to take advantage of the usually higher productivity and prey aggregating effect of these physiographic features. Furthermore, the Macaronesia open ocean oligotrophic waters do not seem to be an important habitat to feed based on the transit behaviour inferred from satellite telemetry.

In summer, Bryde's whales used Macaronesia higher productivity habitats (inshore waters, seamounts and particular oceanographic features), moving away in winter, probably to more productive habitats along the west African coast, as suggested by the photo-identification and satellite telemetry data. However, some animals stayed in the area throughout the winter, especially females with calves.

Baleen whales have traditionally been considered capital breeders, however, the lactation period and the calving intervals estimated in this study support the view that Bryde's whales' breeding strategy is closer to income breeders than to capital breeders. Furthermore, evidence suggests they may feed regularly throughout the year, like income breeders.

Chapter 4


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ABUNDANCE AND SPATIAL AND TEMPORAL DISTRIBUTION OF CETACEANS IN MADEIRA ARCHIPELAGO: HOW DIFFERENT SPECIES SHARE A LIMITED MARINE INSULAR HABITAT

ABUNDANCE AND SPATIAL AND TEMPORAL DISTRIBUTION OF CETACEANS IN MADEIRA ARCHIPELAGO: HOW DIFFERENT SPECIES SHARE A LIMITED MARINE INSULAR HABITAT

4.1 INTRODUCTION

The Madeira archipelago waters are shared among 28 cetacean species (Freitas *et al.*, 2012), with known differences in their patterns of occurrence (common species, regular species, occasional species, rare species), seasonality (year-round presence, seasonal presence, intermittent presence) (Freitas *et al.*, 2004b) and different degrees of site fidelity among individuals of some species (e.g. Alves *et al.*, 2013; Dinis *et al.*, 2016b). Past studies have been mostly focused on single species (e.g. Halicka, 2015; Dinis *et al.*, 2016a), and the few involving multiple species (Freitas *et al.*, 2004b; Alves *et al.*, 2018; Fernandez *et al.*, 2021), had considerable sampling and/or methodological limitations thus restricting inference to allow a better understanding of the habitat preferences and the factors shaping spatio-temporal distribution, considering the marine habitats available to cetaceans in Madeira archipelago.

The description and understanding of the processes that determine the distribution of organisms is a fundamental problem in ecology, with important conservation and management implications (Redfern *et al.*, 2006). Habitat use modelling allows the investigation of the relationship between distribution of observations of a species and environmental variables that may directly or indirectly influence that distribution. There are several modelling approaches (e.g. Elith *et al.*, 2006; Redfern *et al.*, 2006; Fiedler *et al.*, 2018), but generalized additive models (GAMs) are among the commonly used for count data, incorporating search effort. In the last two decades habitat use modelling of cetacean species with GAMs has been used in many studies to address ecological, conservation and management questions (e.g. Cañadas and Hammond, 2008; Baines and Reichelt, 2014; Lambert *et al.*, 2017; Schleimer *et al.*, 2019b).

To understand the spatial and temporal habitat use of cetacean species in Madeira archipelago, it is important to consider the local seasonal patterns of primary productivity (Figure 1.2). In general, the primary productivity reaches its maximum during winter and spring decreasing in summer and reaching its minimum in autumn (Caldeira *et al.*, 2002; Martins *et al.*, 2007). It is also important to have in mind the expected delay in the upwards cascade effect on the local food-webs of the higher primary productivity in winter and spring, measured through chlorophyll-a concentrations. The community of zooplankton, measured in a station south of Madeira island from March to August 2003, showed the highest values of zooplankton biomass in March and April, followed by reduction in subsequent months and a recovery in August (Alves and Kaufmann, 2003).

Furthermore, Caldeira and Sangrà (2012) made a realistic computer simulation of Madeira archipelago to study the island wake problem, i.e., the effect of these physiographic features (islands) on the flow of the currents. Four scenarios were explored to represent the flow regimes affecting the islands, namely, southward current (Canary Current), northward current, eastward current (Azores current) and westward current (West Africa coast filaments), taking into consideration the effect of the islands' shelf. Two phenomena highlighted by the study are probably relevant to explain cetacean use of Madeira archipelago. Firstly, the cyclonic eddy formation, weakening down to a depth of 200 m, associated with anticyclonic vorticity at the surface. These eddies, forming closer to the surface, contribute to export prey biomass in the euphotic zone from Madeira coastal waters to further offshore waters, probably having an impact on the habitat use of surface-dwelling cetacean species. Secondly, the formation of anticyclonic circulation at depths below 300 m contained within a cyclonic rim around the archipelago. This contained anticyclonic circulation at depth probably helps distribute and contain within the rim zooplankton and other mesopelagic/bathypelagic prey, contributing to the islands' aggregating effect. The coastal and sea surface (euphotic zone) primary productivity will not only contribute to the increase of the biomass in the epipelagic layer but also in deeper waters by mixing, downwelling currents and the gradual sinking of plankton in the water column (Mann and Lazier, 1991). This last phenomenon is not only relevant for deep diving species (pilot whale, sperm whale and beaked whales) but also for surface dwelling species that take advantage of the diel migration of the deep scattering layer and mesopelagic fish over the islands slopes (e.g. Bryde's whale, spotted dolphin, common dolphin and bottlenose dolphin).

The small size of the archipelago and its location in relation to nearby continental waters, neighbouring archipelagos (Canary Islands and Azores) and seamounts, and influenced by open ocean dynamic features (Azores current and front; Canaries Current; West Africa productive filaments) (Klein and Siedler, 1989; Zhou *et al.*, 2000; Caldeira and Sangrà, 2012), provide the conditions to investigate the role of open oceans islands in the lives of cetaceans and how they may share or compete for resources in such small insular marine environment. According to ecological theory, for sympatric species with similar ecological requirements to coexist they need some degree of habitat and resource partitioning to minimize competition (Pianka, 1974).

Questions posed by the study

To understand the importance of oceanic islands to cetaceans it is important to understand how the different, apparently competing, species (populations) share those islands' limited inshore marine habitats and surrounding waters over space and time. To address this overarching question, the data collected over the last two decades by multiple surveys carried out in Madeira archipelago waters were combined to:

a) Increase understanding of the seasonal patterns of temporal distribution of cetacean species in the study area;
b) Increase knowledge of the habitat use of cetacean species using the study area, including the underlying ecological and biological drivers, and how that habitat use may change seasonally;
c) Investigate how well primary productivity related covariates may explain the distribution of lower trophic level cetacean species in oceanic islands, considering the delays in propagation of changes through the food web.

The study combined data from dedicated shipboard and aerial line-transect surveys, non-systematic shipboard surveys and observers on whale-watching and fishing boats to model the temporal and spatial use of Madeira archipelago waters by the main cetacean species and to identify their habitat preferences.

4.2 MATERIAL AND METHODS

4.2.1 Study Region

The study was carried out in the coastal waters of the Madeira archipelago, Portugal, from the shore up to a maximum distance of 50 km from land (Figure 4.1). The surveys covered an overall area of 11 923 km^2, and included partially overlapping survey areas, that changed according to the type of survey.

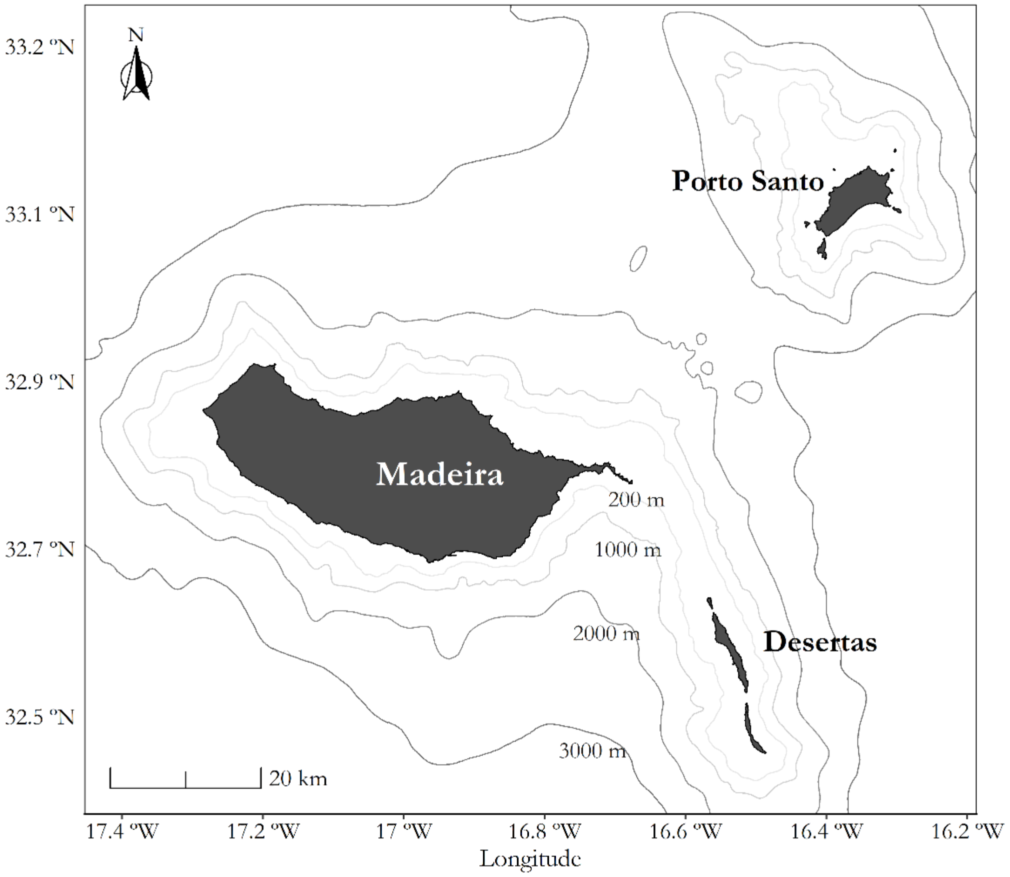


Figure 4.1. The overall study area comprising inshore waters of the Madeira archipelago around the main group of islands (except the Selvagens islands), from shore up to a maximum distance of 50 km from land.

4.2.2 Survey type, survey design, and data collection

Multiple systematic shipboard and aerial line-transect surveys, non-systematic shipboard surveys, data from observers on whale-watching trips and data from observers on fishing vessels were combined to model the habitat use of several cetacean species in the study area over a period of 17 years.

4.2.2.1 Systematic shipboard line-transect surveys

Systematic shipboard line-transect surveys (SLS) were conducted in Madeiran coastal waters in 2001-2002 (Project CetaceosMadeira), 2007-2009 (Project Emecetus) and 2010-2012 (Project CetaceosMadeira II), with year-round coverage and following conventional designed-based distance sampling methodology (Strindberg and Buckland, 2004), to estimate the abundance of cetacean species in the archipelago.

To provide equal coverage probability, replicate random equal spaced zig-zag transects with 8 nautical miles (nm) spacing were generated using either Distance 4.0 or Distance 5.0 (Thomas *et al.*, 2010) for eight blocks, covering all inshore waters up to the 2 000 m depth contour (maximum distance from land between 8 and 20 km)(Figure 4.2). The blocks were laid out so that transects were as perpendicular as possible to the depth contours and a block could be surveyed in one day, allowing the vessel to return every night to harbour. The study area was adjusted in the 2010 – 2012 surveys, with a reduction in sampled area in block 6 (230 km^2) and an increase in blocks 7 and 8 (209 km^2) (Appendix III; Figure 4.2). The 2001 – 2002 and 2007 – 2009 surveys considered a planned monthly coverage of the entire study area (maximum 24 replicates per survey period) while the 2010 – 2012 surveys considered two transects per block every three months (maximum 20 replicates per block). In all survey periods, the transects were carried out as much as possible on days with predicted sea conditions of Beaufort 3 or less.

The 2001-2002 transects were surveyed from a dedicated 12 m open deck wooden fishing vessel ("Calcamar") with a cruising speed of 6 knots, with 4-6 crew of which two took seated position as observers on the bow of the vessel on a platform with a height of approximately 2 m (Figure 4.3). Each observer searched one side of the boat, with the search sector covering the area from 90° to the bow, with the sectors overlapping 20° on track line. The 2007 – 2009 and the 2010 – 2012 transects were carried out on a dedicated 16.5 m steel motorsailer vessel ("Ziphius") with an average cruise speed of 6.5 knots, with a crew of five to seven and with two observation platforms (Figure 4.3). The forward platform, with a height of 3.93 m, had one observer (seated) who searched 30° to each side of the track line, while the aft platform, with a height of 3.52 m, had two observers (standing) who searched a sector each side of the boat from 90° (abeam) forward to 20° from the track line. In all surveys the trained and experienced observers searched with naked eyes, alternating with 7 x 50 binoculars, and rotated with other positions such as data recorder, helmsman or to rest, so that observation periods were between 40 minutes and 2 hours maximum.

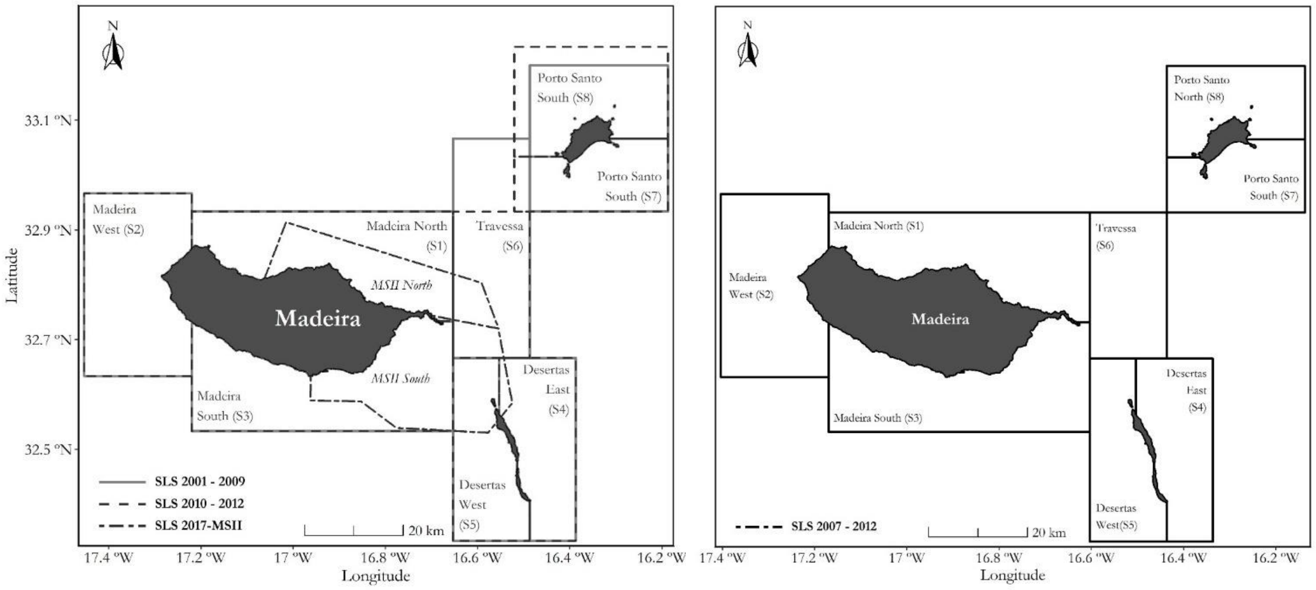


Figure 4.2. Left: Study areas, and respective blocks, of the systematic shipboard line transect surveys (SLS) carried out in the Madeira archipelago from 2001 to 2009, from 2010 to 2012 (changes in blocks S6 (reduced area), S7 and S8 (increased areas) in comparison with 2001-2009 survey area) and 2017 (covering a subarea of the previous surveys). Right: common survey area shared by 2001-2009 surveys and 2010-2012 surveys, for which the sighting and effort data were pulled together to have enough sightings to obtain detection functions in distance sampling analysis and generate abundance estimates for the period 2007-2012.

Sightings, effort and environmental data were recorded in a laptop running LOGGER 2000 software (IFAW, 2020) or, alternatively, on backup paper forms. Global Positioning System (GPS) track lines were recorded in the laptop computer and in a backup portable GPS device internal memory. Effort and environmental data were recorded every hour or whenever the conditions changed. Whenever observers were searching for cetaceans, the survey was in "on effort" mode, either on transect or passage, otherwise it was in "with animals" mode or "off effort" mode. In the SLS between 2001 and 2009, whenever the transect was suspended to be with the animals for photo-identification work or to obtain biopsies, it was recorded as "off effort" rather than "with animals". The environmental data included among others wind direction and strength, sea conditions measured on the Beaufort scale, and swell height. When a sighting was made, angle and distance to the sighted group were recorded, as well as species identification, cue, minimum, average and maximum group size, number of calves, heading of the group, group composition (adults, subadults, juveniles and calves), natural behaviour (e.g. travelling, feeding, resting, socializing) and response behaviour (attracted to the boat, avoiding the boat, neutral, bow-riding). When more than one natural or response behaviour was observed in the group during the sighting it was recorded with the main natural behaviour identified. Whenever the sighting was less than 15 minutes away at the vessel's cruising speed and it was deemed necessary, the vessel would leave the track line temporarily to approach the group for species identification/confirmation, group count and gather sighting-related data, whilst remaining "on effort", returning afterwards to the track line. If the observed sighting was more than 15 minutes away at the vessel's cruising speed or the sighted species was of interest for photo-identification and/or biopsying, effort status would be changed from "on effort" to "with animals" or "off effort".

Figure 4.3. Left: the open deck wooden fishing vessel "Calcamar" used in systematic line-transect surveys (SLS) in Madeira archipelago inshore waters between 2001 and 2002; Centre: the motor-sailer vessel "Ziphius" with a front and aft observation platforms used in SLS to survey inshore waters between 2007 and 2012. Right: the rigid inflatable boat "Kogia" used in SLS in 2017.

Also included in the present study was a line-transect survey (Project Mistic Seas II – coastal subprogram) with multiple random equal spaced zig-zag transects, carried out from August to November 2017 in part of the area sampled by the previously mentioned SLS surveys, covering the northeast, east and southeast waters of Madeira Island and divided in two blocks (15 replicate transects per block)(Figure 4.2). As in the previous surveys, the transects were carried out as much as possible on days with predicted sea conditions of Beaufort 3 or less. This survey's primary aim was to collect data for a photo-identification mark-recapture study based on robust-design (SLS-RD), following an equal coverage probability design and also collecting distance sampling data. The dedicated 6.5 m rigid inflatable boat "Kogia" was used in the survey with an elevated platform (height of 2 m) for two seated observers and a cruising speed of 10 knots (Figure 4.3). Each observer had the same searching sector and search procedure as explained previously for the 2001-2002 surveys, except the observers only searched with naked eye. The team was three or four people rotating between positions (two observers, helmsman or rest), and with periods of observation between 80 minutes and 2 hours' maximum. The surveyed track was recorded with a portable GPS, and sighting, effort and environmental data were recorded on paper forms. Effort and environmental data were recorded every hour, whenever the conditions changed or when the end of a transect leg was reached (waypoint). The sighting form included fields similar to those in the forms of previous surveys, with minor adjustments in the categories defined for some of those fields, but which remained equivalent and comparable. However, unlike previous SLS surveys only the main natural behaviour was recorded. Whenever there was a sighting, the relevant data were recorded and, if needed, the group of interest was approached temporarily. If the sighted species were of interest for photo-identification or to obtain biopsies the effort status would change to "with animals" and the transect was resumed at the point where search effort was interrupted after the work with the group was done.

4.2.2.2 Systematic aerial line-transect surveys

Systematic aerial line-transect surveys (ALS) were also conducted in Madeiran coastal waters in 2002 – 2008, with year-round coverage and following conventional designed-based distance sampling methodology (Strindberg and Buckland, 2004) to complement SLS surveys in the estimation of cetacean species abundance in the archipelago.

To provide equal coverage probability, replicate random equal spaced zig-zag transects with a spacing of 10 nm were generated using Distance 4.0 (Thomas *et al.*, 2010) for four blocks, covering all inshore waters up to the 3 000 m depth contour (maximum distance between 8 and 40 km from land) (Figure 4.4). The blocks were laid out so that transects were as perpendicular as possible to the depth contours and so that one or two blocks would be surveyed completely in one flight, including the distance to start and end points of effort and within the flying endurance capabilities of the aircraft. The survey strategy considered monthly coverage of the entire study area (maximum of 84 replicates for the survey period); however this was dependent on aircraft availability, which was limited by weather, maintenance periods and other planned or priority missions assigned to the aircraft. In all survey periods, the transects were carried out as much as possible on days with predicted sea conditions of Beaufort 2 or less.

The aerial surveys were carried out at an altitude of 500 feet from a Eurocopter AS350 Écureuil helicopter certified for flights up to 20 nm from land and with a flying endurance of 2:30 h and a cruising speed of approximately 100 knots (Figure 4.4). Each survey was conducted with four crew, the pilot and three trained and experienced observers. The observer sitting to the left of the pilot surveyed up to 30° to each side of the track line while the observers sitting behind searched from 20° to 90° of the track line on each side of the aircraft.

In all surveys the observers searched with naked eyes, although 7 x 50 binoculars were used to verify cues sighted further away from the track line. Sightings, effort and environmental data were recorded by the observer sitting aft of the front observer in a laptop running LOGGER 2000 software (IFAW, 2020) or, alternatively, on backup paper forms. GPS track lines were recorded in the laptop computer and in the GPS internal memory as backup. Effort and environmental data were recorded at the beginning of effort and whenever the conditions changed. The environmental data included among others Beaufort and general weather conditions. Whenever a sighting was made, the spotter informed all crew and the helicopter continued the flight path until the animal or group of animals was perpendicular to the aircraft at which time one of the aft observers would measure the vertical angle to the sighting using an inclinometer (Suunto) and the helicopter altitude (measured with the aircraft radar altimeter) was recorded. Afterwards, the effort status was temporarily changed to "with animals" and the helicopter would climb to 700 feet and circle over the observed animal or group for species identification and the best estimate of group size. On completion of time with the sighting, searching was resumed on the track line as close as possible to the point where it was left.

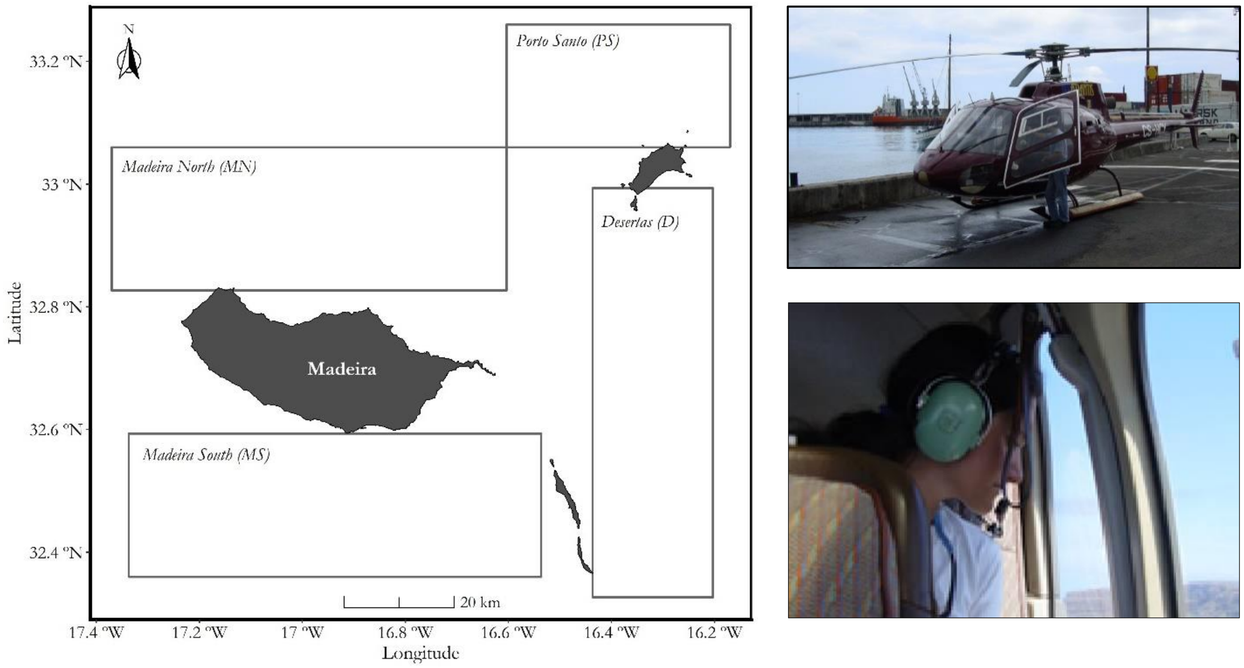


Figure 4.4. Left: systematic aerial line-transect surveys (ALS) study area, and survey blocks, carried out in the Madeira archipelago between 2002 and 2008. Right: the aircraft used in the aerial surveys and a detail of an observer searching for cetaceans.

4.2.2.3 *Non-systematic shipboard surveys*

Non-systematic shipboard surveys (NSS) were conducted in Madeira coastal waters in 2004 – 2012 and 2016, with the purpose of finding cetaceans for photo-identification, skin biopsy sampling and/or deployment of TDR (Time depth recorders) biologgers with suction cups.

There were no pre-established track lines and the search pattern was chosen considering sea and weather conditions and any information relayed by whale-watching boats, lookouts or others regarding the presence of the species of interest to maximize the chances of finding animals. As far as possible the effort was spread among the reference searching blocks (Figure 4.5); however, distance and exposure to prevailing winds limited the survey of the northern most block (Porto Santo) and the northern area of Madeira East Block, and resulted in a higher survey effort in the southern area of the latter block where the boat's mooring was. In the Madeira archipelago, the prevailing winds are from the northeast with the blocks Madeira south and Madeira southwest being usually sheltered. The course of travel could also change if there was new information about sightings from external sources and the search track could go beyond the predefined blocks, for example around the Desertas Islands (Figure 4.1; Figure 4.5). The search effort changed over the years depending on specific project objectives, although with no limitations to year-round coverage. In all survey periods, the transects were carried out as much as possible on days with predicted sea conditions of Beaufort 3 or less.

The 2004 – 2012 transects were surveyed from a 6.5 m rigid-inflatable boat (“Roaz”) equipped with an outboard 115 HP petrol engine with a cruising speed around 12 knots. The crew was usually three or four people, two of whom stood next to each other (the helmsperson and an observer) and searching for cetaceans from the track line up to 90º on their respective side of the track line. They could search both standing on the deck (around sea level) or on a seat at a height of 0.5 m. During the same period, NSS surveys were also carried out with the vessel “Ziphius” with a crew of four to six people following the observer layout and height of sight, as described in subsection 4.

The 2016 transects were conducted on a 5.5 m fiberglass boat (“Biomar”) with an outboard 60 HP petrol engine with a cruising speed of around 10 knots. The crew were also three to four people with the same search pattern as described for “Roaz”, but always searching from the boat deck, from around sea level (Figure 4.5).

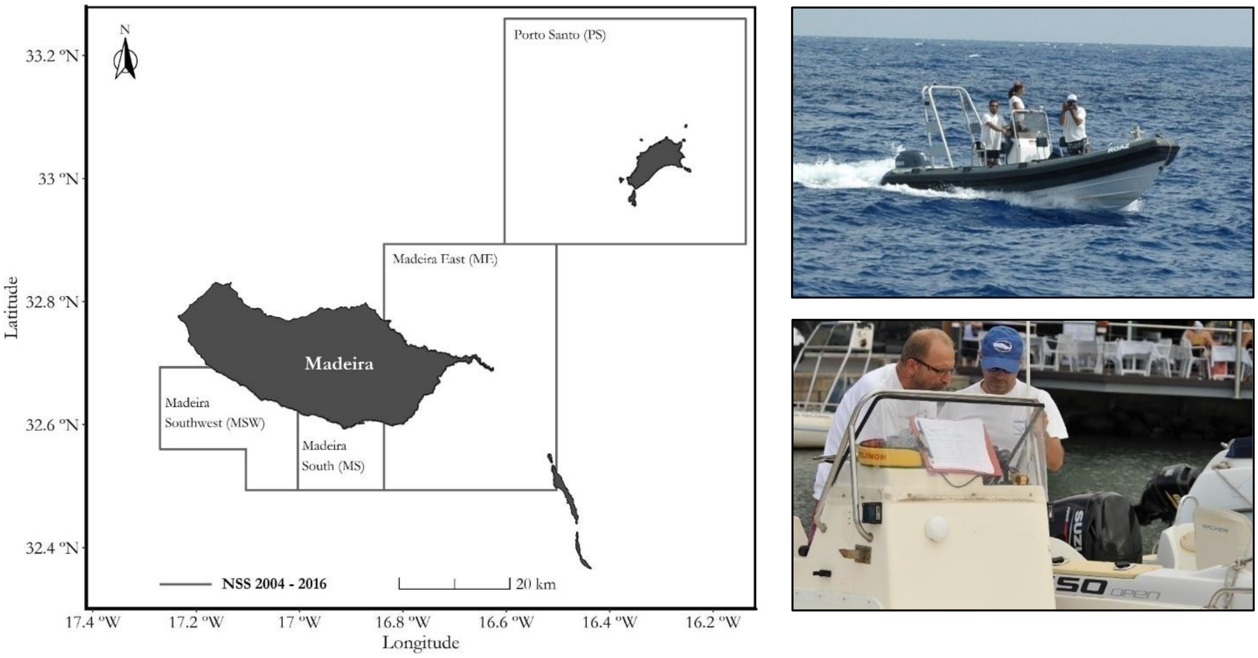


Figure 4.5. Left: Map of the study area, and survey blocks, of the non-systematic surveys for photo-id work (NSS) carried out in the Madeira archipelago between 2004 and 2016. Right: photos of the rigid-inflatable boat “Roaz” (top) and of the fiberglass boat “Biomar” (bottom), both used in the NSS.

Cetaceans were searched for in all these surveys with naked eye and 7 x 50 binoculars were only used for species confirmation and group size estimation, whenever the sighted group was not approached for photo-identification, biopsying or tagging. There was rotation among the crew at the helm and observer positions but without a rigid rotation schedule.

The search track was recorded on a portable GPS and sighting, effort and environmental data were recorded on paper forms. Start and end of search effort were recorded, but not whenever the boat was with animals. Beaufort was the only environmental parameter consistently recorded throughout these surveys, both whenever it changed and whenever there was a sighting. Whenever there was a sighting, the relevant data would be recorded and if needed the group of interest would be approached temporarily. The sighting form was simpler than that used on SLS surveys and included time of sighting, position, species, best estimate of the group size, number of calves, main behaviour observed and degree of group aggregation, and photo-identification related information whenever relevant. If the sighted species was of interest for photo-identification or to obtain biopsies, the group would be followed until the objective or the predefined time limit was reached and the search would resume afterwards from that position.

4.2.2.4 Observers on whale-watching trips

From 2010 onwards the Madeira Whale Museum (MWM) started placing trained volunteer observers regularly on-board whale-watching boats to collect data on cetacean encounters and record the operators' compliance with the volunteer code of conduct in place at the time, and from 2013 onwards, the compliance with whale-watching legislation.

These "whale-watching observers' surveys" (WWO) took advantage of these platforms of opportunity to survey the south coast of Madeira Island for cetaceans between 2010 and 2017. Photo-identification data were collected during these trips as well as effort and sighting data. The survey track was recorded on a portable GPS while the observer's search effort and the corresponding sightings were recorded on paper, whether they were the observer's own detections or by anyone on board. Whenever an encounter with cetaceans occurred, time, geographic position, species, best estimate of group size, observed number of calves, main natural behaviour and behavioural responses to the boat (e.g. bow-riding, avoidance, etc.), degree of group aggregation, environmental conditions at the time and photo-identification related information whenever relevant, were recorded. The species identification and group size were estimated using binoculars whenever the sighted group of animals was not approached. No information regarding the period of time the boat was engaged with a cetacean group was recorded, although from 2013 onwards a limit of 10 minutes was established by law.

The whale-watching boats that participated in the WWO were of three types: mono-hull boats traveling at speeds between 5 and 7 knots and ranging from 10 to 20 m length; catamarans travelling at speeds between 10 and 15 knots and with lengths 12 and 22 m; rigid-inflatable boats (RIB) with speeds of 15-20 knots and ranging from 7 to 10 m length (Figure 4.6). While observers in the mono-hull boats and catamarans searched for animals at heights varying from 1 to 3 m, in RIBs they were lower, usually close to sea level. Whale-watching trips lasted 2 to 3 hours and the boats' search pattern was decided by the skipper of the whale-watching vessel, considering sea and weather conditions and any information relayed by lookouts when they located cetaceans. Nevertheless, all boats kept on board observers searching for cetaceans as they travelled, in addition to the MWM museum observer. Most of the WWO trips started from Funchal harbour although there were a few from Calheta harbour (Southwest Madeira) (Figure 4.6). Some boats (catamarans and mono-hull boats) usually followed a similar search pattern day in day out thus covering the same area general off Funchal city towards the west, sheltered from the northeast prevailing winds. Whenever wind intensity decreased those boats would also search eastwards towards the Desertas Islands. On a few occasions surveys were also conducted on catamarans doing weekly trips to the Desertas Islands nature reserve (southeast of Madeira). The smaller RIBs covered a wider area than the other boats, did not necessarily follow particular search patterns and were also limited by the prevailing sea conditions. The search effort conducted by whale-watching boats was mostly within 6 nm of the coast and usually not going further than 10 nm either side of the boat's mooring harbour. Whale-watching trips were carried out in areas with better sea conditions and usually with Beaufort 3 or less.

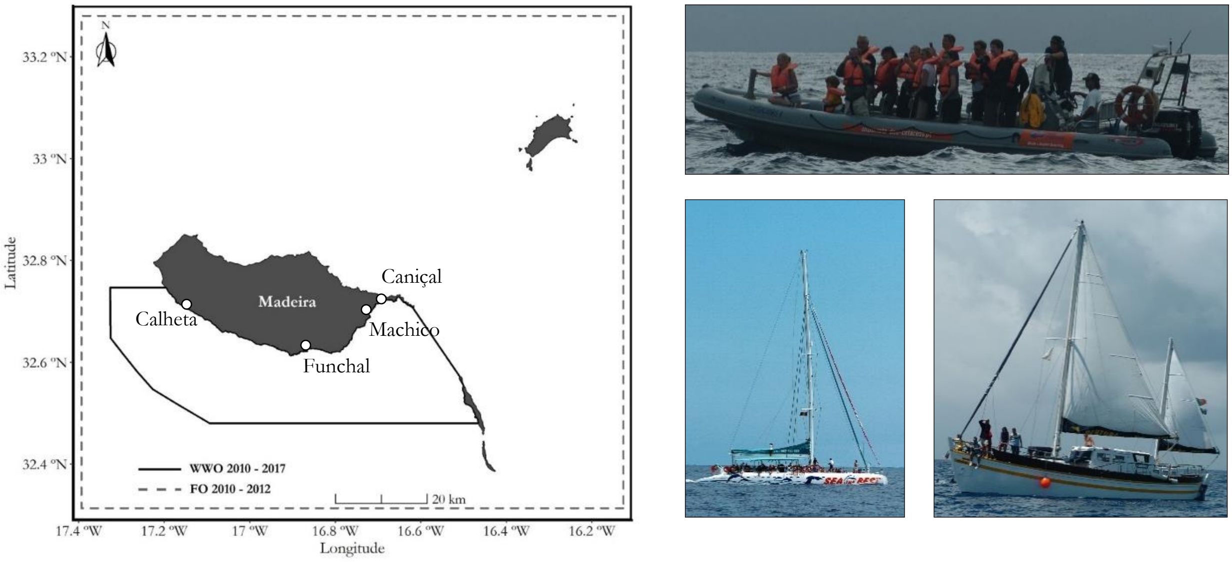


Figure 4.6. Left: Study area, covered by observers onboard platforms of opportunity, namely whale-watching boats (WWO; 2010-12 and 2014-17) and fishing vessels (FO; 2010-12), carried out in the Madeira archipelago. On the map are also identified the harbours from where the whale-watching boats operated. Right: photos of the three types of boats covered by the observers during the WWO, namely, rigid-inflatable boats (top), catamarans (bottom-left) and monohulls (bottom-right).

4.2.2.5 *Observers on fisheries vessels*

Between 2010 and 2012 the MWM placed trained observers on board pole and line tuna fishing boats operating from the Madeira archipelago and covering all months from March to October in those two years (tuna fishing season), both in Madeira EEZ inshore and offshore waters. The aim of the Fisheries Observers program was to record the interactions between cetaceans and the fisheries, including by-catch. In the present study only data collected on effort and inside the study area were used as ”Fisheries Observer surveys” (FO) (Figure 4.6).

A total of nineteen tuna fishing vessels were monitored during the two year survey period, with lengths over 25 m, travelling at cruising speeds between 10 and 15 knots and with bridges and flying bridges from 5 to 9 height above sea level (Figure 4.7). The tuna fishing vessels operated in two distinct modes: “fishing” mode and “search” mode. Whenever a shoal of tuna was located, the fishing vessel would be positioned over the shoal and start drifting or slowly moving to function as a fish aggregating device (FAD) and attract the shoal to the boat. Once this happened, they would fish on the shoal at regular intervals until the whole shoal was fished or the boat was full. In the latter situation, the fishing boat would be replaced by another to keep the shoal aggregated under a vessel. Conversely, at the beginning of the season and whenever a fishing boat did not aggregate a shoal, it would search for tuna in a non-systematic way decided by the skipper or based on information of tuna sightings obtained from other boats. Whenever the fishing vessel was searching for tuna, the observer would spread a minimum of 6 hours of sighting effort throughout the day, from sunrise to sunset, in up to two-hour search periods with minimum resting intervals of 30 minutes. The observer searched for cetaceans from the highest available point on the boat, either the bridge or the flying bridge, in sea conditions of Beaufort 4 or less.

Figure 4.7. Left: Photo of one of the ten tuna fishing boats which had observers on board between 2010 and 2012. Right: the flying bridge was one of the main location from which the observer would search for cetaceans.

The search track was recorded with portable GPS while the observer’s search effort and environmental data were recorded on paper and updated every 30 minutes or every hour, respectively, or whenever there was a change in the corresponding parameters, e.g. direction of travel > 20º (effort) or Beaufort (environment). Sightings were also recorded on paper, whether they were the observer’s own detections or those made by the vessel spotters, while on effort. Whenever cetaceans were sighted, date, time, geographic position, minimum distance to the boat, species, minimum and best estimate of group size, observed number of calves and adults, main natural behaviour and behavioural responses to the boat and degree of group aggregation were recorded. The species identification and group size were estimated using binoculars, whenever the sighted group of animals did not approach or was approached by the fishing vessel.

4.2.3 Data organization, processing and validation

Data were organized, processed and validated prior to habitat use modelling analysis. Although it can be challenging, it is crucial to integrate with coherence and consistency data from multiple surveys, designed and carried out with different purposes, to ensure a valid and robust analysis and meaningful results. Although there was an effort to keep consistency over the years within and across field work and data collection protocols of the different types of surveys, nevertheless, changes, corrections and improvements were incorporated over time as the surveys were implemented, to accommodate lessons learned, crucial specificities of the surveys and platforms utilized, and relevant methodological improvements.

Effort, sightings and environmental tables were compiled for each survey type and checked and corrected for mistakes in data input, consistency across tables and between tracks and sighting positions. Beaufort was the only environmental variable used in the analysis because of its impact on detectability of cetaceans at sea and consistency across all survey types. In the following subsections, it is explained how data from the different survey types were organized, processed, validated and selected for analysis.

4.2.3.1 Sightings and effort data processing, including track segmenting, selection and validation

The tracks of all surveys were recorded at intervals between 10 and 30 seconds using GPS devices, either connected to LOGGER 2000 Software (IFAW, 2020) running in a laptop or saved in the internal memory of portable GPS devices, and downloaded later.

Systematic shipboard and aerial line-transect surveys and fisheries observer surveys

In the SLS and ALS surveys, the data were saved in Microsoft Access relational databases using the software LOGGER 2000. The tables with the relevant data were cross related with the track table (with coordinates of the track points, time, vessel speed and heading) and exported as Excel files. In the FO surveys, all the data recorded on paper sheets were later manually entered into Excel spreadsheets and the tracks downloaded from the portable GPS devices and saved in Excel spreadsheets.

The data tables from all these surveys were checked for mistakes in data entry and for consistency between the track table, the effort and sighting tables and, whenever applicable, to other tables (e.g. turtle sightings, litter). Whenever there were data missing in GPS tracks because of failure in the main GPS device, in the data logging or in the GPS connection to the laptop, track positions from a backup portable GPS device were used. The tracks, effort and sightings were visually checked in ArcGIS 9.3 (ESRI, 2009) and errors (e.g. positions of sightings) were corrected. Final checked and validated transects' points shapefiles with corresponding effort and environmental information (Beaufort) were generated, as well as corrected and validated sightings and effort tables.

Track selection

All SLS and ALS surveys' tracks "on effort" were used in the habitat use modelling analysis. The FO surveys tracks sections selected were those that fell into the inshore waters FO 2010 – 2012 study area (Figure 4.6) and were both in "search mode" and "on effort" (Section 4.2.2.5).

Track segmenting

The SLS, ALS and FO transects were segmented in ArcGIS 9.3. However, the transects of SLS and ALS surveys were first divided into legs, with each leg corresponding to the section between two consecutive way points (WP) of the zigzag transect. The transects of FO surveys were naturally divided in discontinuous "on effort" sections of variable length (legs) as a result of the "on" and "off" search pattern throughout the day of the single observer on board the fishing boats. Afterwards, each leg was segmented in sections of the size of the prediction grid cells (segment unit: 2 nm = 3.704 km; Section 4.2.3.4) or whenever the Beaufort changed. The segmenting of the transects also followed other rules as explained in Figure 4.8.

4.2.3.2 Systematic and non-systematic photo-identification surveys and whale-watching observer surveys

The data collected in NSS surveys (2004 – 2012 and 2016) and WWO surveys (2010 – 2012 and 2014 – 2017) were organized, formatted and consolidated in single effort and sighting tables for each dataset for the corresponding overall periods, and checked for mistakes and consistency. In these surveys, the environmental data were associated with sightings rather than effort. The individual tracks of NSS and WWO surveys were almost all recorded in portable GPS devices by multiple observers in different formats over the years, thus requiring further organization and processing. R code was developed to standardize the format of the track data, relate them with the effort and sightings data and generate track plots with sightings and identify "on effort" track sections for visual inspection, identification of mistakes and overall data validation. Formatted and validated output sightings and track tables with associated effort were generated as well as diagnostic and summary tables for data quality double checking and posterior track selection, respectively.

The available data collected in SLS-RD surveys (2017) were organized differently from the previous datasets. There was a single table with all the track points of all the transects carried out in these surveys and the corresponding effort and environmental data for each track point, ordered sequentially by date/time. The sighting data were organized in a separate table. As for the previous surveys, R code was developed to standardize the format of output sighting and track table. It also generated track plots with sightings and identified "on effort" track sections for visual inspection, identification of mistakes and overall data validation as well as diagnostic and summary tables for data double checking and posterior track selection, respectively.

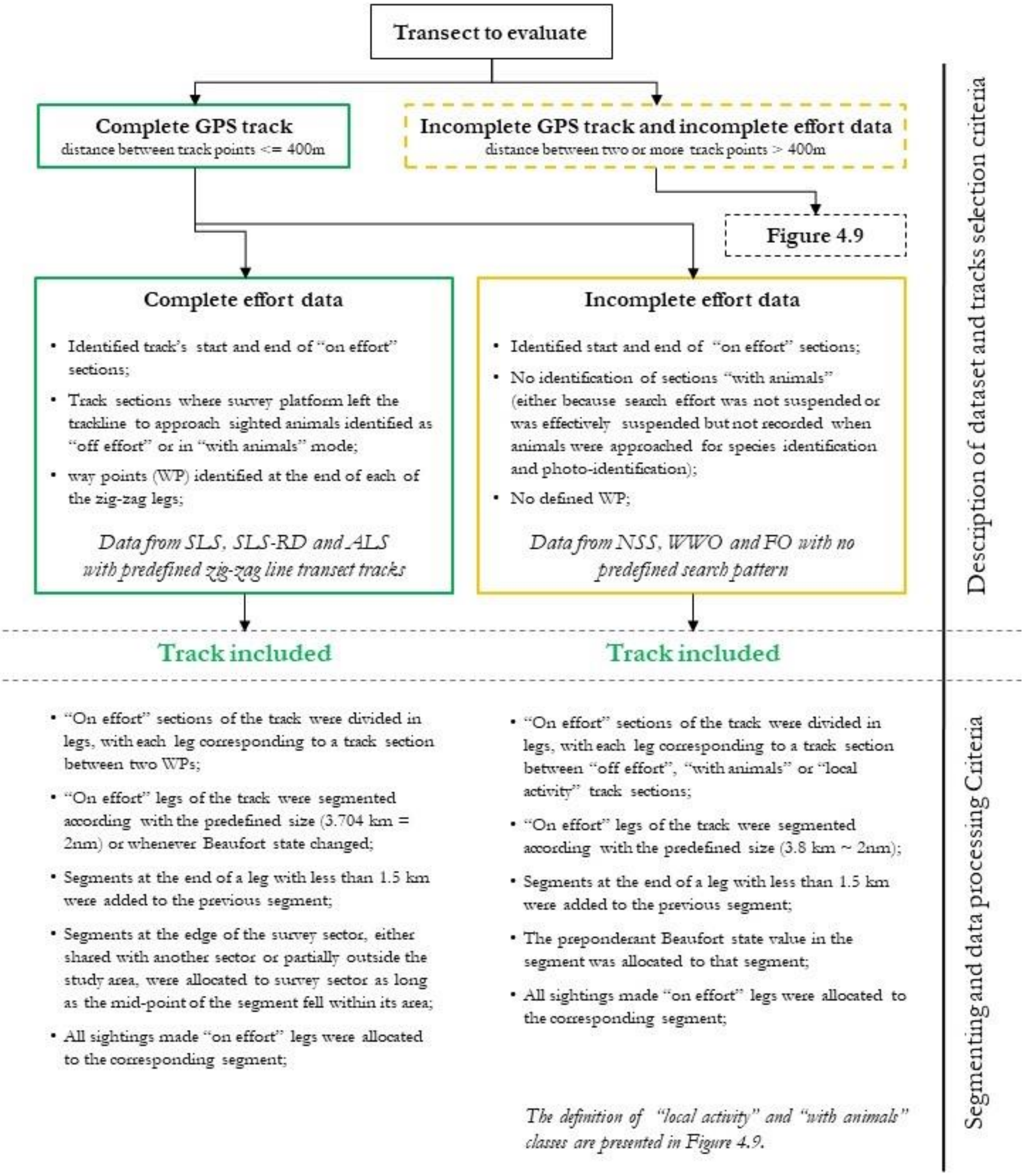
Although latitude and longitude were recorded on the paper forms for most sightings in the previous datasets, the final positions of the sightings were systematically allocated using date/time to relate the sightings data with the corresponding track positions. This approach was taken to overcome geographic position writing errors in the field. The final positions of all sightings were checked visually in plots generated in R against the track line and the original positions recorded in the field to ensure consistency and coherence in the datasets.

Track selection

All SLS-RD survey tracks "on effort" were used in the habitat use modelling analysis (Figure 4.8). The tracks of NSS and WWO were first visually checked for consistency with their known patterns of operation, namely start and end of effort close to harbours, and then checked against a set of criteria, as explained in Figure 4.8 and Figure 4.9, implemented through an R-script to select out incomplete tracks. Unlike other surveys, in NNS and WWO surveys no backup GPS devices were used, resulting in a number of survey tracks with incomplete GPS records. Failure to address this issue would result in an over estimation of encounter rate of cetaceans.

Firstly, the GPS tracks were checked for the presence of two consecutive track positions distanced more than 400 m apart. If present, those tracks were considered "incomplete" and were further checked, otherwise they were selected for segmenting and analysis.

The "incomplete" tracks were next checked for large sections of missing track and were excluded if one or more sections were larger than 25% of the overall minimum length of the track (calculate by summing all the linear distances between geographic positions recorded in the GPS track) or larger than approximately two segment units (7.6 km). These two values set a relative and absolute limit, respectively, to the maximum section length missing from a track to be considered for analysis.



Complete effort data

- Identified track's start and end of "on effort" sections;
- Track sections where survey platform left the trackline to approach sighted animals identified as "off effort" or in "with animals" mode;
- way points (WP) identified at the end of each of the zig-zag legs;

Data from SLS, SLS-RD and ALS with predefined zig-zag line transect tracks

Incomplete effort data

- Identified start and end of "on effort" sections;
- No identification of sections "with animals" (either because search effort was not suspended or was effectively suspended but not recorded when animals were approached for species identification and photo-identification);
- No defined WP;

Data from NSS, WWO and FO with no predefined search pattern

Track included

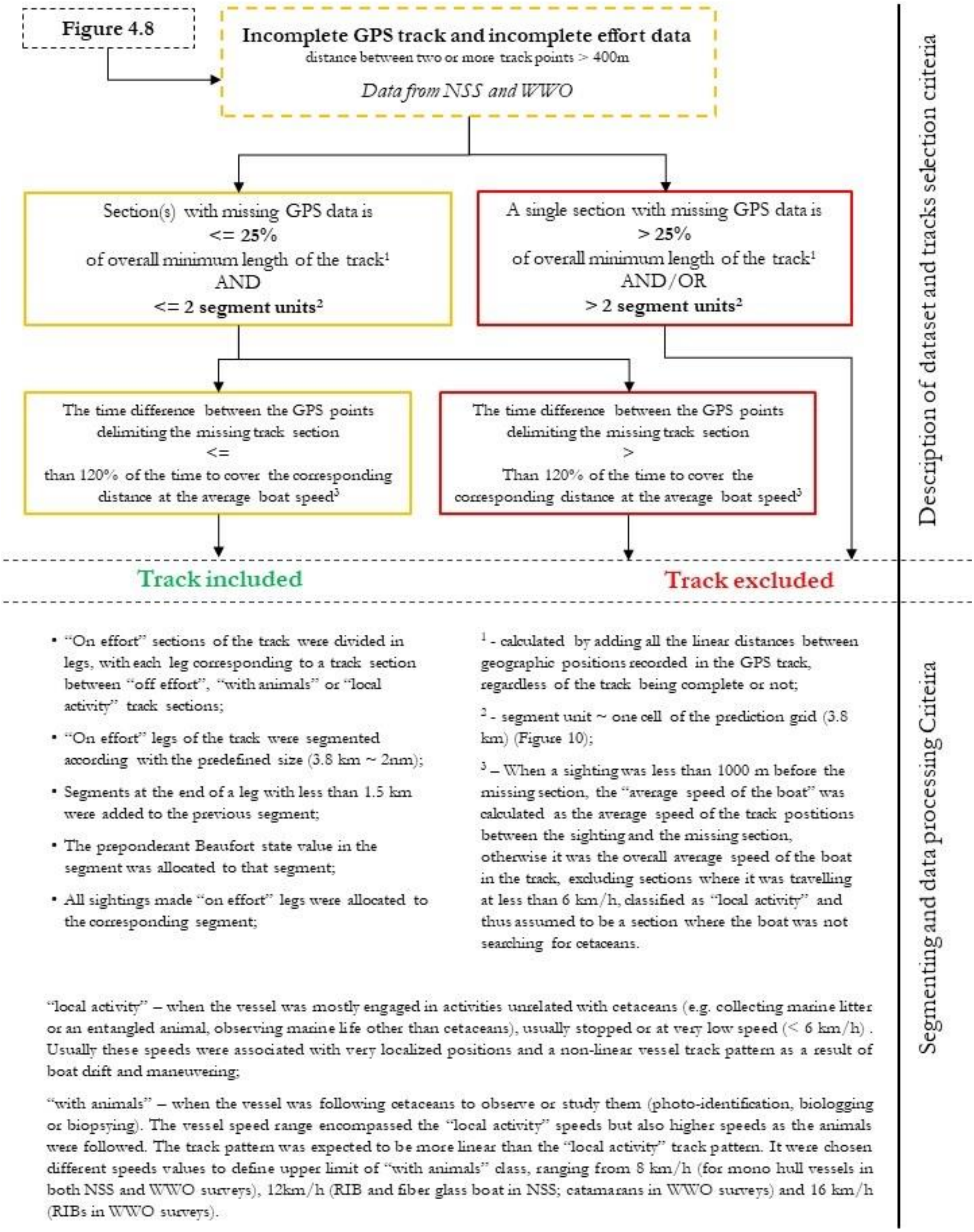
- "On effort" sections of the track were divided in legs, with each leg corresponding to a track section between two WPs;
- "On effort" legs of the track were segmented according with the predefined size (3.704 km = 2nm) or whenever Beaufort state changed;
- Segments at the end of a leg with less than 1.5 km were added to the previous segment;
- Segments at the edge of the survey sector, either shared with another sector or partially outside the study area, were allocated to survey sector as long as the mid-point of the segment fell within its area;
- All sightings made "on effort" legs were allocated to the corresponding segment;

Track included

- "On effort" sections of the track were divided in legs, with each leg corresponding to a track section between "off effort", "with animals" or "local activity" track sections;
- "On effort" legs of the track were segmented according with the predefined size (3.8 km ~ 2nm);
- Segments at the end of a leg with less than 1.5 km were added to the previous segment;
- The preponderant Beaufort state value in the segment was allocated to that segment;
- All sightings made "on effort" legs were allocated to the corresponding segment;

The definition of "local activity" and "with animals" classes are presented in Figure 4.9.

Figure 4.8. Flowchart describing the steps and criteria to select, process and segment tracks from the different surveys transects used in the several analyses done in the present study. SLS - Systematic shipboard line-transect surveys; SLS-RD - Systematic shipboard line-transect surveys for photo-identification mark-recapture study based on robust-design; ALS - Systematic aerial line-transect surveys; NSS - Non-systematic shipboard surveys for photo-identification, biologging and skin biopsy sampling; WWO - whale-watching observers' surveys; FO - Fisheries Observers program.



- "On effort" sections of the track were divided in legs, with each leg corresponding to a track section between "off effort", "with animals" or "local activity" track sections;
- "On effort" legs of the track were segmented according with the predefined size (3.8 km ~ 2nm);
- Segments at the end of a leg with less than 1.5 km were added to the previous segment;
- The preponderant Beaufort state value in the segment was allocated to that segment;
- All sightings made "on effort" legs were allocated to the corresponding segment;

[1] - calculated by adding all the linear distances between geographic positions recorded in the GPS track, regardless of the track being complete or not;

[2] - segment unit ~ one cell of the prediction grid (3.8 km) (Figure 10);

[3] – When a sighting was less than 1000 m before the missing section, the "average speed of the boat" was calculated as the average speed of the track positions between the sighting and the missing section, otherwise it was the overall average speed of the boat in the track, excluding sections where it was travelling at less than 6 km/h, classified as "local activity" and thus assumed to be a section where the boat was not searching for cetaceans.

"local activity" – when the vessel was mostly engaged in activities unrelated with cetaceans (e.g. collecting marine litter or an entangled animal, observing marine life other than cetaceans), usually stopped or at very low speed (< 6 km/h) . Usually these speeds were associated with very localized positions and a non-linear vessel track pattern as a result of boat drift and maneuvering;

"with animals" – when the vessel was following cetaceans to observe or study them (photo-identification, biologging or biopsying). The vessel speed range encompassed the "local activity" speeds but also higher speeds as the animals were followed. The track pattern was expected to be more linear than the "local activity" track pattern. It were chosen different speeds values to define upper limit of "with animals" class, ranging from 8 km/h (for mono hull vessels in both NSS and WWO surveys), 12km/h (RIB and fiber glass boat in NSS; catamarans in WWO surveys) and 16 km/h (RIBs in WWO surveys).

Figure 4.9. Continuation of the flowchart of Figure 4.8, describing the steps and criteria to select, process and segment tracks from the different surveys transects used in the several analyses done in the present study.

The remaining "incomplete" tracks, with sections more than 400 m in length but less than the maximum limits specified above, were checked to confirm if those distances could be covered at the vessel's average speed in the time interval (recorded in the GPS) between the two geographic positions delimiting those sections. If so, it was assumed that the vessel had travelled in a more or less linear path between those two positions and thus it would be possible to reconstruct its path in that section with a relatively high degree of confidence. A tolerance of 20% below average speed was considered to accommodate slight changes in vessel speed in those sections. The vessel's track average speed was calculated as the average of the speed values recorded with each geographic position by the GPS, excluding the positions "off effort" or with speeds of 6 km/h or less and with no sightings recorded in the previous 1 000 m, classified as "local activity" (see below).

Whenever there was a sighting less than 1 000 m before the missing section, the "average speed of the boat" was calculated using the speed values from that stretch of track, as one would expect a change in speed (usually slowing down) as a reaction to the detection. It is expected that if the vessel is searching for cetaceans, it will travel usually close to the average "on effort" track speed, excluding all the sections when the boat was on "local activity", or with animals.

All tracks, both those selected for segmenting and those excluded, were visually checked for coherence and consistency in the application of the above-mentioned criteria, in plots in which sightings, the "on effort" and "off effort" stretches of track as well as the sections that were selected according with the criteria previously explained were identified.

Track segmenting

The SLS-RD, NNS and WWO survey tracks were segmented in R using purpose-written code. The SLS-RD survey equal-spaced zig-zag tracks followed the same segmenting criteria as the SLS and ALS surveys (Figure 4.8).

Unlike the other types of surveys, in NNS and WWO the change in effort status to "with animals" or "off effort" was not recorded whenever search effort was temporarily suspended, either to approach cetaceans for photo-identification, observation or another purpose, or for other reasons (e.g. collect litter from the sea, approach a turtle or observe other marine life). Failure to address this issue may have resulted in a serious under estimation of encounter rate. To minimize this issue, the speed patterns of the survey platforms were investigated in an attempt to associate specific vessel speed ranges to specific activities while "on effort". Three classes of activities were defined *a priori* to be identified through the vessel speed, namely:

- "local activity" – when the vessel was engaged in activities mostly unrelated with cetaceans, usually stopped or at very low speeds, such as collecting marine litter or an entangled marine turtle, observing other marine life other than cetaceans (e.g. turtle, monk seal), communication at close distance between boats. Usually, these speeds are expected to be associated with very localized positions and a non-linear vessel track pattern as a result of boat drift and maneuvering;
- "with animals" – when the vessel was following cetaceans to observe or study them (photo-identification, biologging or biopsying). It was expected for the vessel speed to be in range that encompassed the "local activity" speeds but also higher as the animals were followed. The track pattern was expected to be more linear than the "local activity" track pattern;
- "on search" – remaining stretches of track "on effort" with speeds higher than the "with animals" threshold or the "local activity" threshold, whenever there were sightings or there were no sightings of cetaceans in the previous 1 000 m, respectively. The track pattern was expected to have more or less linear sections combined with changes in direction.

A subset of tracks of both NSS and WWO surveys were plotted with the speed of each track position represented in different speed class colours together with the corresponding sightings. Different arrangements of speed classes were tested and visualized. As a result, it was found that 6 km/h was an appropriate speed value to define the upper limit of the "local activity" class, identifying well the non-linear stretches of track for both survey types, with no sightings in the previous 1000 m. There was also consistency in the upper vessel speed limit for the "with animals" class, within and across these two survey types. For mono-hull vessels the speed of 8 km/h identified well the speed below which these boats would engage with cetaceans, both in NSS (vessel "Ziphius") and WWO (all mono-hull vessels) surveys, while for all catamarans used in WWO surveys the threshold speed was 12 km/h. For NSS survey smaller boats (RIB "Roaz" and fiber glass boat "Biomar") the threshold speed was also 12 km/h while for the RIBs used in WWO surveys it was 16 km/h. To deal with transient changes in vessel speed, the switch between speed classes in a track was only considered if the change in vessel speed, below or above a threshold, persisted for stretches of track longer than 200 m.

As a result, the tracks of these surveys were naturally divided in discontinuous "on effort/on search" sections (legs) of variable length between stretches of "off effort", "with animals" and/or "local activity" track sections, following more or less a similar segmenting pattern with FO surveys. The segmenting of these survey tracks was done according to the criteria explained in Figure 4.8 and Figure 4.9.

4.2.3.3 *Group size*

In all surveys, the protocol was for minimum, maximum and mean group size (or best estimate of group size) to be recorded. However, these values were not always consistently recorded. As a result, criteria were defined to obtain the best estimate of group size to use in analysis. Whenever, mean or best group size was recorded, that was the final selected group size value. If these were missing but there were minimum and maximum group size estimate values, the average of these two values was used. Finally, if only the minimum or maximum group size estimate was available then that was the value used as the best group size estimate for the corresponding sighting.

4.2.3.4 *Final output tables for analysis*

A grid was prepared for the overall study area with 38 x 29 grid cells with a resolution of 3.7 km x 3.7 km (2 x 2 nm), as shown in Figure 4.10. This grid was used to predict the distribution of abundance within the spatial modelling analysis, defining the resolution of predictions and also the sampling units (segments). The choice of grid cell size and the segment length were a compromise based on the range of the dynamic variables' resolution used in the study (1 – 9 km) (Table 4.1).

A prediction table was produced based on the prediction grid, with each row corresponding to a grid cell and with fields to characterize it such as, unique ID indicating the position in the grid, the effective area of the grid cell (removing land) and multiple fields with the mean value of the covariates used in the spatial modelling analysis (see below).

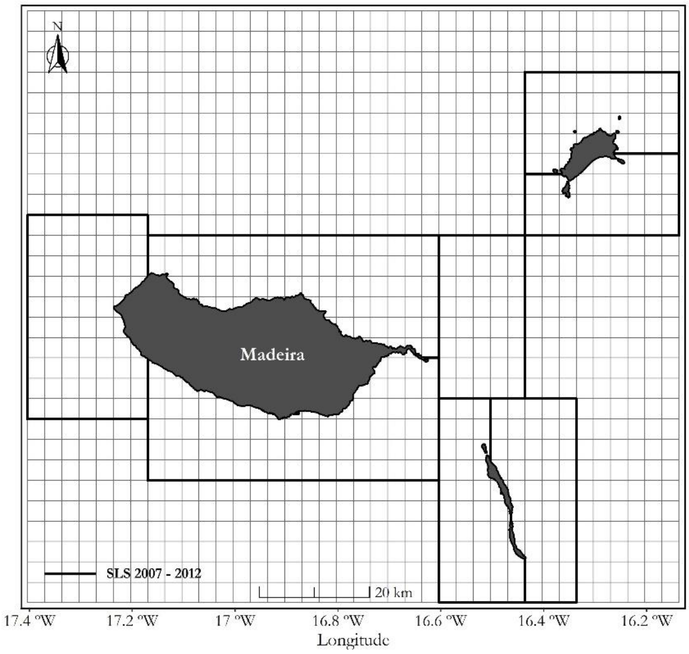


Figure 4.10. Map showing the prediction grid with 38 x 29 grid cells with a resolution of 2 x 2 nm (3.704 km x 3.704 km), covering the study area for which habitat use models predicted the distribution of encounter rates of groups and/or individuals.

Final standard output tables for habitat use analysis were generated for all types of surveys, one to model the distribution of groups or individuals encounter rates (ER) and another to model group size. The output tables for different surveys were consolidated in two final tables, one to model the distribution of groups or individual ER and another to model group size.

4.2.4 Environmental variables

The selection of environmental variables to test as covariates in the habitat use models is important and should reflect, as much as possible, knowledge of the ecology of the species to be modelled (Redfern *et al.*, 2006). However, there is often a limited local knowledge of this and also a limited number of variables for which there are available data with a spatial resolution and temporal and spatial coverage matching those of the study.

In spite of the general knowledge on the ecology and habitat use of cetacean species utilizing Madeira archipelago inshore waters (Chapter 2), little is known in detail about their local distribution, habitat use or the environmental features driving these. Furthermore, there is a wide diversity of cetacean species using the study area, with a wide range of ecological requirements, including oceanic dolphins, deep diving species and baleen whales. As such, a relatively wide range of physiographic, oceanographic and biological variables representing potentially important environmental features, or proxies of important features, were chosen.

In total, 40 covariates were used in the analysis, both static (physiographic; e.g. Harris *et al.*, 2014) and dynamic variables. Table 4.1 gives the list of covariates selected, with a brief description of how they were calculated and their characteristics. There was some difficulty in identifying dynamic covariates for the study that covered the overall study period (2001 – 2017) and with an adequate spatial resolution (3,7 km).

Among those covariates with available data, it was necessary to make in some cases compromises to have a wider number of covariates in the analysis. Covariates included: those such as "mixed layer depth" or "sea surface height" with a spatial resolution (9 x 9 km) lower than the prediction grid resolution (3.7 x 3.7 km, Figure 4.10); those with a temporal coverage that missed the first one of two years of the study (2001 and/or 2002), such as "primary productivity" or "particulate organic matter"; and those in which datasets were combined with equivalent data covering a complementary period of the study such as "mixed layer depth" and "sea surface height" (Table 4.1).

Table 4.1. List of the covariates used in the spatial modelling analysis to explain the distribution of cetaceans in the study area, including a brief description of how it was calculated and characteristics, namely measurement unit, spatial and temporal resolution, period covered and source. Sources: EMEPC - Portuguese Task Group for the Extension of the Continental Shelf ("Estrutura de Missão para a Extensão da Plataforma Continental" of Portugal);

NOAA (https://coastwatch.pfeg.noaa.gov/erddap/griddap/index.html?page=1&itemsPerPage=1000)
COPERNICUS (http://marine.copernicus.eu/services-portfolio/access-to-products/)
Blue Habitats (https://www.bluehabitats.org/?page_id=58/)

	Covariate					**Resolution**		**Data Series**		**Source**
#	Name	Abrev.	Description	Type	Units	Spatial	Temporal	Start	End	
Dynamic variables										
1	Chlorophyll A	chl-a	North Atlantic surface chlorophyll concentration from satellite observations (daily average) reprocessed L4 (ESA-CCI)	Numeric	mg m^{-3}	1 km	monthly	2001	2017	COPERNICUS
2	Mixed layer depth	Mld	Mean montly values for 2002 - 2017 of ocean mixed layer thickness defined by sigma thet obtained by the combination of reanalysed data (L4) from products IBI_REANALYSIS_PHYS_ 005_002 (2002 - 14) and GLOBAL_ANALYSIS_FORECAST_PHY_001_024 (2015 - 2017)		m	0.083º (~9km)		2002 2015	2014 2017	COPERNICUS
3	Particulate organic carbon	Poc	MODIS Aqua, Level-3 SMI, Global (Monthly Composite)		mg m^{-3}	4.64 km		2003	2017	NOAA
4	Primary productivity	Pp	Primary Productivity, Aqua MODIS, NPP, Global (Monthly Composite)		mg C m^{-2} day^{-1}	0.0125º (~1.3 km)		2003	2017	NOAA
5	Sea surface height	Ssh	Mean montly values for 2002 - 2017 of sea surface height obtained by the combination of reanalysed data (L4) from products IBI_REANALYSIS_PHYS_ 005_002 (2002 - 2014) and GLOBAL_ANALYSIS_FORECAST_PHY_001_024 (2015 - 2017)		m	0.083º (~9km)		2002 2014	2013 2017	COPERNICUS
6	Sea surface temperature	Sst	Satellite measured sea surface temperature, Multi-scale ultra-high resolution (MUR)		ºC	0.01º (~1 km)		2002	2017	NOAA
7	Sea surface temperature anomaly	Sst-a	Multi-scale Ultra-high Resolution (MUR) SST Analysis Anomaly fv04.1, Global		ºC	0.01º (~1 km)		2002	2017	NOAA
Static variables										
8	Minimum depth	-	Variables values calculated for each grid cell in ArcGIS 9.3.1 from a sample of 81 regularly spaced depth readings per grid cell obtained from high resolution side scan sonar surveys of the study area (EMEPC depth data) Aspect (the orientation of the sea floor slope in relation to the true north) in degrees was measured from clockwise from 0º to 359º	Numeric	m	3.704 km	-	-	-	Depth data from EMEPC
9	Average depth									
10	Maximum depth									
11	Depth standard deviation				-					
12	Minimum slope				%					
13	Average slope									
14	Maximum slope									
15	Slope standard deviation				-					
16	Minimum aspect				degree					
17	Average aspect									
18	Maximum aspect									
19	Aspect standard deviation									
20	Contour index		$CI = \frac{max.depth - min.depth}{max.depth}$ x 100		-					
21	Escarpment		Classification of grid cells according to presence/absence of sea floor physiography classes, namely, shelf, escarpment, slope and abyss.	binary			-	-	-	Blue Habitats (Harris et al. 2014)
22	Abyss									
23	Slope									
24	Shelf									
25	Escarpment area		Percentage of area of each sea floor physiographic class, namely, shelf, slope, escarpment and abyss, in the grid cells	Numeric	%					
26	Abyss area									
27	Slope area									
28	Shelf area									
29	Distance to escarpment		Minimum distance of each grid cell mid-point to the mid-point of a grid cell with the corresponding sea floor physiographic classes		m					
30	Distance to slope									
31	Distance to shelf									
32	Distance to coast									
33	Distance to 100 m isobath		Minimum distance of each grid cell mid-point to different depths contours were calculated in ArcGIS 9.3.1 using navigation chart 101 of Madeira archipelago				-	-	-	Isobath data from navigation Chart 101 of Madeira archipelago from Portuguese Hydrographic Institute (IH)
34	Distance to 200 m isobath									
35	Distance to 500 m isobath									
36	Distance to 1000 m isobath									
37	Distance to 1500 m isobath									
38	Distance to 2000 m isobath									
39	Distance to 2500 m isobath									
40	Distance to 3000 m isobath									

The monthly values of each dynamic covariate were averaged across the periods defined for each of the analysis datasets (Section 4.2.5.3 and Figure 4.11), namely, the overall study period (2001 –2017) and by season (winter, spring, summer and autumn). The covariate monthly values matched the months sampled by the surveys across the periods of each dataset or were time lagged in relation to those months. For the species with a strong and well defined seasonal presence in Madeira archipelago inshore waters (Bryde's whale and common dolphin, Section 4.2.5.3), specific covariates were prepared to cover each dataset period but including only the months when the species was present in the study area.

Primary productivity related covariates were also averaged for the overall period (2004 – 2017), by month (April to November) and bi-monthly (Mar-Apr, May-Jun, Jul-Aug, Sept-Oct) to explore how well time-lagged (monthly and bi-monthly) covariates may explain the distribution of the Bryde's whale, a relatively low trophic level species, taking into consideration the propagation of changes through the food web over time.

4.2.5 Data Analysis

4.2.5.1 Relative importance and Encounter rates

To have a basic understanding of the relative importance of the cetacean species in the study area, the ER of groups were calculated for each species, expressed in number of sightings/100 km of effort, including all the transects selected for analysis regardless of survey type (Section 4.2.3). In this preliminary approach, differences in detection probability intrinsic to each species or associated with survey types and/or platforms used and strong differences between species in their yearly use of the study area were not considered. The ER per month for all species was also calculated (100 * number of sightings of a species /effort in km of the month).

4.2.5.2 Group size

Group size statistics were calculated using data from all types of surveys, except FO surveys. Unlike the other surveys, in FO surveys the platform of observation usually did not change its course to approach the sighted group and thus in many cases group size counts are expected to be negatively biased, especially for groups sighted further away. Furthermore, FO surveys did not have year-round coverage, potentially skewing group size estimates for species with seasonal changes in group size.

The distribution of group sizes of different species was confirmed to be non-normal by visually checking with QQ-plots and testing using a Shapiro-Wilk test. Consequently, a Kruskal-Wallis test was used to check if there were significant differences ($p < 0.05$) in mean group size between types of surveys (SLS, SAS, NSS, WWO) and seasons (winter, spring, summer and autumn), while a Wilcoxon rank sum test was used to investigate significant differences between periods. The statistical tests were done in R (R Core Team, 2019).

4.2.5.3 Datasets

To address the questions considered in this study, the data collected during the multiple surveys were organized in different datasets (Figure 4.11).

To model habitat use, all pre-selected transects of all types of surveys covering the period 2001 – 2017 were combined to increase the number of observations (sightings of a particular species) in the analysis and thus maximise the number of species for which an acceptable final model could be obtained. To study seasonality, the analysis was done using subsets that combined all transects carried out in each season (Figure 4.11). In the case of the Bryde's whale, a species feeding low in the trophic chain, the importance of time lagged covariates to explain the distribution of animals in the study area at finer temporal scale was investigated. As such, models for the periods June/July, August/September and October/November, combining data from 2004 – 2017, were run with dynamic covariates with no time-lag, and also one- and two-month lags, using the average of the two-month values (e.g. June/July).

All datasets were visually checked for consistency in their spatial and temporal coverage, i.e., the transects of the different surveys selected for a dataset had an acceptable coverage of the study area (or of the part of the study area over which predictions would be made) and, overall, they covered reasonably well the dataset's time period. Maps of distribution of effort in the study area were produced for each dataset as well as plots of distribution of effort per year. A consistent spatial and temporal coverage of each dataset is important to ensure, as far as possible, an acceptable coverage of the range of values of each of the explanatory variables to be tested in the models.

For the species with a very marked seasonal presence in the archipelago, habitat use was modelled using a subset of the data that excluded the months the animals were absent or had a very low monthly ER. As a result, the estimated relative abundance given by the models reflect the abundance while the species is present in the study area and not the year-round average. A species was considered as having a very marked seasonality when the average of the three months with highest ER was at least tenfold greater than the three months with lowest ER (excluding months with no sightings) (Appendix IV.3). For species with sightings in fewer than six months of the year, the calculation was made by comparing the average of the months with the lowest 50% of ER values with the months with the highest 50% of ER values. However, to model each species year-round seasonality, i.e. using month as a circular covariate, all data were used.

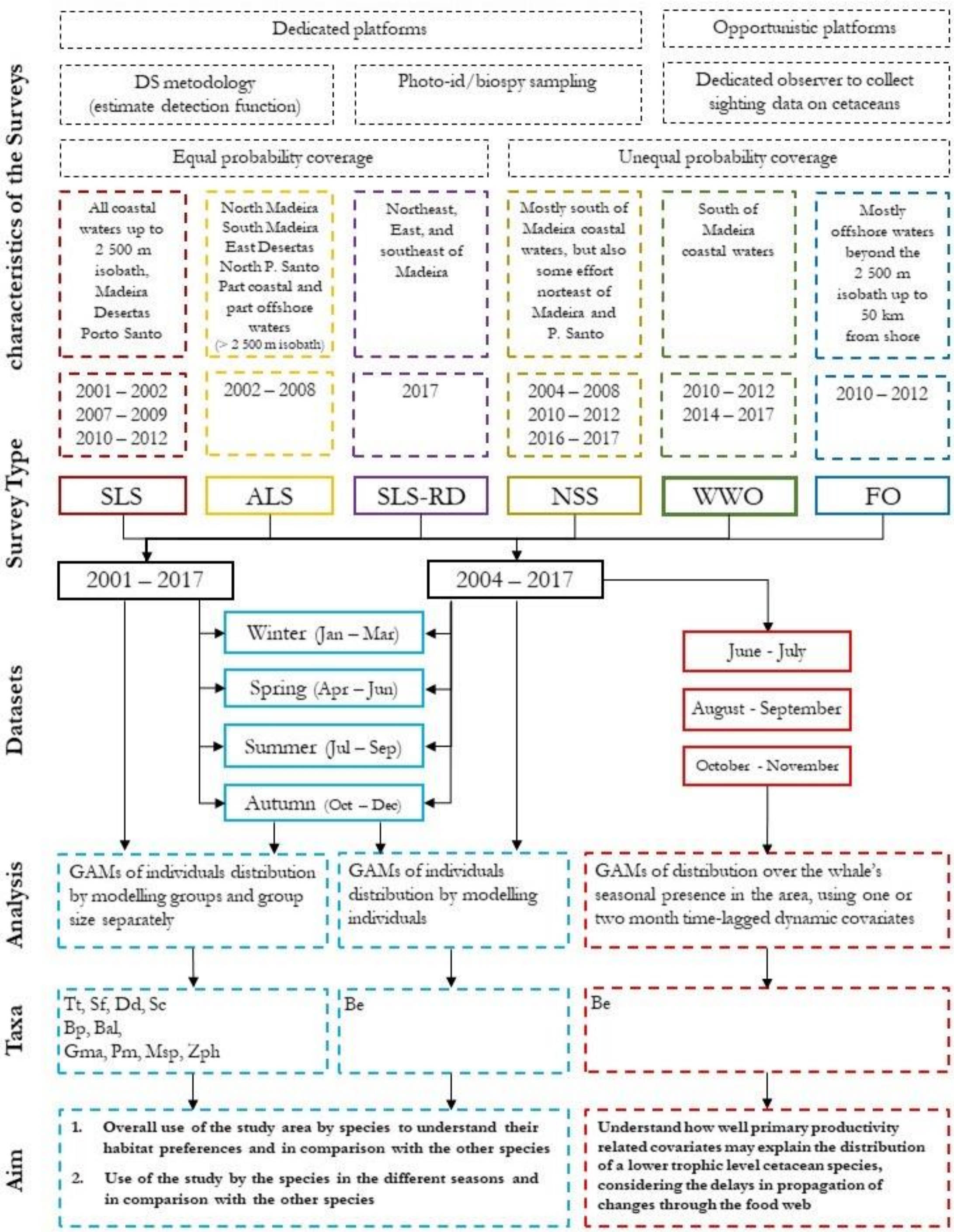


Figure 4.11. Flowchart explaining the datasets used in the analysis, namely, type of surveys and their characteristics (spatial and temporal coverage), period covered by each dataset (years and/or seasons), the analysis carried out, taxa analysed and aim of the analysis. SLS – systematic line-transect surveys; ALS – aerial line-transect surveys; SLS-RD – systematic line-transect surveys for photo-identification using robust design; NSS – non-systematic surveys (photo-identification and biopsy sampling); WWO – observers on whale-watching vessels; FO – observers on tuna fishing vessels. Tt – *Tursiops truncatus*; Gma – *Globicephala macrorhynchus*; Sf – *Stenella frontalis*; Dd – *Delphinus delphis*; Sc – *Stenella ceoruleoalba*; Be – *Balaenoptera edeni*; Bp – *Balaenoptera physalus*; Pm – *Physeter macrocephalus*; Msp – *Mesoplodon* sp.; Bal – Balaenoteridae; Zph – Ziphiidae. For Bryde's whale, the datasets include only surveys from 2004 onwards, when the species started being recorded separately.

The common dolphin and the Bryde's whale are the species with a very marked seasonal presence following the criteria explained previously. The habitat use models of common dolphin used sub datasets covering the months of December to June, while the sub dataset for Bryde's whale covered the period from May to January, to exclude the months when the species were absence or had very low ER.

The models of Bryde's whale habitat use only included surveys from 2004 onwards because that was the year the species was first recognised in the Madeira archipelago and started being recorded separately during the surveys and not as "unidentified balaenopteridae".

4.2.5.4 Data exploration, preparation and exploratory analysis

Exploratory data plots were made for all datasets to check both for outliers and for the spread of the observations over the range of the covariates, as well as to understand the relationships between the response variables and the explanatory variables (Zuur *et al.*, 2009).

Collinearity between explanatory variables was checked visually through pairplots (Zuur et al., 2009) and matrices of correlation between covariates were generated for each dataset to identify highly correlated covariates. Two explanatory variables were considered highly correlated if the estimated Pearson correlation coefficient exceeded 0.7 (Model selection, see below).

Preliminary generalized additive models (GAMs, see below) were run for several datasets to develop and test the R scripts for analysis, as well as to familiarize with and investigate the suitability/efficiency of modelling approaches, such as forward and backwards model selection and selecting covariates based on null space penalties (shrinkage and double penalty approaches) (Marra and Wood, 2011; Wood, 2017). These preliminary models were also used to test and choose the error distribution families for the response variables (individuals, groups and group size) of the different datasets, considering the nature of the data (i.e. non-negative counts, possibly over dispersed and zero-inflated). The exponential distribution families Quasi-Poisson, Negative Binomial (with the parameter θ estimated during fitting –function nb() in R) and Tweedie (with the parameter p estimated during fitting – function tw() in R) were tested and the distribution was selected based on visual observation of QQ plots. Results showed that the error distribution that generally had better fit for the different response variables was the Tweedie distribution, which is appropriate to model zero-inflated and over dispersed data (Miller et al., 2013).

The aim was to model the relative abundance of individuals in the study area for all the modelled taxa, either by modelling individuals (counts of individuals as the response) or modelling groups (counts of groups as the response) and group size. Most response variables modelled were characterized by a high frequency of zeros (e.g. for the bottlenose dolphin, the species with most sightings in the period 2001 – 2017, there were 15 116 segments without sightings compared to 377 with sightings) and/or over dispersion in the data (e.g. group size of the spotted dolphin ranges from 1 to 500 animals). To minimize problems of modelling over dispersed data, species with wider group size ranges had the relative abundance of groups and group sizes modelled separately and the respective predictions combined to predict the distribution of individuals. For species with smaller group size ranges (sperm whales, baleen whales and beaked whales), it was attempted to model individuals as well as groups and group size. Preliminary models were run and, based on their performance (model fit assessed by visual inspection of QQ plots and the model's convergence), it was decided to model groups and group size rather than individuals for all taxa but the Bryde's whale. To address differences in the detection probabilities, "type of survey" and "platform type" were included as candidate factor covariates in the models.

During exploratory analysis, it was noticed that some of the transects of NSS and WWO surveys (both without predefined search patterns) had the search effort terminated soon after a sighting, potentially resulting in a positive bias in ER. It was suspected, especially for WWO surveys, that the end of effort was dictated by the platform of observation pattern of operation (search for animals would cease whenever the trip objective was reached, e.g., tourists had seen cetaceans), rather than a predefined or random event. To investigate whether the average transect lengths were significantly different between both types of transects (those ending soon after a sighting and the others), their mean lengths in NSS and WWO surveys were tested with the two sample Student's t-test and the Wilcoxon rank sum test, respectively. The normal distribution of their data was checked previously with QQ-plots and tested using a Shapiro-Wilk test. The statistical tests were done in R (R Core Team, 2019). Furthermore, in the preliminary GAMs it was realised that there was not always a linear relationship between increase in segment length and increase in sightings ER. To account for these issues in the models, effort was incorporated as a covariate in the models, rather than as an offset.

4.2.5.5 Habitat use modelling

Modelling approach and parameterization

The habitat use of different cetacean species in Madeira inshore waters was investigated by modelling their relative abundance using GAMs (Hastie and Tibshirani, 1990; Wood, 2017), either by modelling individuals or by modelling groups and group size. This modelling exercise will contribute to increase knowledge of the ecological and biological drivers of the local distribution of cetacean species. This modelling approach was followed considering that several explanatory variables may influence the distribution of the response variable and that the relationships between response variable and predictors may not be linear.

These models have the following structure:

$$g(\mu_i) = A_i\theta + f_1(x_{1i}) + f_2(x_{2i}) + f_3(x_{3i}, x_{4i}) + \cdots$$

where g(.) is a specified link function of $\mu_i \equiv \mathbb{E}(Y_i)$ and $Y_i = \text{EF}(\mu_i, \emptyset)$, where Y_i (i = 1,….,n) is the response variable that follows an exponential family distribution with mean μ_i and scale parameter $\emptyset$, A_i is a row of the model matrix for any strictly parametric model components, θ are their associated coefficients, and the f_i are smooth functions of the covariates, x_k (Wood, 2017; Miller, 2019). The smooth terms are sums of simple basis functions where the smooth s of covariate x has the following structure:

$$s(x) = \sum_{K=1}^{K} \beta_k b_k(x)$$

where β_k are the coefficients to be estimated and b_k are the fixed basis functions (Wood, 2017; Miller, 2019).

Most smooth functions were fitted to the data using thin plate regression splines with a penalized null space through the shrinkage approach (expressed in R gam function as bs="ts")(Marra and Wood, 2011; Wood, 2017). Variables such as month, minimum, average and maximum aspect (0 – 360º) were modelled as cyclic covariates with the smooth functions fitted using cyclic cubic regression splines (expressed in R gam function as bs="cs"), including the species with strong seasonality (common dolphin and Bryde's whale) as in both cases the datasets included the months at the beginning and end of the year (January and December). The smoothness selection method of the models' smooth terms was the restricted maximum likelihood (REML) (Marra and Wood, 2011; Miller et al., 2013). Several methods may be used in multiple smoothing parameter estimation, among the GCV, AIC or REML. However, at finite sample sizes GCV or AIC are more likely to develop multiple minima and more prone to undersmoothing than REML (Marra and Wood, 2011; Wood, 2017).

The relative abundance of groups or individuals was modelled using a GAM with a logarithmic link function and the Tweedie error distribution, and where the response was counts of groups or counts of individuals, respectively. The models had the following general structure (adapted from Cañadas and Hammond, 2008):

$$n_i = exp\left[\theta_0 + \sum f_k(z_{ik}) + b_i\right]$$

where n_i is the number of groups or individuals detected in the i^{th} effort segment, θ_0 is the intercept, f_k are smoothed functions of the explanatory environmental covariates, z_{ik} is the value of the k^{th} explanatory covariate in the i^{th} segment, and b_i is the type of survey in the i^{th} effort segment. The "type of survey" was included in these models as a factor covariate to account for differences in detection probabilities associated with each of the types of surveys. It was chosen over "platform type" because it has one level less and the differences in the percentage of deviance explained between the two options was negligible (usually less than one percent). Other covariates were also considered in all these models such as: Beaufort to account for changes in detection under different weather conditions; month and year to account for changes in relative abundance of groups or individuals throughout the year and the study period, respectively; and effort, for reasons explained previously (Section 4.2.5.4).

The group size was modelled using also a GAM with a logarithmic link function and the Tweedie error distribution. The models had the following general structure (adapted from Cañadas and Hammond, 2008):

$$E(s_j) = exp\left[\theta_0 + \sum f_k(z_{jk}) + b_i\right]$$

where s_j is the number of animals counted in the j^{th} group (response variable), θ_0 is the intercept, f_k are smoothed functions of the explanatory environmental covariates, z_{jk} is the value of the k^{th} explanatory covariate in the j^{th} group, and b_i is the type of survey in the i^{th} effort segment. The "type of survey" was included in these models as a factor covariate to account for differences in group size associated with each of the types of surveys. Other covariates were also considered in the group size models such as: Beaufort to account for differences in group size under different weather conditions; month and year to account for changes in group size throughout the year and the study period, respectively.

GAM models were fitted using the "mgcv" package (version 1.3-28) (Wood, 2017) in the software R 3.5.3 (R Core Team, 2019), using RStudio (version 1.2.1335, RStudio Team 2019).

Model selection

A full model was run for each response variable with all the covariates of the subset being analysed (e.g. year-round 2001 – 2017, 2001 – 2017 winter) (Figure 4.11) to select covariates through smoother shrinkage selection. Covariates with the effective degrees of freedom (edf) shrunk to zero or close to zero (i.e. that had no effect on the response variable; edf < 0.1), were excluded from subsequent models. Variable selection has the objective of determining which covariates have the strongest effects on the response of interest, trying at the same time to achieve a balance between goodness of fit and parsimony (Marra and Wood, 2011). Shrinkage methods and methods like subset selection and stepwise procedures can be employed, however, the former methods have proved to be a valid alternative to the latter procedures in terms of stability and prediction, with the advantage of carrying out variable selection in one single step as opposed to subset selection and stepwise algorithms (Marra and Wood, 2011).

Next, models were run with the remaining selected covariates, but excluding combinations of highly correlated (Pearson correlation coefficient > 0.7) or related/derived covariates (e.g. chlorophyll-a and primary productivity; average depth and maximum depth; distance to 100 m and to 200 m isobaths). Models were run by removing one by one smooth terms shrunk to zero or close to zero.

The chosen final model was the one with lowest corrected conditional AIC (Wood *et al.*, 2016), provided it was not over fitted (Marra and Wood, 2011), had acceptable diagnostic plots of the model residuals (i.e. the assumptions of normality and variance homogeneity were not violated), and predictions plots (see below) had no serious edge effects or unrealistic predictions. If there was more than one model with equivalent AIC values (Δ AIC < 2) that met the other selection criteria, the model with highest deviance explained was chosen. Temporal and spatial autocorrelation in the model residuals was assessed using the "acf" function of the "stats" R package (R Core Team, 2019) and the variogram function of the "gstat" R package, respectively (Zuur *et al.*, 2009).

Predictions and estimation of uncertainty

Relative abundance of individuals was predicted from the model of individuals for the Bryde's whale, or as the product of the predicted relative abundance of groups and the predicted group size (when a final group size model was chosen) per grid cell, for the remaining taxa. If the best group size model did not include any covariates or did not follow the model selection criteria (see above), the relative abundance of individuals was calculated as the product of the predicted relative abundance of groups per grid cell and the observed mean group size of the taxon for the period in question. The relative abundance (individuals or groups) and group size was predicted over a grid of 2 x 2 nm resolution (Section 4.2.3.4) using the function predict.gam of R package "mgcv". The overall predicted relative abundance of individuals is the average of the predicted values per grid cell in the study area. The prediction was based on the average values of the environmental variables per grid cell of a particular dataset for the period being modelled (e.g. 2001 – 2017; 2004 – 2017; winter 2001 – 2017; June/July 2004 – 2017) (Section 4.2.5.3).

For covariates associated with effort or without a spatial expression in the prediction (without a specific value attributable to each cell of the prediction grid) such as "month", "year", "Beaufort", "effort" and "type of survey", it was necessary to select a value or category over which to predict them. The selected values (quantitative variables) or categories (qualitative variables) are presented in Table 4.2. The months selected for predictions took into consideration the strong seasonal presence of some species such as the common dolphin and the Bryde's whale. In models of individuals or abundance of groups, when the covariate "effort" was excluded in the selection process, effort was incorporated in the final model as an offset, thus assuming a linear relationship (1:1) between the response variable (count) and segment length (Effort).

Table 4.2 –Values or categories of non-spatial covariates used to predict group size and relative abundance of groups or individuals taking in consideration the temporal coverage of each dataset analysed and species with a very marked seasonal presence in Madeira, such as *Delphinus delphis* (Dd) and *Balaenoptera edeni* (Be). In the case of the prediction of time-lag models, the covariate month was not considered because it had less degrees of freedom (2) than necessary to run the GAM models (>=3). SLS stands for systematic line-transect surveys.

Period	**Dataset**	**Beaufort**	**Effort**	**Type of survey**	**Year**	**Month**		
						Other	Dd	Be
2001 - 2017	Overall	2	1 km	SLS surveys	2010	7	3	7
	Winter (Jan - Mar)					2	2	-
	Spring (Apr - Jun)					5	5	5
	Summer (Jul - Sep)					8	-	8
	Autumn (Oct - Dec)					11	-	11
	Jun - Jul - time lag (Be)					-	-	-
	Aug - Sept - time lag (Be)					-	-	-
	Oct - Nov - time lag (Be)					-	-	-

The models of habitat use of Bryde´s whales at a smaller seasonal temporal scale (June/July, August/September; and October/November) with time-lagged covariates were predicted for the period of the corresponding datasets (June/July, August/September; and October/November). In these models, the covariate month was not considered because it had less degrees of freedom (2) than allowed to run in the GAM models (>=3).

The coefficient of variation (CV) and the percentile based 95% confidence intervals of the models were obtained by posterior simulation, following the Metropolis-Hastings approach (Miller, 2019, 2020). A total of 2 000 simulations were run for each model using transect as the resampling unit. For the taxa where relative abundance of individuals was estimated as the product of the predicted relative abundance of groups and the observed mean group size, and thus group size variability was not taken into account in the simulation process, the corresponding total CV was estimated using the delta method (Seber, 1982), as follows:

$$\widehat{CV}\ (n_{ind}) = \sqrt{\widehat{CV}^2(n_{grp}) + \widehat{CV}^2(s)}$$

where n_{ind} is the estimated relative abundance of individuals, n_{grp} is the estimated relative abundance of groups and S is the observed group size. The $\widehat{CV}(s)$ was calculated as the ratio of the standard error (SE) to the observed mean group size.

The CV values of relative abundance of individuals were plotted as maps of the variability distribution (Appendix IV).

4.3 RESULTS

A total of 56 127 km of effort from different types of survey were combined in this analysis (Table 4.3). All types of survey had year-round coverage and sampled multiple years, except for SLS-RD that sampled a single year (2017) from August to November and FO that covered from March to October in 2010, 2011 and 2012.

Table 4.3 – Effort (km) and number of sightings by type of survey done between 2001 and 2017 and modelled in this study. The types of surveys were: SLS – shipboard line transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line-transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; FO – fisheries observers program; and WWO – whale-watching observers program. Tt – *Tursiops truncatus*; Gma – *Globicephala macrorhynchus*; Sf – *Stenella frontalis*; Dd – *Delphinus delphis*; Sc – *Stenella ceoruleoalba*; Gg – *Grampus griseus*; Be – *Balaenoptera edeni*; Bp – *Balaenoptera physalus*; Pm – *Physeter macrocephalus*; Zc – *Ziphius cavirostris*; Msp – *Mesoplodon* sp.; Ksp – *Kogia* sp.; Bal – Balaenoteridae; Zph – Ziphiidae.

Effort type	**Project**	**Sampling period**	**Effort (km)**	**Effort by survey type (km)**	**nº of sightings/species**														
					Tt	**Gma**	**Sf**	**Dd**	**Sc**	**Gg**	**Be**	**Bp**	**Pm**	**Msp**	**Zc**	**Ksp**	**Bal**	**Zph**	**All**
SLS	CetáceosMadeira	2001-04	5 133	17 780	19	9	22	42	5	4	0	7	5	2	2	2	15	8	119
	Emecetus	2007-09	3 656		25	13	23	20	11	0	6	0	8	5	2	3	15	9	116
	CetáceosMadeira II	2010-12	5 441		45	18	26	51	7	0	1	8	9	7	3	2	22	19	177
SLS - RD	Mistic Seas II	2017	3 550		27	28	15	5	1	0	24	0	8	0	0	0	25	0	108
ALS	MBM	2002-2008	17 323	17 323	29	13	26	50	9	1	10	0	13	1	5	1	19	6	158
NSS	Macetus	2004-05	1 689	8 408	11	9	37	1	1	1	9	0	9	0	0	0	14	1	78
	Golfinicho	2006	1 421		6	9	23	11	1	0	10	0	2	1	0	2	16	2	65
	Emecetus	2007	420		4	3	5	3	0	0	6	0	1	0	0	0	10	1	22
	CetáceosMadeira II	2010-12	4 374		68	45	25	42	9	1	5	2	2	3	0	2	16	4	204
	OceanWebs	2016-17	505		10	2	9	0	0	0	0	0	4	2	0	0	0	2	27
FO	CetáceosMadeira II	2010-12	3 689	3 689	5	3	5	61	3	0	2	0	2	2	0	0	33	2	83
WWO	CetáceosMadeira II	2010-12	3 886	8 927	76	30	53	23	8	4	12	1	5	2	0	0	18	5	214
	MBM	2014-17	5 041		70	54	115	48	4	0	37	10	17	7	1	1	47	8	364
Total		**2001-17**		**56 127**	**395**	**236**	**384**	**357**	**59**	**11**	**122**	**28**	**85**	**32**	**13**	**13**	**250**	**67**	**1 735**
Total (without ALS)		**2001-17**		**38 804**	**339**	**195**	**343**	**302**	**49**	**10**	**88**	**28**	**64**	**31**	**8**	**12**	**206**	**61**	**1 469**

Figure 4.12 shows the spatial coverage of the types of surveys used in the analysis (datasets) to model the habitat use of cetacean species, for the periods 2001 – 2017 and by season. In Appendix III are shown maps with effort per type of survey for 2001-17.

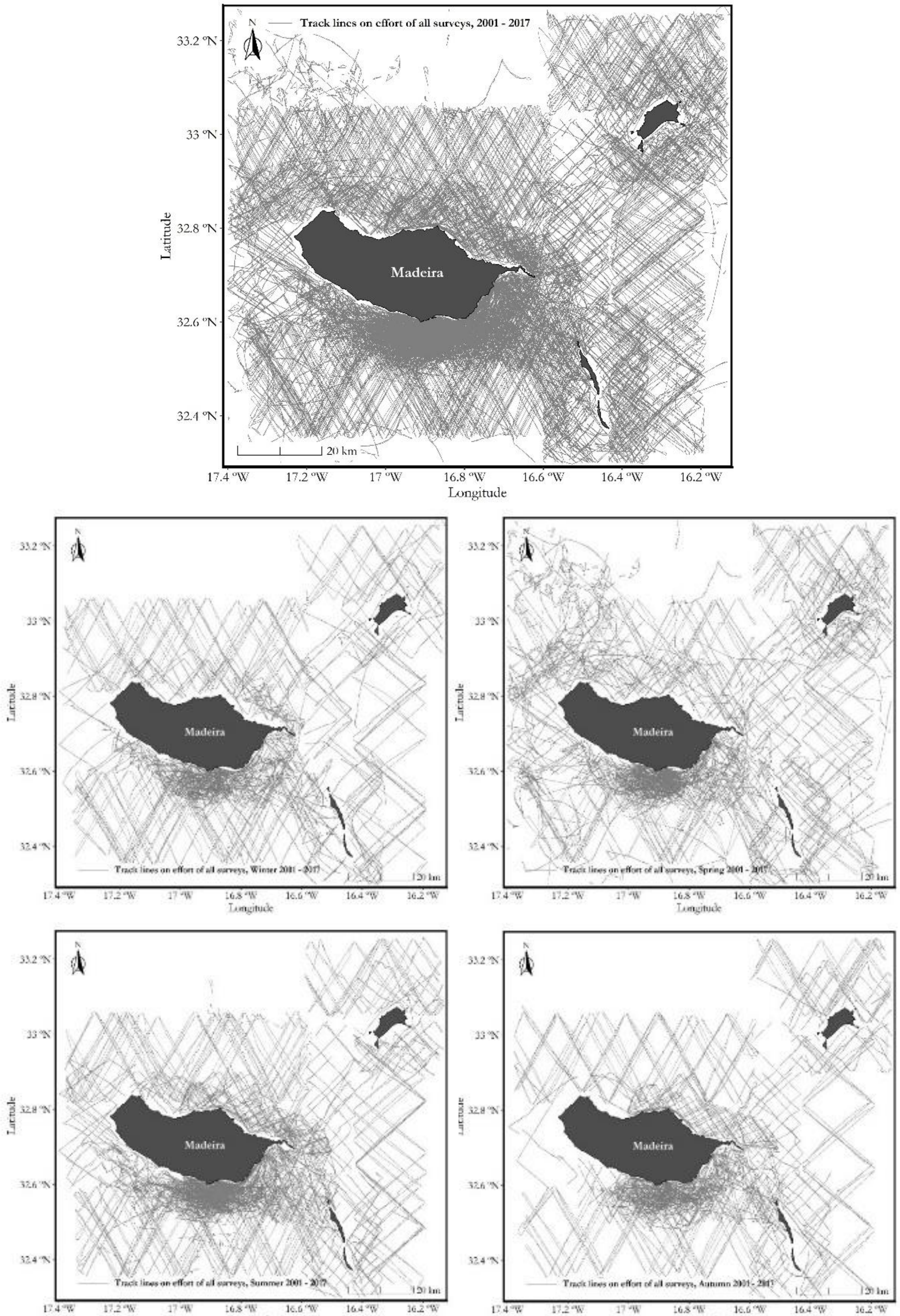


Figure 4.12. Spatial coverage of the study area given by the track lines on effort of all surveys used to model habitat use of cetacean taxa (species, genera or families) for the periods 2001 – 2017 (top) and by season, namely, winter (center-left), spring (centre-right), summer (bottom-left) and autumn (bottom-right).

4.3.1 Relative importance

A total of 28 cetacean species have been mentioned for Madeira archipelago, 26 of which are confirmed records (Freitas *et al.*, 2012; Ferreira *et al.*, 2017). During the surveys, 25 cetacean taxa were identified, 21 to species, two to genus and two to family level (Figure 4.13). The remaining species attributed to Madeira are either very rare, regionally extinct or extra-limital records.

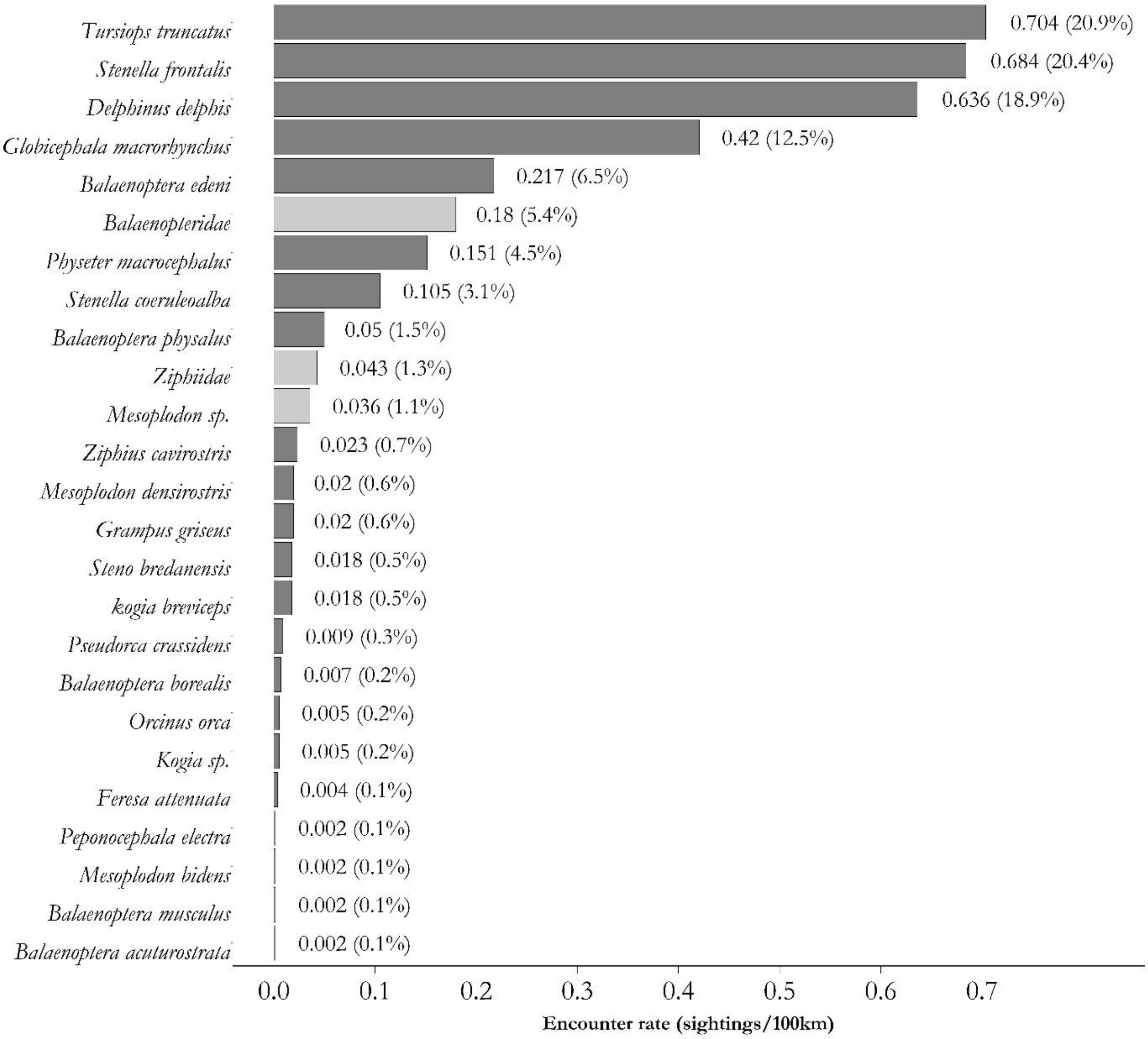


Figure 4.13. Average encounter rate (sightings/100km) of cetacean groups sighted during the different types of survey around Madeira coastal waters between 2001 and 2017 and covering all months of the year, identified down to the lowest taxonomic level. In parenthesis are given the percentage of sightings of each taxon.

The most sighted species were the bottlenose dolphin (*Tursiops truncatus*), the Atlantic spotted dolphin (*Stenella frontalis*) (henceforward called spotted dolphin), the common dolphin (*Delphinus delphis*) and the short-finned pilot whale (*Globicephala macrorhynchus*) (henceforward called pilot whale), with encounter rates (ER) ranging from 0.7 sightings/100 km down to 0.42 sightings/100 km. The next group of species, with ER between 0.22 sightings/100 km and 0.05 sightings/100 km, were the Bryde's whale (*Balaenoptera edeni*), the sperm whale (*Physeter macrochephalus*), the striped dolphin (*Stenella coeruleoalba*) and the fin whale (*Balaenoptera physalus*). The beaked whales, namely Cuvier's beaked whales (*Ziphius cavirostris*) and Blainville's beaked whale (*Mesoplodon densirostris*), Risso's dolphin (*Grampus griseus*), rough-toothed dolphin (*Steno bredanensis*) and pygmy killer whale (*Kogia breviceps*) formed a third group with lower ER that ranged from 0.023 sightings/100 km to 0.018 sightings/100 km.

Finally, the last group included rarer species such as the false killer whale (*Pseudorca crassidens*), the sei whale (*Balaenoptera borealis*), the killer whale (*Orcinus orca*), the pygmy killer whale (*Feresa attenuata*), the melon-headed whale (*Peponocephala electra*), Sowerby's beaked whale (*Mesoplodon bidens*), the blue whale (*Balaenoptera musculus*) and the minke whale (*Balaenoptera acutorostrata*), with ER from 0.009 sightings/100 km down to 0.002 sighting/100 km.

4.3.2 Group size

Figure 4.14 and Figure 4.15 show the group size for the cetacean species observed in Madeira inshore waters between 2001 and 2017 including all the surveys, except FO. Tables with group size statistics by type of survey, season and period are presented in Appendix IV.

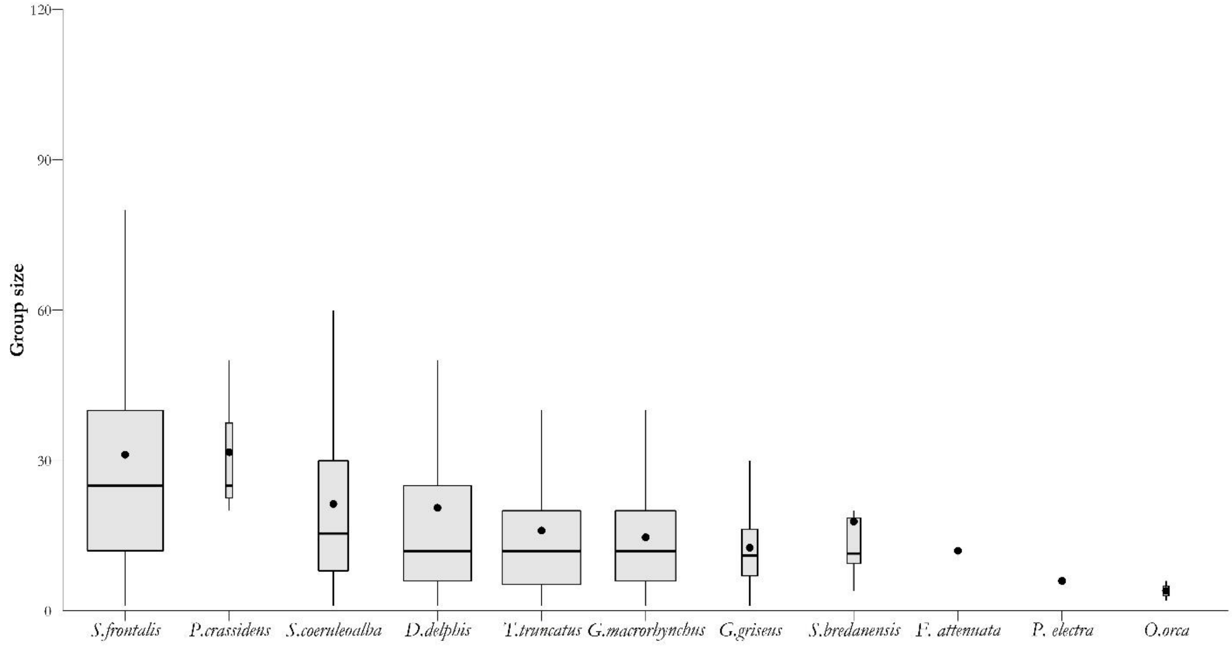


Figure 4.14. Mean (dot), median (line), interquartile range (IQR; grey box), and minimum and maximum (calculated as the 25th percentile – 1.5* IQR and the 75th percentile + 1.5*IQR, respectively; vertical lines) group sizes of dolphin species in Madeira inshore waters based on data covering the period 2001-2017 from all types of surveys, except fisheries observer surveys. Potential outlier maximum values (> 75th percentile + 1.5*IQR) were not represented for the sake of clarity of the graph. The width of the grey box reflects the relative number of sightings upon which the statistics are calculated.

Among the regularly sighted species in the study area, the spotted dolphin had the highest mean (36.6), median (25) and range (1 – 500) of group sizes, followed by the striped and common dolphins with similar means (21.4 and 21.5, respectively), although the former had a higher median and narrower ranges (16; 1 – 70) when compared to the latter (12; 1 – 170). The bottlenose dolphin and the pilot whale had similar means (16 and 14.7 animals, respectively) and medians (12), with the former having a wider range of group sizes (1 – 90; 1 – 60) (Figure 4.14).

The mean group size of species seen occasionally in Madeira inshore waters was variable, with 31.7 animals for false-killer whales (median =25), 17.8 for rough-tooted dolphin (median = 12), 12.6 for Risso's dolphin (median = 8) and 4 for killer whale (median = 4) (Figure 4.14). The group size ranges were smaller than in the common species.

Several odontoceti species sightings had some atypically high group sizes (not represented in Figure 4.14), including the spotted dolphin (35 groups with sizes between 90 and 500 animals out of the 378 recorded), common dolphin (42 groups between 45 and 170 animals out of the 294 recorded), bottlenose dolphin (25 groups between 45 and 90 animals out of the 390 recorded), pilot whale (nine groups between 45 and 60 animals out of the 233 recorded), striped dolphin (two groups of 70 animals out of the 56 recorded) and rough-toothed dolphin (two groups of 40 and 60 animals out of the 12 recorded).

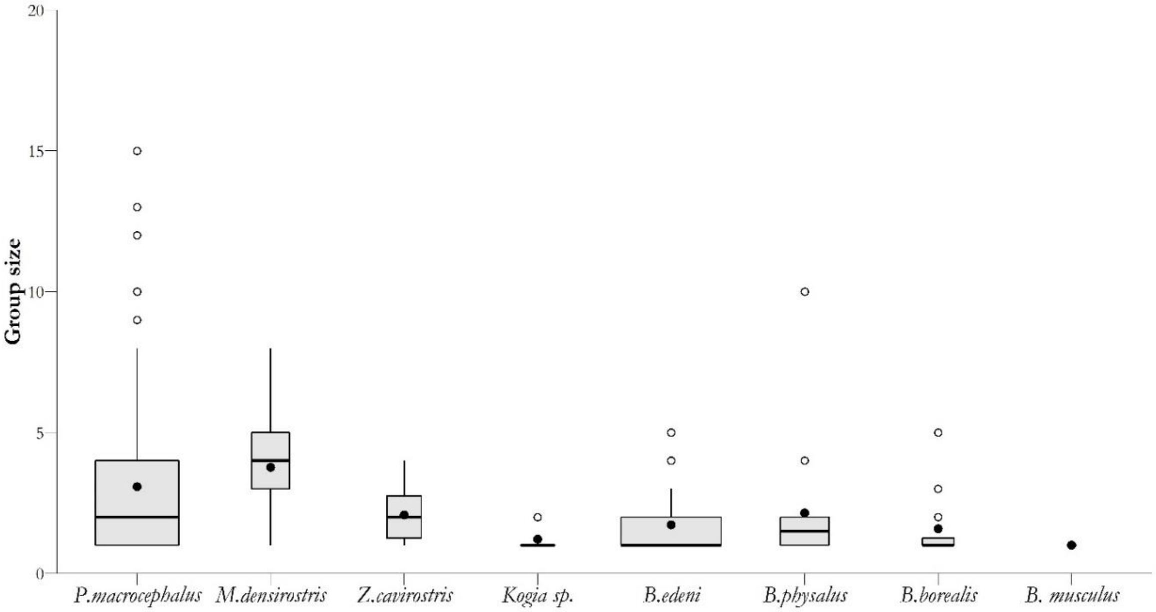


Figure 4.15. Mean (dot), median (line), interquartile range (IQR; grey box), minimum and maximum (calculated as the 25th percentile – 1.5*IQR and the 75th percentile + 1.5*IQR, respectively; vertical lines), and potential outliers (> 75th percentile + 1.5*IQR; open circles), of group sizes of baleen whales and deep diving species in Madeira inshore waters based on data from systematic line-transect surveys, systematic aerial line-transect surveys, non-systematic surveys and whale-watching observer surveys covering the period 2001-2017. The width of the grey box reflects the relative number of sightings upon which the statistics are calculated.

Sperm whales were seen in groups with a mean size of 3 animals (median = 2), but with quite a wide range (1 – 15, n = 85). Beaked whales were also seen in small groups, with Blainville's beaked whales forming groups with a mean of 3.8 animals (median = 4; range = 1 – 8; n = 17), while Cuvier's beaked whale groups had a mean size of 2.1 animals (median = 2; range = 1 – 4; n = 14). Sightings of *Kogia* sp. were mostly of single individuals (mean = 1.2; median = 1; n = 14), although there were occasional sightings of two animals (Figure 4.15).

The group size of baleen whales was also small, with Bryde's whales (mean =1.7; mean = 1; range = 1 – 5; n = 120) and sei whales (mean = 1.6; median = 1; range = 1 – 5; n = 12) having similar group sizes statistics. Fin whales had slightly bigger groups in the area (mean = 2.1; median = 2; range = 1 – 10; n = 28).

4.3.2.1 Group size by season

The group sizes of different cetacean species by season (winter, spring, summer and autumn) are presented in Figure 4.16 and Figure 4.17. Seasonal variation in group sizes of the species with sufficient sightings were also modelled using GAMs for 2001 – 2017, and 2004 – 2017 in the case of the Bryde's whale. The fitted smooths of group size as a function of month are shown in Figure 4.18.

Bottlenose dolphin group size shows a clear seasonal pattern, with the smallest group sizes in April and the largest in September (Figure 4.18). Group sizes of spotted dolphin and common dolphin show the same general pattern as for the bottlenose dolphin, with the first species having larger group sizes in October/November and the second in August/September (Figure 4.18). Despite some variation in the data, there was no support for seasonal variation in striped dolphin group size (Figure 4.18).

Pilot whale, *Mesoplodon* sp. and other beaked whales as a whole show seasonal variation in group size, which is larger in spring and summer compared to autumn and winter (Figure 4.18). Conversely, there was no indication of seasonal variation in sperm whale group size.

Fin whale group size also shows a clear seasonal pattern, with larger group sizes in spring compared to the rest of the year, while the Bryde's whale shows no clear seasonal pattern in group size (Figure 4.18).

There were insufficient data to model with GAMs the seasonal variation of group size of *Kogia* sp., Risso's dolphin, rough-tooted dolphin and sei whale.

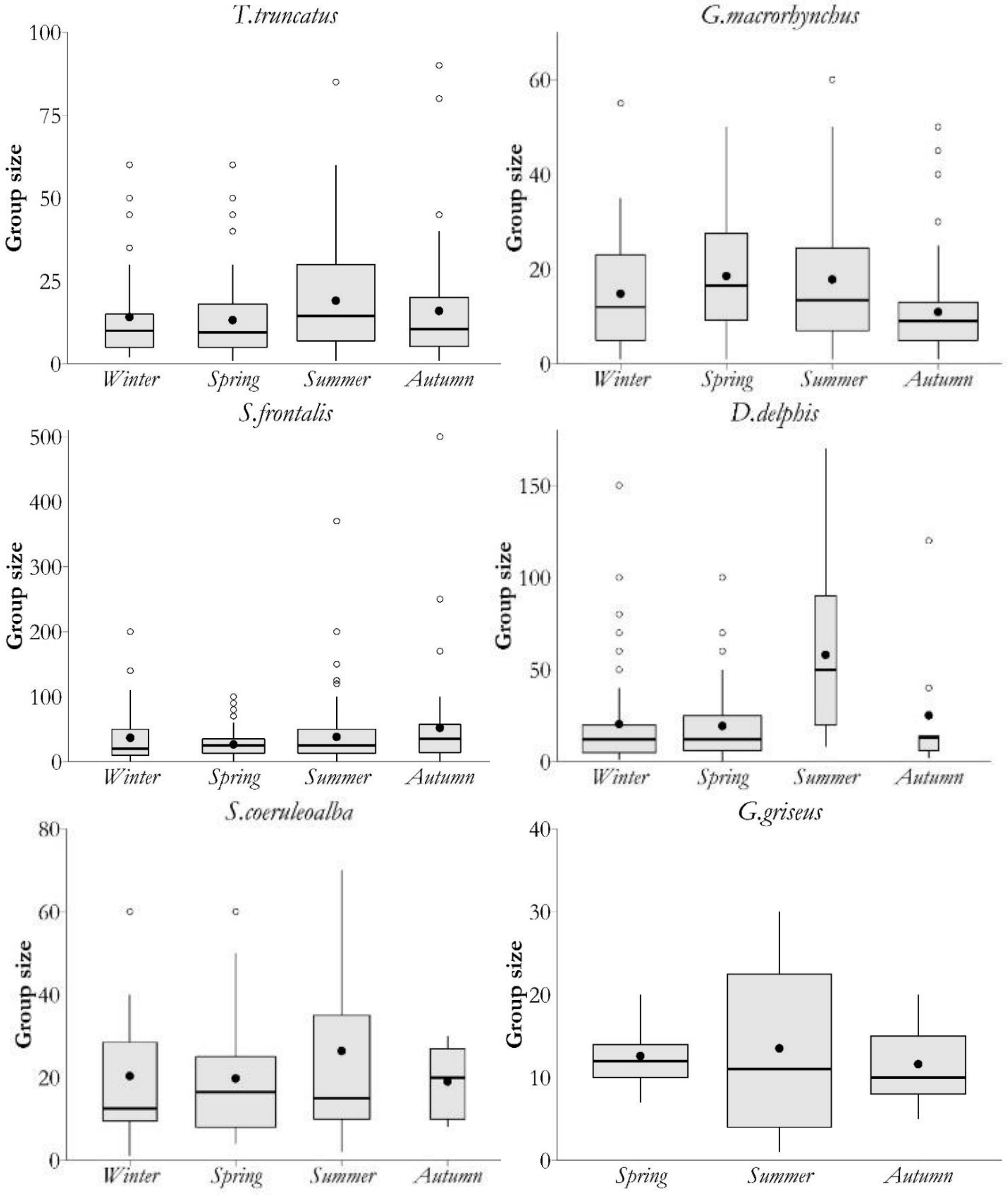


Figure 4.16. Mean (dot), median (line), interquartile range (IQR; grey box), minimum and maximum (calculated as the 25th percentile – 1.5*IQR and the 75th percentile + 1.5*IQR, respectively; vertical lines), and potential outliers (> 75th percentile + 1.5*IQR; open circles) by season (winter, spring, summer and autumn) for different dolphin species and the short-finned pilot whale in Madeira inshore waters based on data from systematic shipboard and aerial line-transect surveys, non-systematic surveys and whale-watching observer surveys covering the period 2001-2017. The width of the grey box reflects the relative number of sightings upon which the statistics are calculated.

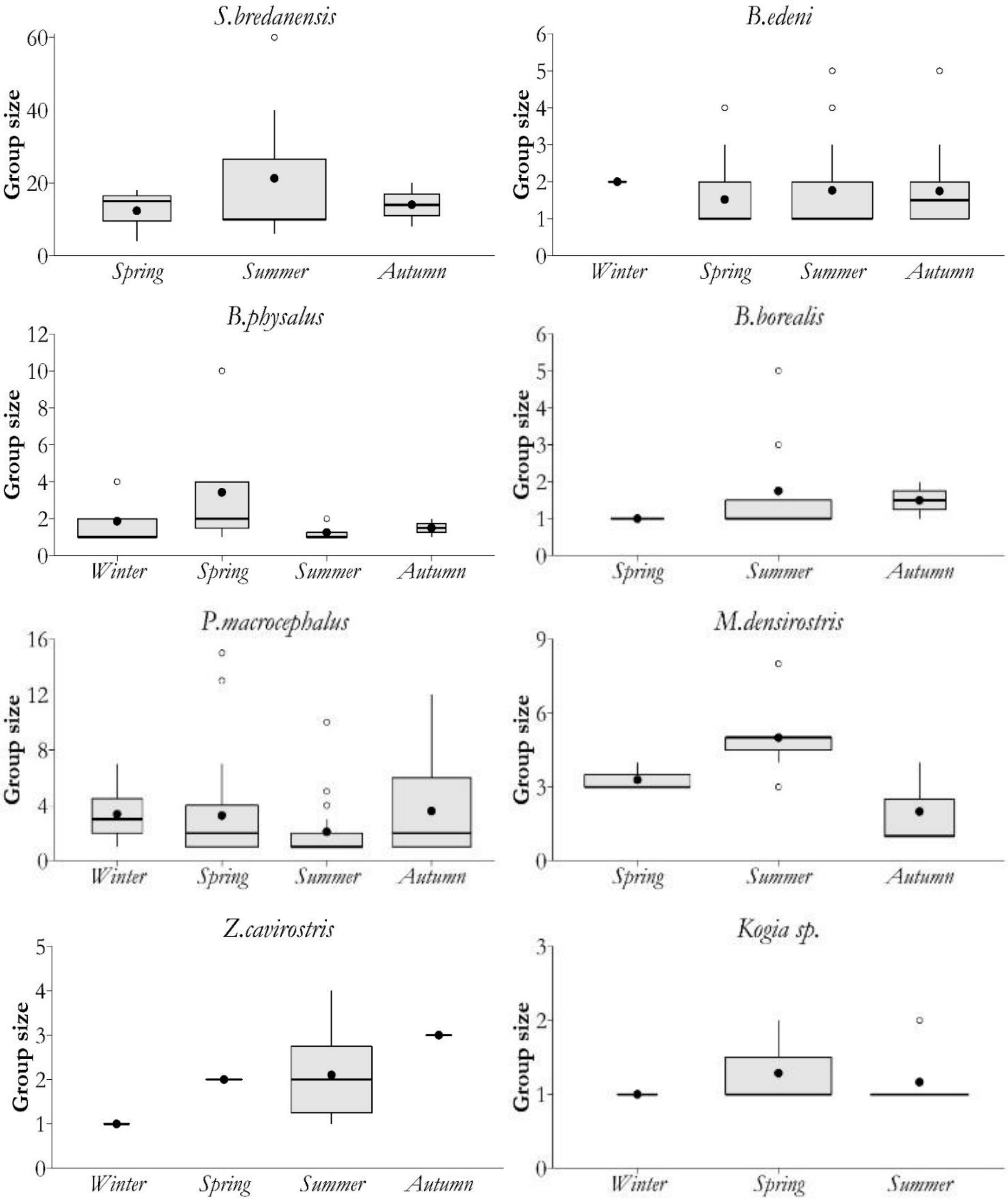


Figure 4.17. Mean (dot), median (line), interquartile range (IQR; grey box), minimum and maximum (calculated as the 25th percentile – 1.5*IQR and the 75th percentile + 1.5*IQR, respectively; vertical lines), and potential outliers (> 75th percentile + 1.5*IQR; open circles) by season (winter, spring, summer and autumn) for rough-toothed dolphin, baleen whales, sperm whale, beaked whales and *Kogia sp.* in Madeira inshore waters based on data from systematic shipboard and aerial line-transect surveys, non-systematic surveys and whale-watching observer surveys covering the period 2001-2017 (2004 – 2017 for Bryde's whale). The width of the grey box reflects the relative number of sightings upon which the statistics are calculated.

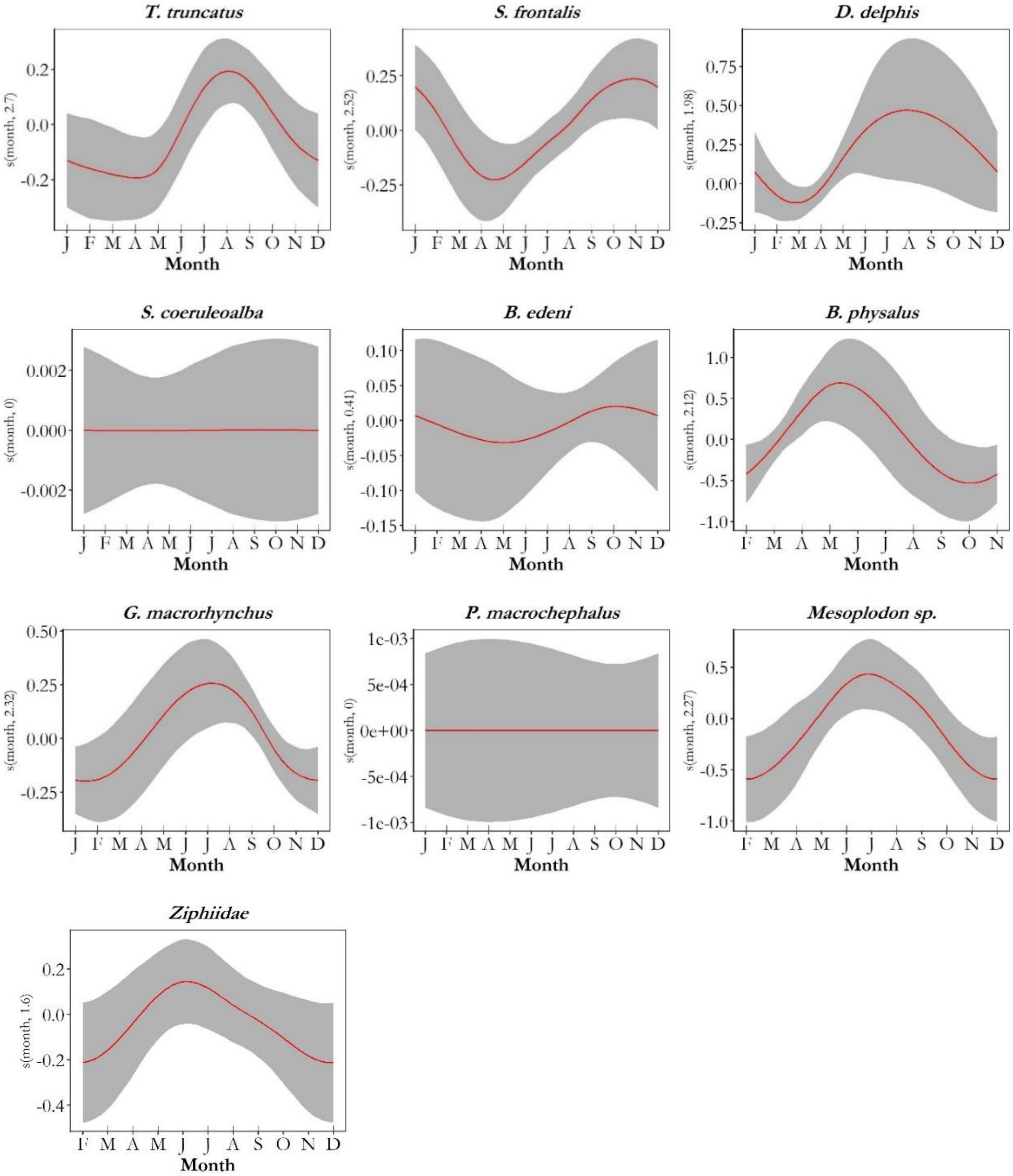


Figure 4.18. Smooths of generalized additive models of several cetacean species where the group size is the response variable and month the explanatory variable. The data were collected by systematic shipboard and aerial line-transect surveys, non-systematic surveys and whale-watching observer and fisheries observer surveys covering the period 2001-2017 (2004 – 2017 for Bryde's whale). The month of January is absent in some plots because of the absence of sightings of the corresponding taxon in that month.

4.3.3 Overall relative temporal distribution (2001 – 2017)

The group ER distribution per month for the same species as the previous section is shown in Figure 4.19 and the corresponding GAM model smooth curves of the group and individuals relative abundance as a function of "Month" in Figure 4.20 and Figure 4.21, respectively.

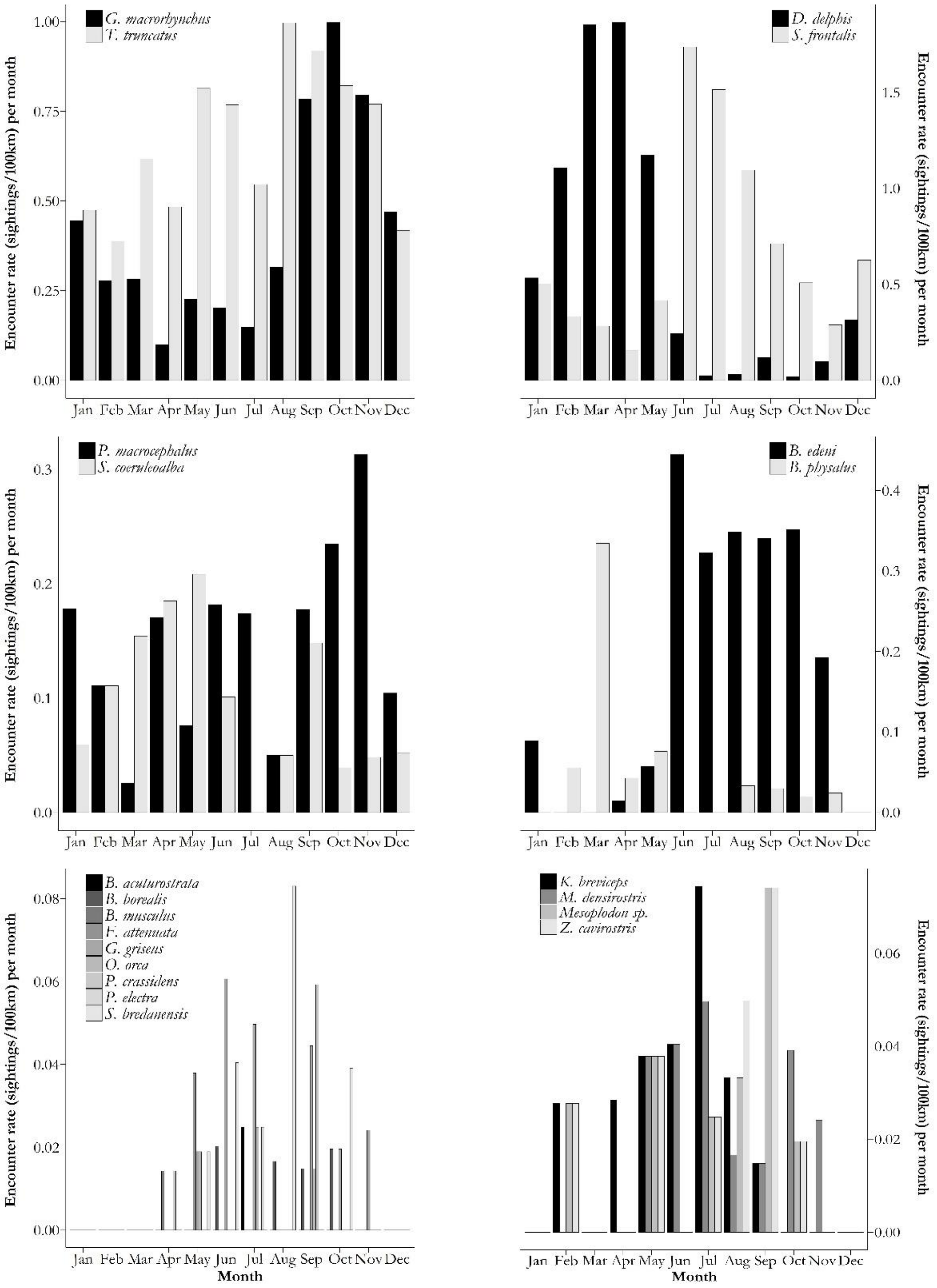


Figure 4.19. Average monthly encounter rate (sightings/100 km) of the cetacean species identified during the surveys carried out by the Madeira Whale Museum between 2001 and 2017.

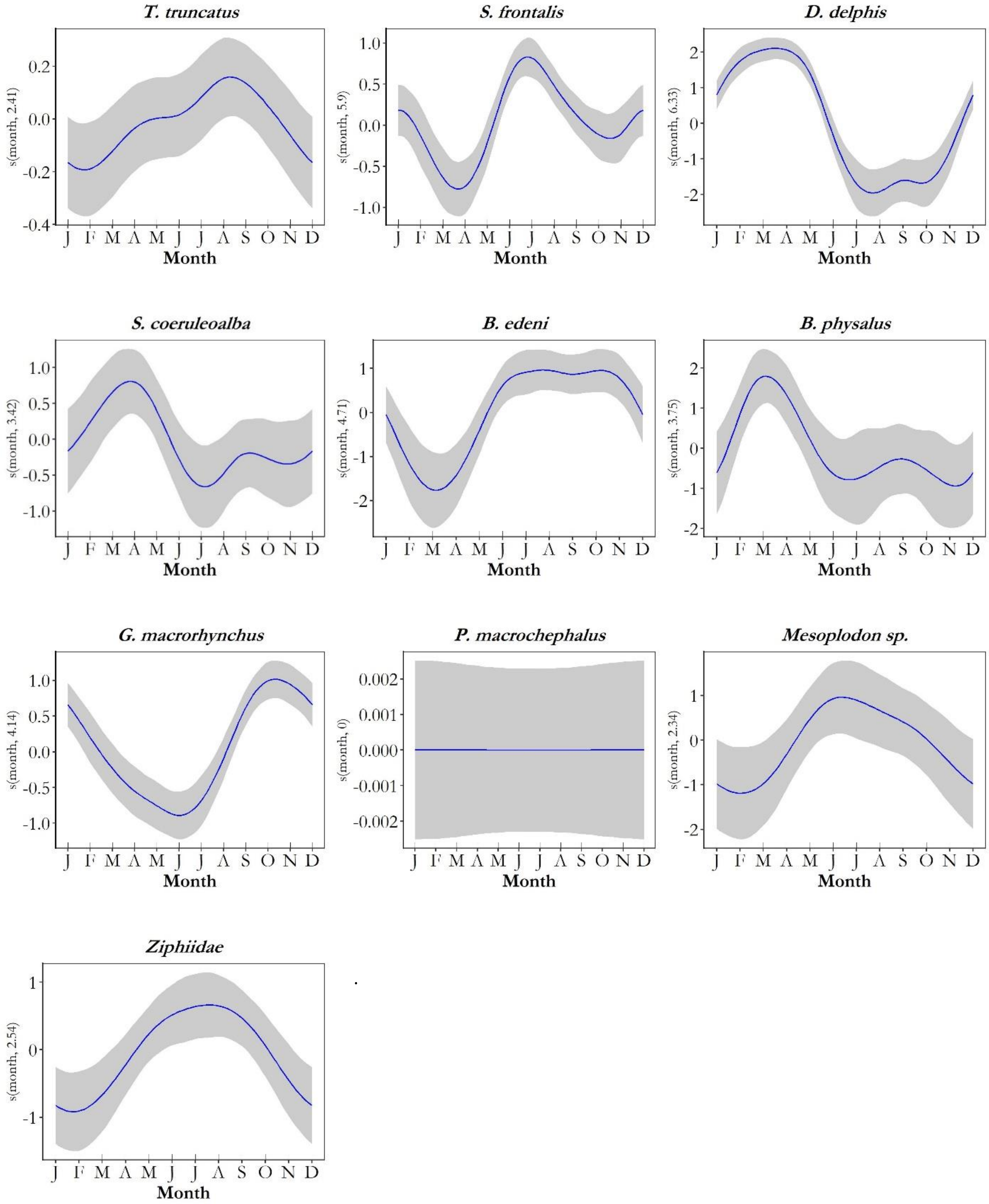


Figure 4.20. Smooths of generalized additive models of several cetacean species where the encounter rate of groups is the response variable and month the explanatory variable. The data were collected by systematic shipboard and aerial line-transect surveys, non-systematic surveys and whale-watching observer and fisheries observer surveys carried out by the Madeira Whale Museum between 2001 and 2017.

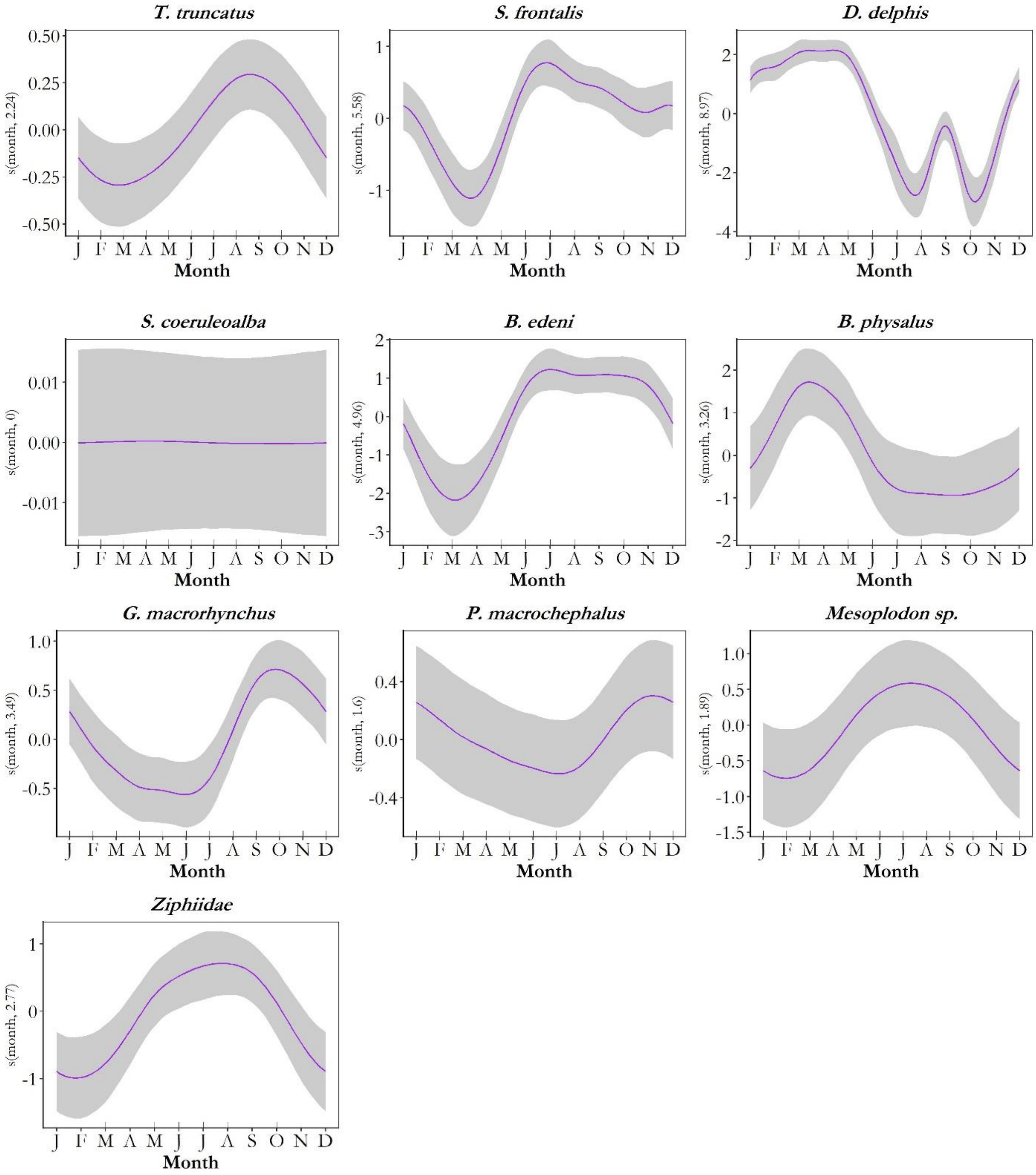


Figure 4.21. Smooths of generalized additive models of several cetacean species where the encounter rate of individuals is the response variable and month the explanatory variable. The data were collected by systematic shipboard and aerial line-transect surveys, non-systematic surveys and whale-watching observer and fisheries observer surveys carried out by the Madeira Whale Museum between 2001 and 2017.

Bottlenose dolphin and pilot whale have a seasonal variation in relative abundance of groups (Figure 4.20) and individuals (Figure 4.21), with the latter species showing a more marked seasonal pattern. The bottlenose dolphin reaches the maximum relative abundance of groups in August – September and the minimum in January – February, while the pilot whale reaches the maximum in October – November and the minimum in May – July. The seasonal variations of relative abundance of individuals, i.e. the combined seasonal fluctuations of relative abundance of group and group size, shows the same general seasonal pattern, but with slight variation in the months when the maximum and minimum relative abundance is reached (Figure 4.21) .

The common dolphin and the spotted dolphin have a clear complementary seasonal presence in the Madeira inshore waters, with the former having a higher relative abundance of groups and individuals from late autumn to late spring, while the latter reaches its highest relative abundance in the summer months (Figure 4.20 and Figure 4.21). When comparing the smooth of relative abundance of groups with the smooth of relative abundance of individuals per month for both species, the effect of group size emerges; the spotted dolphin's December peak of relative abundance present in the smooth of groups dissipates in the smooth of individuals, while a clear peak in common dolphins relative abundance of individuals emerges in September (Figure 4.20 and Figure 4.21).

The striped dolphin and the common dolphin have a more or less similar pattern of relative abundance of groups over the year, although less defined in the former species as suggested by the 95% confidence limits of the smooths (Figure 4.20). Like the common dolphin, the striped dolphin relative abundance of groups over the year mirrors that of the spotted dolphin, with its peak in March/April and a trough in July at the lowest and highest presence of spotted dolphin, respectively. However, that pattern is not confirmed by the smooth of individuals (Figure 4.21).

Bryde's whale and the fin whale also have complementary seasonal patterns of presence in Madeira archipelago. The relative abundance of groups and individuals of fin whale is highest between February to May, with a clear peak in March, while the Bryde's whale has a marked seasonal presence, arriving in June and using these waters until November (Figure 4.20 and Figure 4.21).

There was no support in the data for seasonal variation in relative abundance of sperm whale groups in Madeira archipelago (Figure 4.20). However, when modelling the relative abundance of individuals over the year a seasonal pattern emerged (peak in November), but with some uncertainty (Figure 4.21). Conversely, beaked whales of the genus *Mesoplodon* and beaked whales as a whole (Ziphiidae) show an increase in relative abundance of groups and individuals during late spring and summer. For the remaining species, there were insufficient data to model with GAMs the seasonal variation in relative abundance of groups and individuals.

4.3.4 Modelling habitat use and predicting distribution of relative abundance

Although a total of 21 species were recorded during the surveys, it was only possible to model the habitat use of eight of those species because of the low number of sightings of the remaining ones. To partially overcome this limitation, species of the same genera or family, with expected close ecological requirements, were modelled together in some cases (e.g. genus *Mesoplodon* and family Ziphiidae). The habitat modelling analysis covered the period 2001 – 2017 for all taxa, except Bryde's whale that covered the period 2004 – 2017 (Section 4.2.5.3).

The results of the habitat use modelling analysis are presented by groups of species, i.e. oceanic dolphins, baleen whales and deep divers, with closer ecological needs and biological characteristics, and thus more likely to compete locally for resources. For each group of species, a table is presented with the description of the selected models, including the percentage of deviance explained by the models, the effective degrees of freedom and the number of models that were run for each species. The number of models ran gives an indication of the number of combinations of covariates tested for a particular response variable being modelled, having in consideration the covariates available to model and the steps and rules of the model selection process (shrinkage; related, derived or highly correlated covariates; Section 4.2.5.5). Also presented is a table with the corresponding observed and predicted mean ER of groups and mean group size (when applicable), and the observed and predicted mean ER of individuals and its average uncertainty (mean CV) in the study area. The observed ER of individuals was calculated by multiplying the observed ER of groups by the observed mean group size in the study area. The predicted ER of individuals for most taxa was calculated by multiplying the predicted group size (or the overall mean group size when no final group size model was selected) and the predicted ER of groups of each grid cell of the prediction grid (Figure 4.10), averaged for the whole area. In the case of the Bryde's whale, where count of individuals was the response variable rather than count of groups (as for all other taxa), the predicted ER of individuals was given by the model. The mean CV was obtained by averaging the CV values of each grid cell of the prediction grid, calculated from the model's variance estimated by posterior simulation (Section 4.2.5.5).

Also shown for each taxon is the smooth of each covariate of the corresponding model, ordered by decreasing importance of its effect on the response variable and the predicted distribution map of relative abundance of individuals in the study area. The relative abundance values of the predicted distribution maps are not comparable among taxa and season (Section 4.3.5) because of the survey factor covariate, which is specific to each model. It accounts for differences in the detection probabilities among the type of surveys within the study area for a particular taxon at the expense of the comparability of relative abundance between taxa. The comparison among the predicted distribution maps should be qualitative, i.e., comparison of the pattern of distribution of higher and lower relative abundance within the study area, having in consideration that the relative abundance scales are specific to each map. The observed ER of groups and individuals, presented in Table 4.5, Table 4.7, Table 4.9, Table 4.11, Table 4.13, Table 4.15, Table 4.17 and Table 4.19, are also not comparable with the corresponding predicted ER of groups and individuals in those tables. The observed ER are the average of all types of surveys, while the predicted ER are the prediction for one of the levels of the factor covariate (SLS – systematic line-transect surveys). In the Appendix V.1 are presented tables with the parametric and smooth terms values, diagnostic plots and uncertainty plots of each of the selected models.

4.3.4.1 Oceanic dolphins

The habitat use models selected for the bottlenose dolphin, the spotted dolphin, the common dolphin and the striped dolphin are presented in Table 4.4, and the respective observed and predicted relative abundance in Table 4.5. The final models have values of percentage of deviance explained from 12.43 % for common dolphin to 25.50 % for spotted dolphin (Table 4.4).

As expected, "Month" was among the covariates of the selected models of the species with seasonal presence in Madeira archipelago and its smooth shape reflected each species seasonal local presence pattern (Table 4.4; Figure 4.24, Figure 4.26 and Figure 4.28). The bottlenose dolphin, with a known year-round presence, did not include this covariate in the final model (Figure 4.22).

Effort and Beaufort were also among the covariates of these species' final models. Effort accounts for the non-linear relationship between the number of groups (response variable) and the sampling units (segments) length and the Beaufort accounts for the effect of sea conditions on the detection of these species' groups during the surveys. As expected, the ER of groups decreases with increasing Beaufort, in all the dolphin species models.

Table 4.4 – Summary table of the selected habitat use models of relative abundance of groups and models of group size (when applicable) of the bottlenose dolphin, spotted dolphin, common dolphin and striped dolphin, and the respective selected model main characteristics; * - significant relationship between covariate and response (p<0.05).

Species	Nº of segments	Nº of observ.	Response variable	model selected	% Dev. Explained	edf model	Nº models
Tursiops truncatus	15493	395	Groups	factor(Type of survey) + s(Distance to coast)* + s(Year)* + s(Beaufort)* + s(Effort)*	15.77%	16.7	>100
Stenella frontalis	15493	384	Groups	factor(Type of survey) + s(Slope area)* + s(Distance to escarpment)* + s(Poc 2001-17)* + s(Ssh 2001-17)* + s(Aspect std dev) + s(Contour index) + s(Month)* + s(Year)* + s(Beaufort)* + s(Effort)*	22.50%	27.0	68
Delphinus delphis	8291	341	Groups	factor(Type of survey) + s(Slope area)* + s(Average slope)* + s(Chl-a 2001-17)* + s(Sst-a 2001-17)* + s(Month)* + s(Beaufort)* + s(Effort)*	12.43%	18.5	16
Stenella coeruleoalba	15493	59	Groups	factor(Type of survey) + s(Average depth)* + s(Chl-a 2001-17)* s(Sst 2001-17)* + s(Month)* + s(Beaufort)* + s(Effort)*	12.56%	13.5	32

Table 4.5 – Summary table of the observed and predicted encounter rates (ER) of groups and individuals per kilometre, as well as observed mean group size, of bottlenose dolphin, spotted dolphin, common dolphin and striped dolphin. The observed ER of individuals = observed ER group * observed mean group size; predicted ER of individuals = predicted ER of groups * observed mean group size (no final group size models were selected). The CV was calculated from the models' variance estimated by posterior simulation.

Species	Nº of observ.	ER groups		Group size		ER individuals		
		Observed	Predicted	Observed	Predicted	Observed	Predicted	CV
Tursiops truncatus	395	0.0070	0.012	15.92	-	0.112	0.191	1.17
Stenella frontalis	384	0.0068	0.031	36.39	-	0.249	1.142	1.05
Delphinus delphis	341	0.0114	0.052	19.04	-	0.216	0.982	0.75
Stenella coeruleoalba	59	0.0011	0.002	20.63	-	0.022	0.051	0.66

Tursiops truncatus

The habitat use of the bottlenose dolphin was investigated by modelling the relative abundance of groups and group size, separately. No group size model fulfilled the model selection criteria (Section 4.2.5.5), thus the relative abundance of individuals was obtained by multiplying the predicted ER of groups by the observed mean group size in the study area for 2001 – 1017.

The final group model explained 15.77 % of the deviance in the data and included only the environmental covariate "Distance to coast", in spite of the high number of observations in the dataset (395). Although many models (>100; Table 4.4) were tested including combinations of all non-highly correlate environmental variables available, the best model (lowest AIC) excluded those covariates. The other relevant covariate of the final model is "Year", suggesting a linear increase in ER of groups during the study period (Figure 4.22). The scale of the vertical axis is an indication of the strength of the effect of the covariate on the response variable. In this case, the range is quite narrow, indicating the effect is not strong, thus suggesting a moderate increase in ER of groups over time.

The predicted distribution of relative abundance of bottlenose dolphin was higher closer to the coast, decreasing gradually towards offshore waters (Figure 4.23).

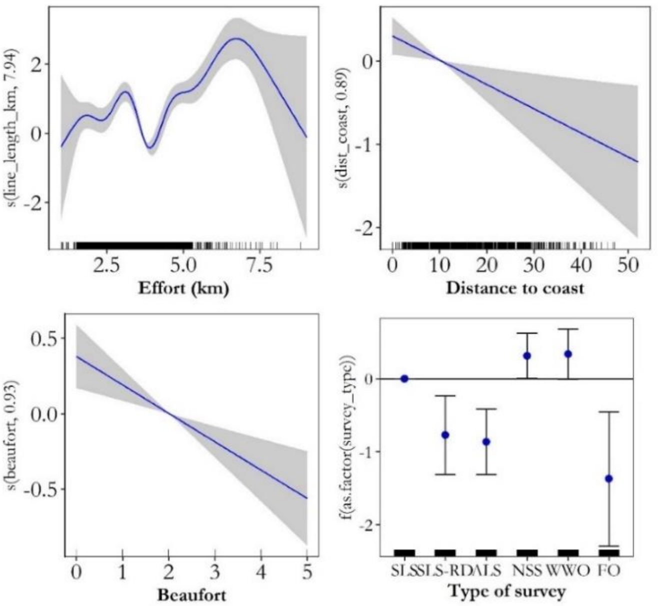


Figure 4.22. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of bottlenose dolphin groups (relative abundance) in the Madeira inshore waters for the period 2001 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – fisheries observers program.

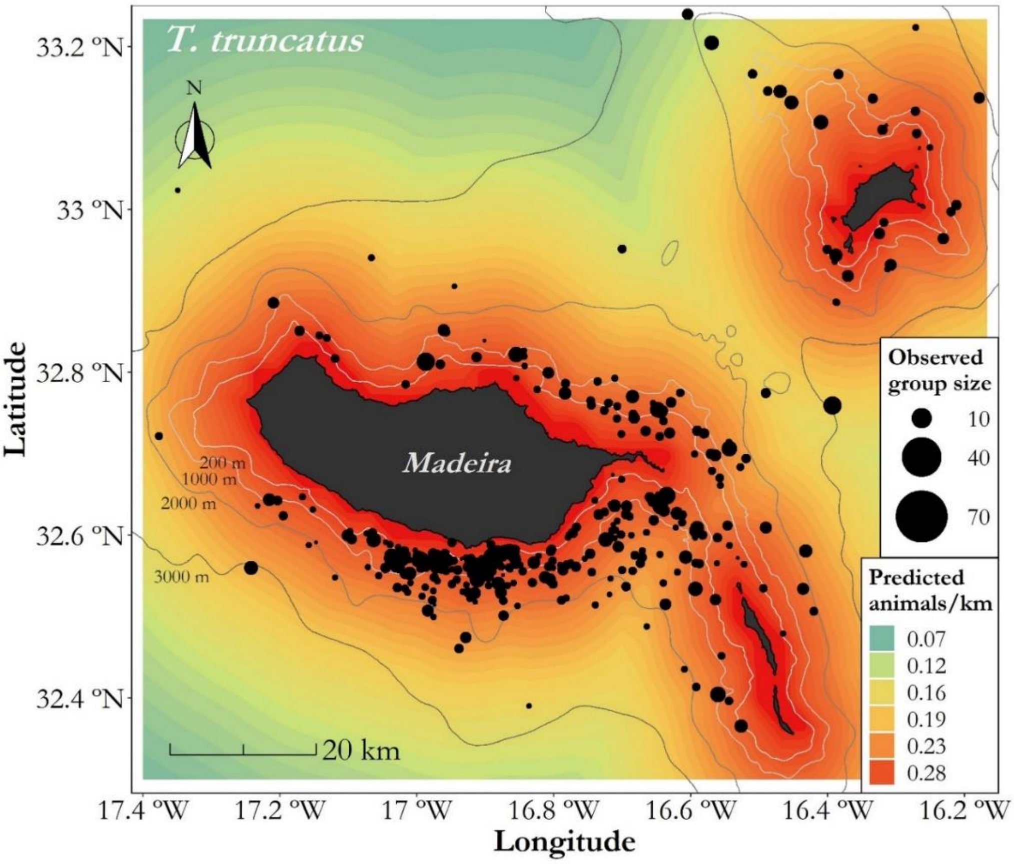


Figure 4.23. Predicted distribution of relative abundance (animals per km of transect line) of bottlenose dolphins in the Madeira inshore waters for the period 2001 – 2017, as a result of the combination of predicted relative abundance of groups and observed mean group size.

Stenella frontalis

The habitat use of the spotted dolphin was explored by modelling the relative abundance of groups and group size separately. No group size model fulfilled the model selection criteria (Section 4.2.5.5), thus the relative abundance of individuals was obtained by multiplying the predicted ER of groups by the observed mean group size in the study area for 2001 – 1017.

The use of habitat by spotted dolphins appears to be driven by static physiographic variables (similar to the bottlenose dolphin), but to a less extend also by dynamic variables (Figure 4.24). The variables in the model with most effect on the number of groups were "Distance to escarpment" followed by "slope area", with the first one having a negative relationship and the second a positive relationship with the response variable, respectively. The final model also included the covariates "Poc 2001-17" (particulate organic carbon) and "Ssh 2001-17" (sea surface height) but with less effect on the response. The negative slope of the "Poc 2001-17" smooth suggests a preference of the species for clearer waters.

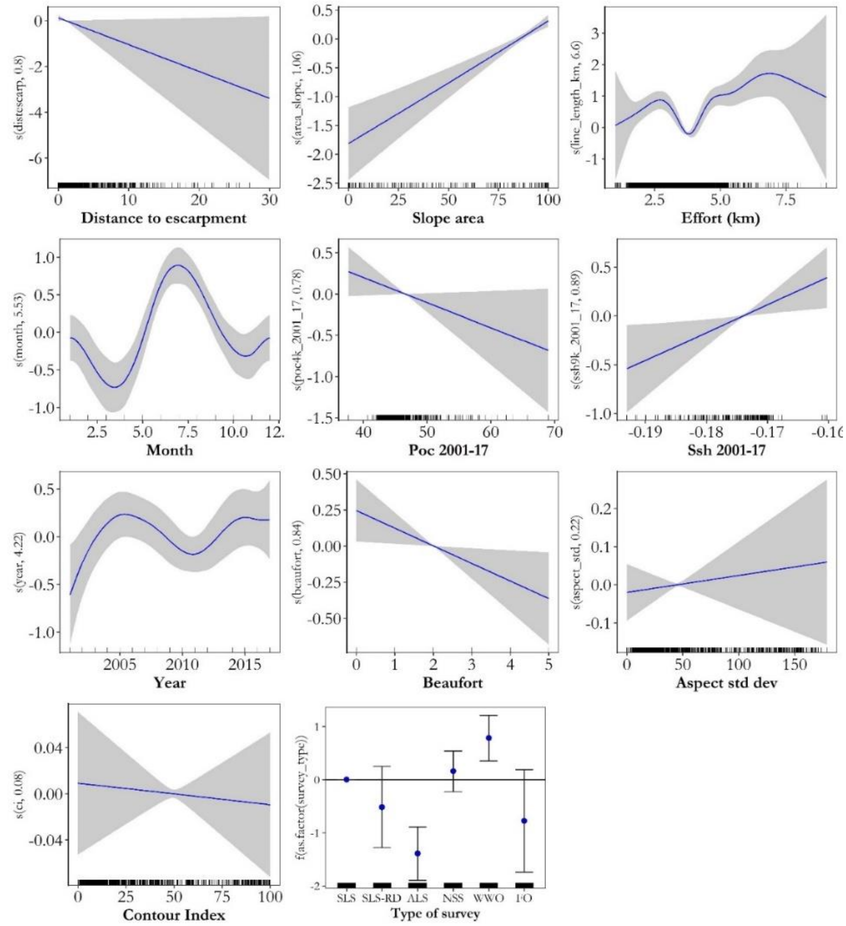


Figure 4.24. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Atlantic spoted dolphin groups (relative abundance) in the Madeira inshore waters for the period 2001 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – fisheries observers program.

The slope of the "Ssh 2001-17" smooth indicates a positive relationship between ER of groups and areas with higher sea surface height, indicative of a warmer water column.

As expected, the temporal covariate "Month" is present in the model reflecting the known seasonal presence of the species in these waters. However, "Year" was also selected suggesting a pattern of fluctuation in the ER of groups with a cycle of several years during the study period.

The spotted dolphin's predicted distribution in the study area is further offshore than the bottlenose dolphin. The prediction showed, on average, a preference of the species for the waters around Madeira Island, but also around Porto Santo and in the channel between these islands (Figure 4.25). The predicted ER of animals decreased in the southeast of the study area, around the neighbouring Desertas Islands, especially on the east side. These dolphins, mostly with a seasonal presence in the archipelago, seem to prefer slope habitats around the islands with clear waters, although to a less extent in slope areas in southeast part of the study area.

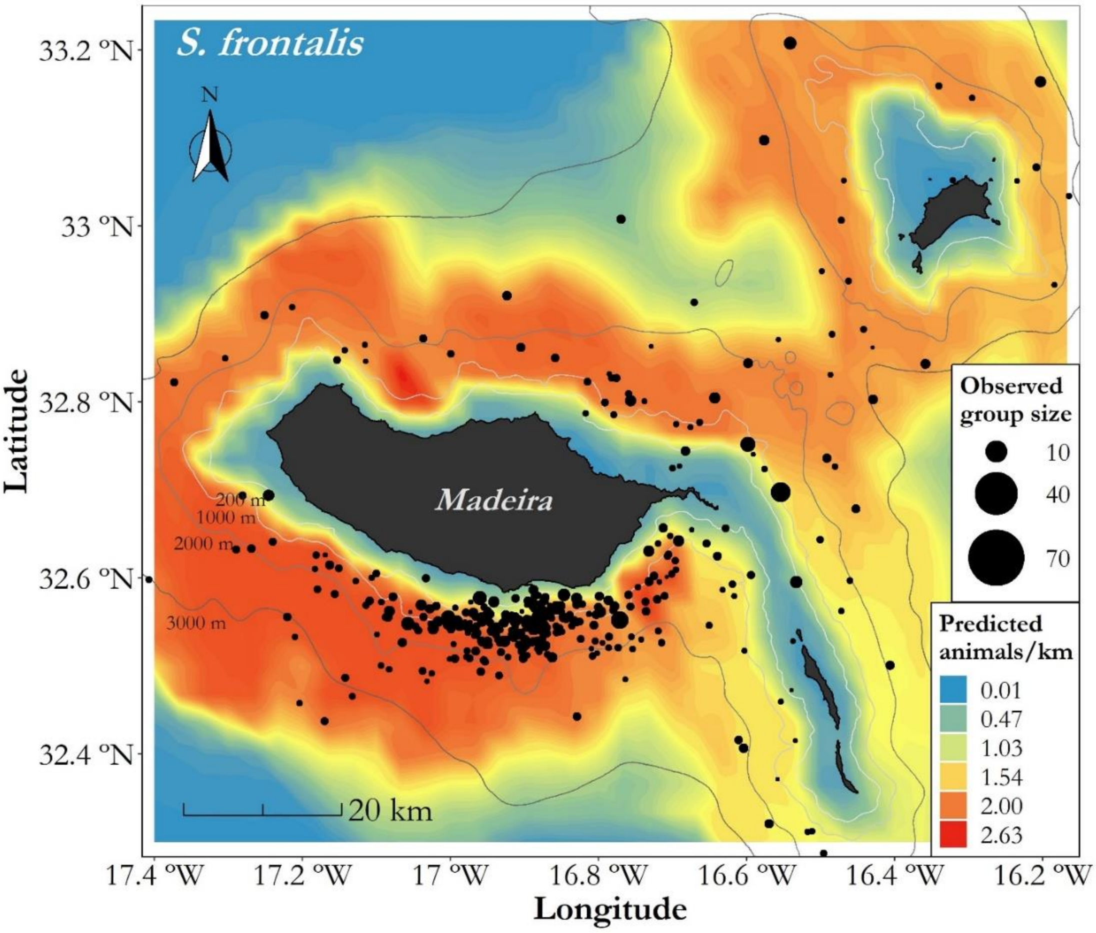


Figure 4.25. Predicted distribution of relative abundance (animals per km of transect line) of Atlantic spotted dolphins in the Madeira inshore waters for the period 2001 – 2017, as a result of the combination of predicted relative abundance of groups and observed mean group size.

Delphinus delphis

The habitat use of the common dolphin was investigated by modelling the relative abundance of groups and group size separately. As for the previous species, no group size model fulfilled the model selection criteria (Section 4.2.5.5), thus the relative abundance of individuals was obtained by multiplying the modelled ER of groups by the observed mean group size in the study area for 2001 – 1017.

Unlike the previous dolphin species, the habitat use by this species seems to be driven primarily by dynamic covariates such as "Chl-a 2001-17" and "Sst-a 2001-17", followed by the physiographic covariates "Average slope (%)" and "Slope area" (Figure 4.26). All these covariates were significant and had a positive relationship with the response variable.

The common dolphin is also known as a seasonal species in Madeira waters. The species final model for the period 2001-2017 reflects that strong seasonality by incorporating the covariate "Month", which is the one with strongest effect on the response (Figure 4.26).

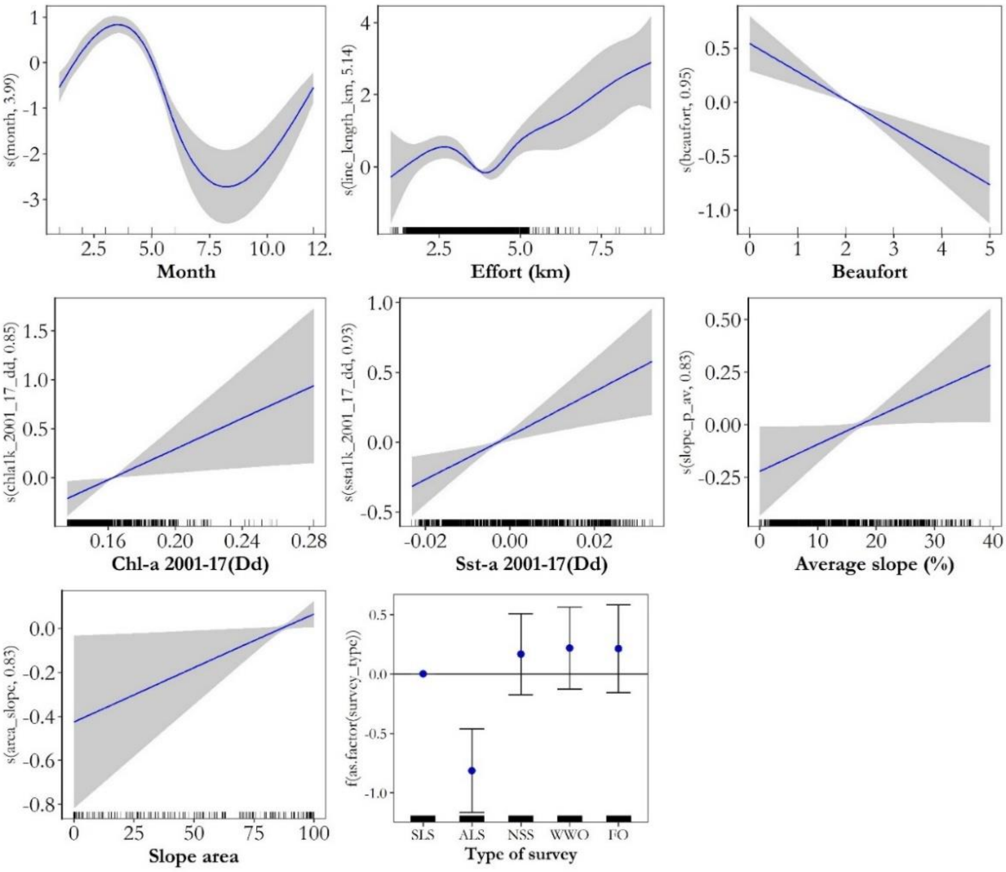


Figure 4.26. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of common dolphin groups (relative abundance) in the Madeira inshore waters for the period 2001 – 2017. SLS – shipboard line-transect surveys; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – fisheries observers program.

The common dolphin's distribution predicted by the model shows a preference of the species for the eastern side of the islands, namely, southeast of Madeira and Porto Santo, east of Madeira and Desertas Islands and northeast of Porto Santo Island (Figure 4.27) and also northwest of Madeira, balanced by a lower ER of groups southwest of that island. The model's prediction of distribution and the observations also suggests a wider and more dispersed presence of common dolphin in the study area when compared with the spotted and bottlenose dolphins. The common dolphins appear to prefer the habitats with steeper slopes in areas with higher concentration of chlorophyll-a. In Figure 4.27 and in prediction maps of other species (below) there is an apparent mismatch between the areas with higher concentration of observations and the areas where higher relative abundance is predicted. Despite the higher concentration of observations south of Madeira, the predicted relative abundance is lower than other areas with fewer sightings because there is much more search effort in that area (Figure 4.12).

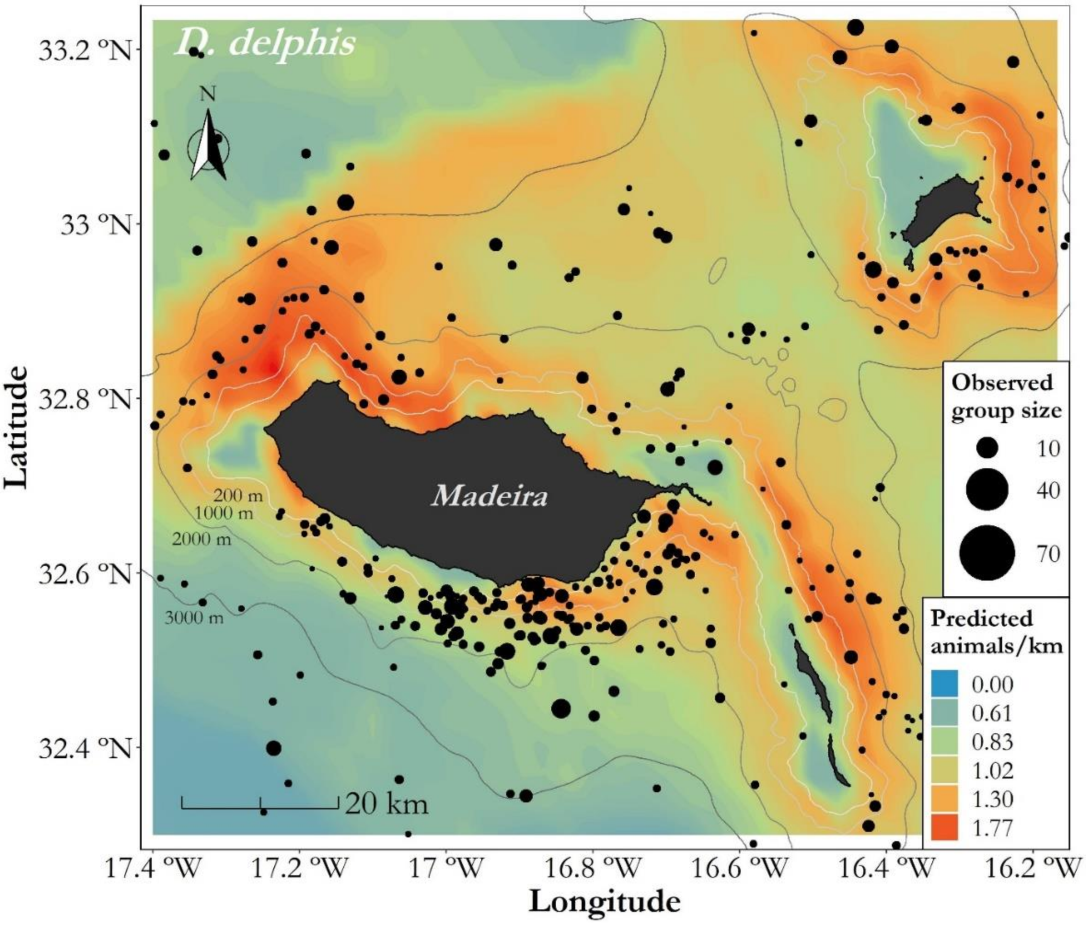


Figure 4.27. Predicted distribution of relative abundance (animals per km of transect line) of common dolphins in the Madeira inshore waters for the period 2001 – 2017, as a result of the combination of predicted relative abundance of groups and observed mean group size.

Stenella coeruleoalba

The habitat use of the striped dolphin was explored by modelling the relative abundance of groups and group size separately. However, no group size model fulfilled the model selection criteria (Section 4.2.5.5), thus the relative abundance of individuals was obtained by multiplying the predicted ER of groups by the observed mean group size in the study area for 2001 – 1017.

The percentage deviance explained by the group model was 12.50 %. The covariate with the strongest effect on the response variable were "Chl-a 2001-17" and "Average depth". These variables linear smooth with a negative relationship with the response indicate a preference of the species for deeper waters with lower concentration of chlorophyll-a. Water temperature may also be influencing, directly or indirectly, the species local distribution, as expressed by the covariate "Sst 2001-17" that shows a preference of the species for colder waters.

Although without a clearly marked seasonal presence in the archipelago as the common dolphin and spotted dolphin, the smooth of the covariate "Month" indicates a weak increase in the presence of striped dolphin in late winter and early spring, when compared with the rest of the year (Figure 4.28).

The predicted habitat use of the striped dolphin in the study area suggests a preference for waters that are further offshore than the previous dolphin species and a much lower presence or even absence in the shallower waters around the islands (Figure 4.29). Overall, the striped dolphin seems to have a preference in the study area for offshore habitats with colder waters, being less present in shallow depth areas close to the islands.

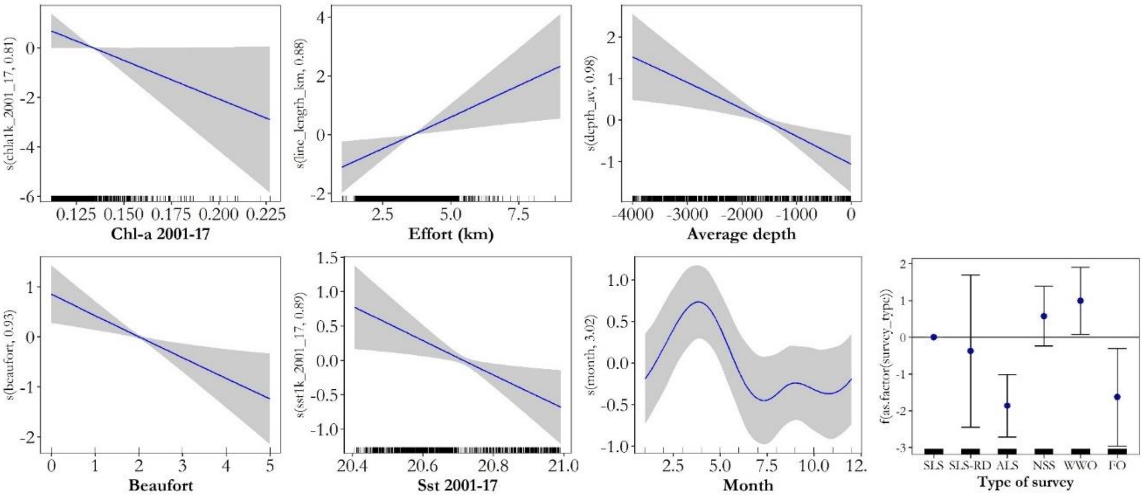


Figure 4.28. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of striped dolphin groups (relative abundance) in the Madeira inshore waters for the period 2001 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – Whale-watching observers program; and FO – Fisheries observers program.

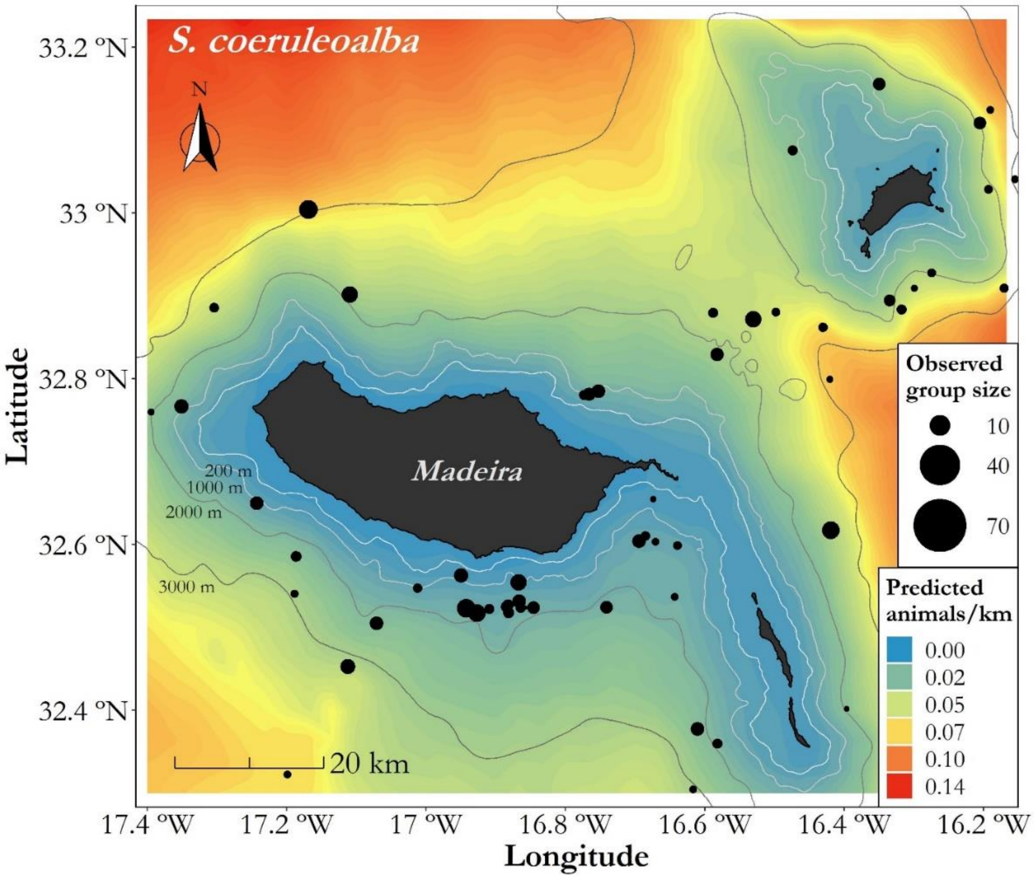


Figure 4.29. Predicted distribution of relative abundance (animals per km of transect line) of striped dolphins in the Madeira inshore waters for the period 2001 – 2017, as a result of the combination of predicted relative abundance of groups and observed mean group size.

4.3.4.2 Deep divers

The habitat use models selected for the pilot whale, the sperm whale, the *Mesoplodon sp.* and Ziphiidae are presented in Table 4.6, and the respective observed and predicted relative abundance in Table 4.7.

The covariate "Month" was selected for the pilot whale and Ziphiidae, reflecting a seasonal trend in these taxa relative abundance (Table 4.6 and Figure 4.36). Although the *Mesoplodon sp.* show a similar seasonal trend in ER of groups to Ziphiidae and the covariate "Month" was among those selected, it was not included in the model with lowest AIC (selected) due to the low number of observations (32), to avoid having an overfitted model. The same reason justifies why neither Effort nor Beaufort were selected in the beaked whales' final models.

Table 4.6 – Summary table of the selected habitat use models of relative abundance of groups and models of group size (if applicable) of short-finned pilot whale, sperm whale, *Mesoplodon sp.* and Ziphiidae family, and respective main model parameters; * - significant relationship between covariate and response ($p<0.05$).

Species	Nº of segments	Nº of observ.	Response variable	model selected	% Dev. Explained	edf model	Nº models
Globicephala macrorhynchus	15493	236	Groups	factor(Type of survey) + s(Distance to 1500m isobath)* + s(Maximum aspect)* + s(Mld 2001-17)* + s(Poc 2001-17)* + s(Contour index)* + s(Month)* + s(Year)* + s(Beaufort)* + s(Effort)*	31.70%	27.3	64
	-	236	Group size	factor(Type of survey) + s(Chla-a 2001-17)* + s(Poc 2001-17)* + s(Distance to 2000 isobath)* + s(Sst 2001-17)* + s(Maximum slope) + s(Month)*	21.10%	12.5	> 100
Physeter macrocephalus	15493	85	Groups	factor(Type of survey) + s(Slope area)* + s(Average aspect)* + s(Sst 2001-17)* + s(Effort)*	13.66%	14.8	20
Mesoplodon sp.	15493	32	Groups	factor(Type of survey) + s(Aspect std dev)* + s(Mld 2001-17)* + s(Year)* + offset(log(Effort))	9.99%	10.6	11
Ziphiidae	15493	67	Groups	factor(Type of survey) + s(Aspect std dev)* + s(Mld 2001-17)* + s(Month)* + s(Year)* + offset(log(Effort))	10.55%	11.0	6

Table 4.7 – Summary table of the observed and predicted encounter rates (ER) of groups and individuals per kilometre, as well as observed and predicted (when applicable) group size, of short-finned pilot whale, sperm whale, *Mesoplodon sp.* and Ziphiidae family. The observed ER of individuals =observed ER group * observed mean group size; predicted ER of individuals = predicted ER of groups * predicted group size (observed mean group size whenever a group size model was not selected). The CV was calculated from the models' variance estimated by posterior simulation.

Species	Nº of observ.	ER groups		Group size		ER individuals		
		Observed	Predicted	Observed	Predicted	Observed	Predicted	CV
Globicephala macrorhynchus	236	0.0042	0.00025	14.75	12.57	0.062	0.004	2.83
Physeter macrocephalus	85	0.0015	0.00187	3.02	-	0.005	0.006	1.47
Mesoplodon sp.	32	0.00057	0.0015	3.06	-	0.0017	0.005	0.40
Ziphiidae	67	0.00119	0.0055	2.37	-	0.0028	0.013	0.25

Globicephala macrorhynchus

The habitat use of the pilot whale was investigated by modelling the relative abundance of groups and group size separately. Unlike other species, a group size model of pilot whales was selected. The group relative abundance and group size models accounted for 31.70 % and 21.10% of the deviance in the data, respectively (Table 4.6). The relative abundance of individuals was obtained as the product of the predicted relative abundance of groups and the predicted group size for the period 2001 – 2017.

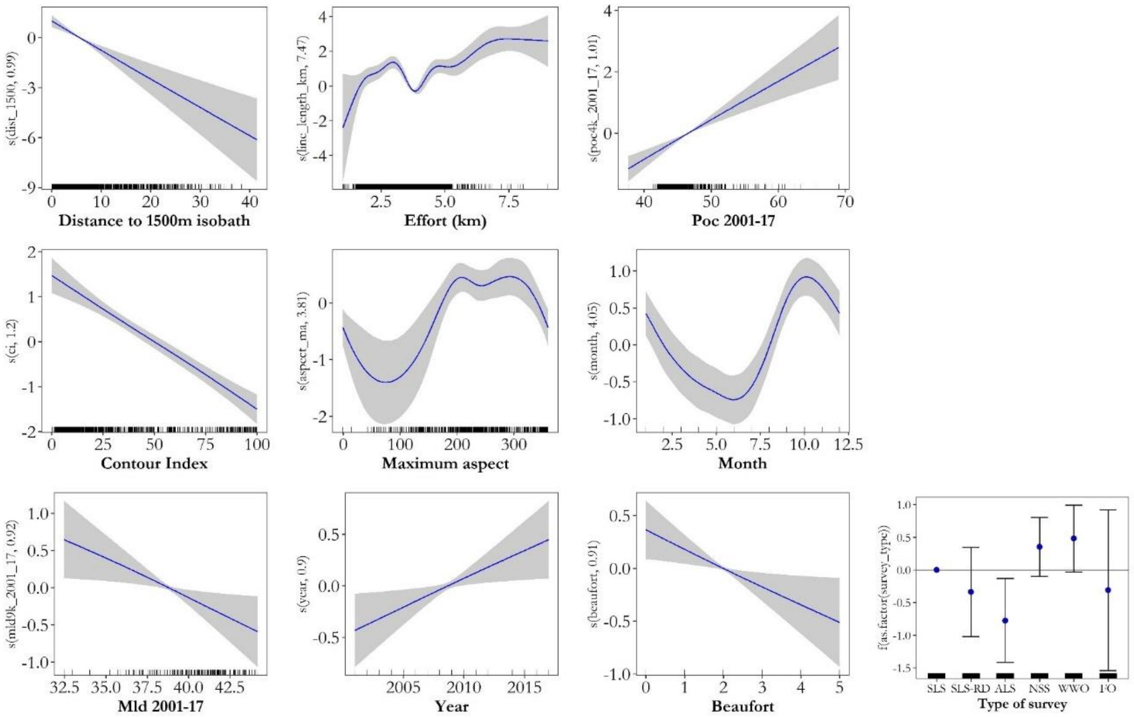


Figure 4.30. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of short-finned pilot whale groups (relative abundance) in the Madeira inshore waters for the period 2001 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – fisheries observers program.

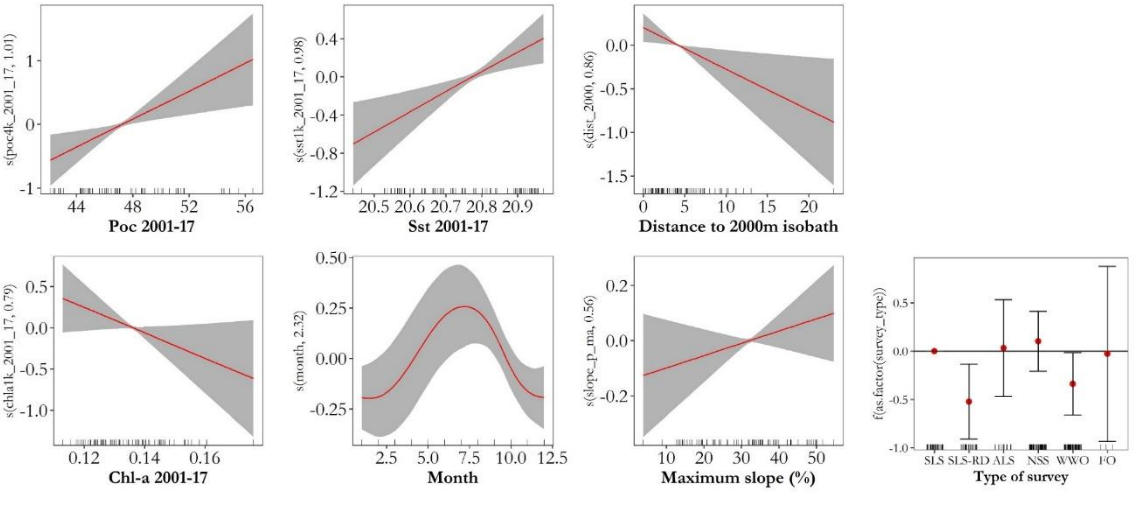


Figure 4.31. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explain the distribution of short-finned pilot whale group size in the Madeira inshore waters for the period 2001 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – fisheries observers program.

Pilot whale groups had a preference for waters with depths around 1 500 m, as indicated by the strong effect of the covariate "Distance to 1500m isobath" on the response (Figure 4.30). Other environmental covariates with a strong effect were "Poc 2001-17", "Contour index" and "Maximum aspect", suggesting a preference for waters richer in organic matter and on average flatter than the surrounding sea floor areas. The covariate "Maximum aspect" may not have an ecological meaning but is indicative of the sea floor orientation of the area where this species is mostly concentrated in the study area, the bay southeast of Madeira (Figure 4.32). The covariate "Mld 2001-17" had a significant negative relationship with the response, indicating a preference of the pilot whales for waters where the mixed layer depth shallower than the surrounding waters. The smooth of the covariate "Year" indicates an increase in the relative abundance of groups during the study period (Figure 4.30).

Figure 4.31 shows the smooths of the covariates selected in the group size model. The dynamic covariates "Poc 2001-17" and "Sst 2001-17" had the strongest effect over the response followed by "Distance to 2000m isobath", unlike the model of relative abundance of groups, in which the depth related covariate had the strongest effect. This suggests that local environmental conditions may influence the dynamics of group size or the distribution of groups, with larger groups preferring warmer waters with more particulate organic matter.

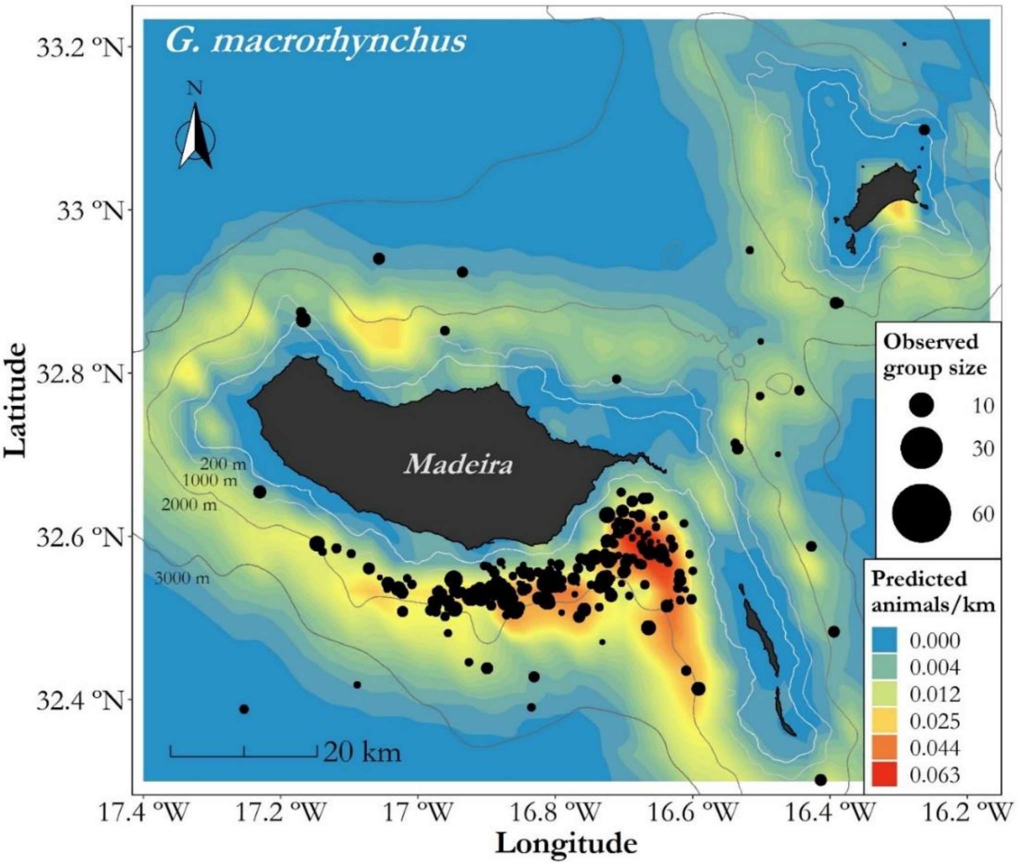


Figure 4.32. Predicted distribution of relative abundance (animals per km of transect line) of short-finned pilot whales in the Madeira inshore waters for the period 2001 – 2017, as a result of the combination of predicted relative abundance of groups and predicted group size.

Larger groups also seem to prefer deeper (further offshore) waters in relation to the average group, as suggested by the "Distance to 2000m isobath" covariate. The seasonal fluctuations in the relative abundance of groups and group size is accommodated through the covariate "Month" in both models.

The map of predicted distribution (Figure 4.32) indicates the pilot whale's preference for the waters 1 000 – 2 000 m deep around the islands, but concentrated in the southeast of Madeira, between this island and Desertas, with a decrease in ER of individuals towards the southwest of Madeira and southwards along the west coast of Desertas.

Physeter macrocephalus

The habitat use of the sperm whale was explored by modelling the relative abundance of groups and group size separately. However, no group size model fulfilled the model selection criteria (Section 4.2.5.5), thus the relative abundance of individuals was obtained by multiplying the predicted ER of groups by the observed mean group size in the study area for 2001 – 1017.

The selected model of groups explained 13.66 % of the deviance in the data (Table 4.6). The covariate "Slope area" has a positive smooth with a very strong effect on the response (Figure 4.33). The covariate "Average aspect" probably does not have a direct ecological meaning but indicates the sea floor orientation of the areas where this species was mostly found, the northern facing sides of the islands. There is a positive relationship between relative abundance of groups and "Sst 2001-17", reflecting a preference for warmer waters.

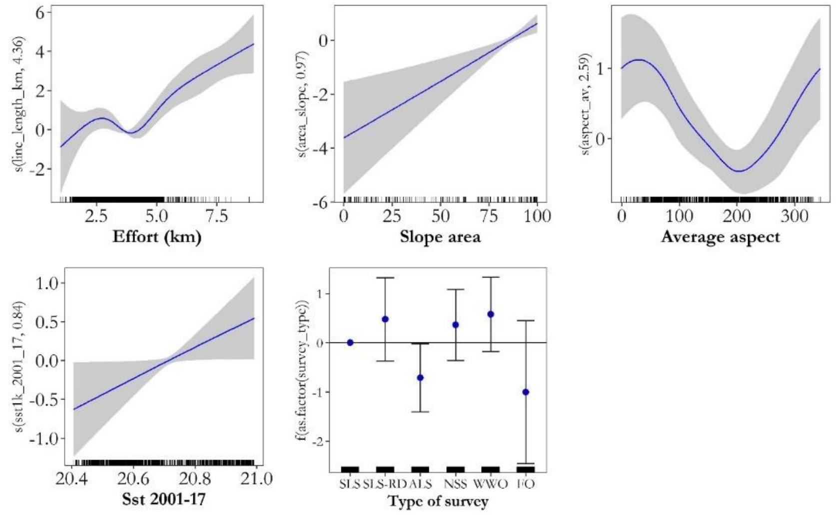


Figure 4.33. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of sperm whale groups (relative abundance) in the Madeira inshore waters for the period 2001 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – fisheries observers program.

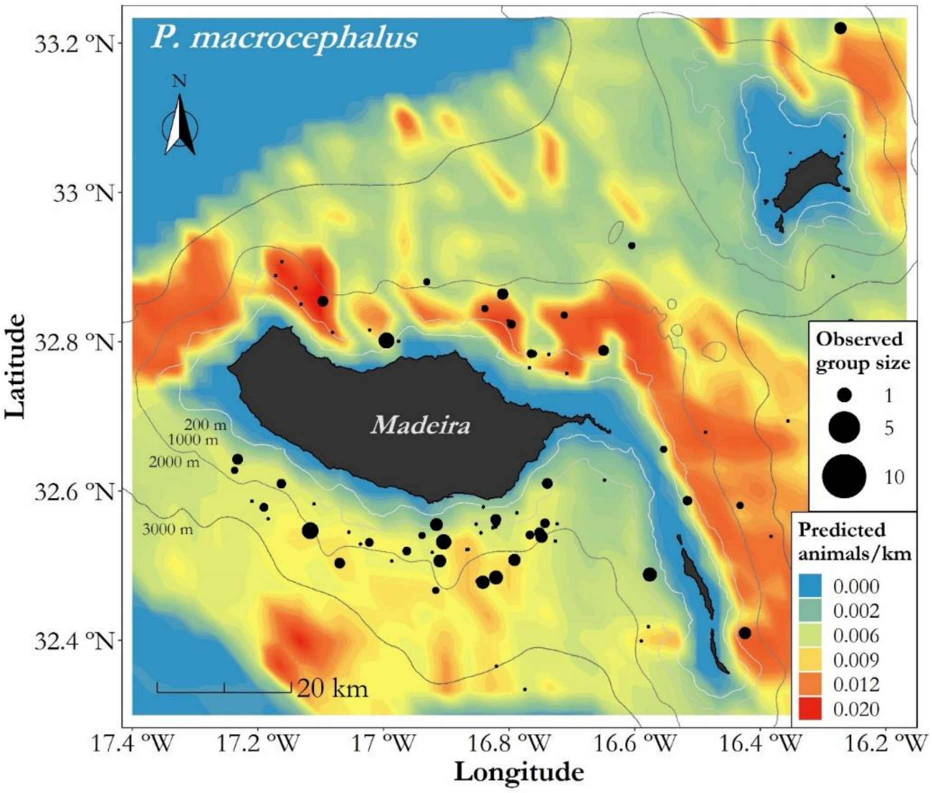


Figure 4.34. Predicted distribution of relative abundance (animals per km of transect line) of sperm whales in the Madeira inshore waters for the period 2001 – 2017, as a result of the combination of predicted relative abundance of groups and observed mean group size.

The predicted distribution of sperm whales in the study area is shown in Figure 4.34. These animals are predicted to be concentrated in the slope areas off the northern side of the islands, although their presence is also predicted and observed in the southern parts. The model predicted the species absence from the shallow waters over the insular shelf. The model also predicted a drop in the species relative abundance of individuals further away from shore, i.e. in the transition between the slopes of the islands and the abyssal plain, and beyond, in the waters over the abyssal plain.

Beaked whales

The habitat use of *Mesoplodon sp.* and *Ziphiidae* was investigated by modelling the relative abundance of groups and group size separately. However, no group size model fulfilled the model selection criteria (Section 4.2.5.5), thus the relative abundance of individuals was obtained by multiplying the predicted ER of groups by the observed mean group size in the study area for 2001 – 1017.

Models of habitat use were selected for both *Mesoplodon sp.* and for all beaked whales combined (Ziphiidae), which included sightings of *Mesoplodon sp., Z. cavirostris* and of animals only identified at sea as beaked whales. The selected models of relative abundance of groups of both *Mesoplodon sp.* and Ziphiidae explained very similar percentages of deviance in the data, 9.99 % and 10.55 % respectively (Table 4.6). Similar covariates were selected in both models, possibly driven by the sightings of *Mesoplodon* used in both models (Table 4.6).

The environmental covariates “Mld 2001-17” and “Aspect std dev” were common to both models, with the first covariate having the strongest effect on the response in both cases (Figure 4.35 and Figure 4.36). The “Mld 2001-17” and “Aspect std dev” smooths, with a positive and negative relationship with the response, respectively, indicate an increase in relative abundance of groups in waters with deeper mixed layer depth and where the sea floor orientation is more constant.

The other selected covariates were “Year” and “Month”, the first included in both models and the second in the model of Ziphiidae (Figure 4.35 and Figure 4.36). The ER of groups increased during the survey period for both taxa. As suggested for the other covariates, it is possible that the relationship found between the response and the covariate “Year” may be driven, at least partially, by the *Mesoplodon* sightings. The covariate “Month” was selected in the model of Ziphiidae and suggests a seasonal pattern in the relative abundance of groups, with a maximum in summer and a minimum in winter.

The factor covariate plots (“Type of survey”) of both the *Mesoplodon* and the Ziphiidae models, have one level (SLS-RD) with very wide confidence limits because of very few sightings of these taxa recorded in that type of survey. Consequently, the plot’s y-axis scale is very wide, masking the differences among the other factor covariate levels. This representation issue also occurs in the factor covariate plot of other models below.

The smaller number of sightings of these taxa in the dataset, especially of *Mesoplodon*, did not limit the number of covariates selected in the final models, because most covariates were selected out previously during the shrinkage process and thus not considered in the final models, as the small number of final models run suggest (Table 4.6).

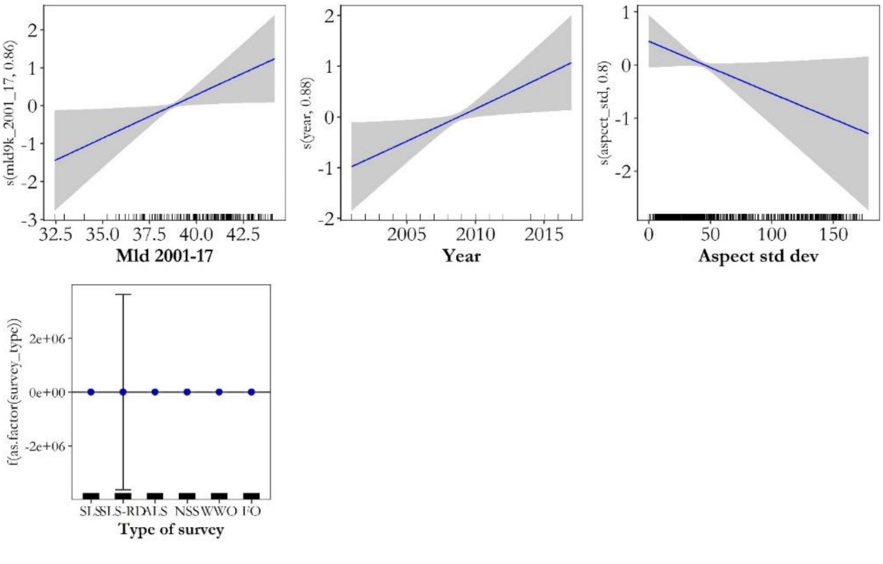


Figure 4.35. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of *Mesoplodon sp.* groups (relative abundance) in the Madeira inshore waters for the period 2001 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – fisheries observers program.

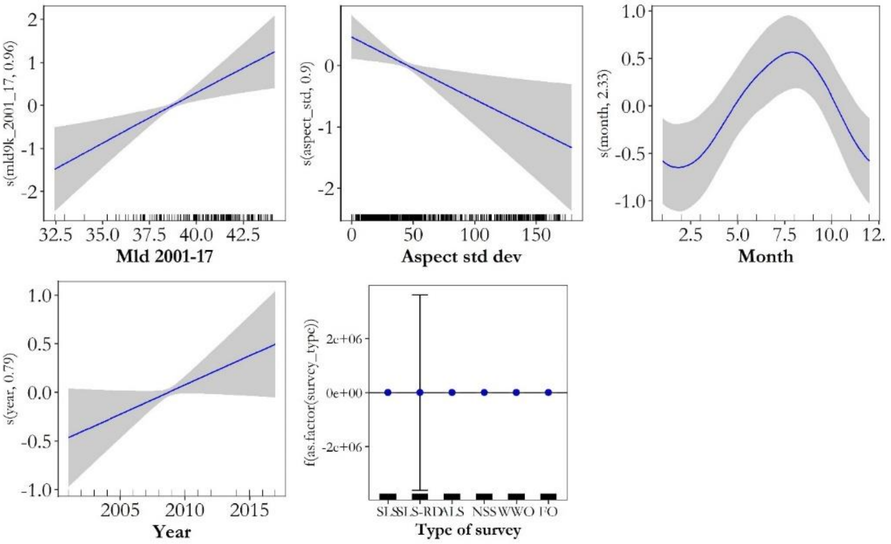


Figure 4.36. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Ziphiidae groups (relative abundance) in the Madeira inshore waters for the period 2001 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – fisheries observers program.

The plots of predicted distribution (Figure 4.37) suggest a preference of both taxa for offshore waters, especially around Porto Santo, east of Madeira and Desertas and southwest of Madeira Island. Although the predicted distribution seems reasonable for this taxon, the prediction does not reflect very well the distribution of the observed sightings.

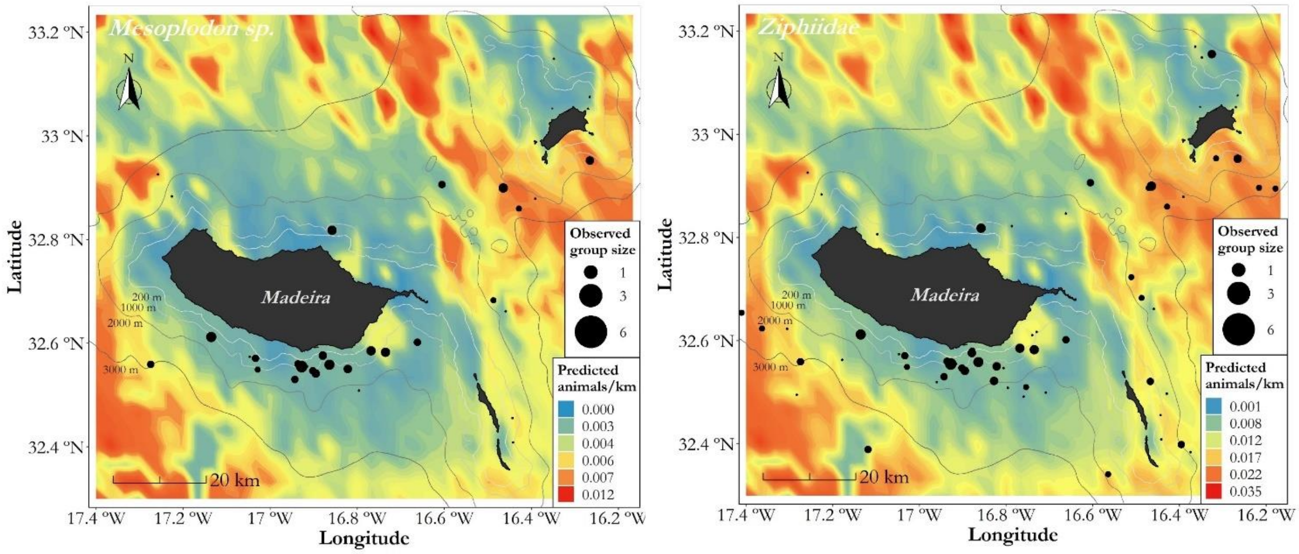


Figure 4.37. Predicted distribution of relative abundance (animals per km of transect line) of *Mesoplodon sp.* (left) and Ziphiidae (right) in the Madeira inshore waters for the period 2001 – 2017, as a result of the combination of predicted relative abundance of groups and observed mean group size. The relative abundance scales are specific to each predicted distribution map and not directly comparable among each other. The comparison among the predicted distribution maps should be qualitative, i.e., comparison of the pattern of distribution of higher and lower relative abundance areas within the study area.

4.3.4.3 *Baleen whales*

The habitat use of the fin whale and Bryde's whale was investigated by modelling the relative abundance of groups and group size separately for the former, and the relative abundance of individuals for the latter. However, no group size model fulfilled the model selection criteria (Section 4.2.5.5) for fin whale. Thus, the relative abundance of individuals was obtained for this species by multiplying the predicted ER of groups by the observed mean group size in the study area for 2001 – 1017, while for the Bryde's whales it obtained directly from the model.

Habitat use models were attempted for Bryde's whale, fin whale and all Balaenopteridae combined. Acceptable final models were obtained for the two species individually but not for all Balaenopteridae. The selected models are presented in Table 4.8, and the respective observed and predicted relative abundance in Table 4.9.

Although Bryde's whale has a strong seasonal presence in the study area, the covariate "Month" was not selected because the data used in the analysis was a subset that excluded the months the animals were absent or had a very low monthly ER, as explained in Section 4.2.5.3. In the case of the fin whale, "Month" was incorporated in the model, reflecting the preferential time they pass by Madeira (Table 4.8 and Figure 4.40).

Table 4.8 – Summary table of the selected habitat use models of relative abundance of groups/individuals of Bryde's and fin whales, and respective main model parameters; * - significant relationship between covariate and response (p<0.05).

Species	Nº of segments	Nº of observ.	Response variable	model selected	% Dev. Explained	edf model	Nº models
Balaenoptera edeni	9801	122	Individuals	factor(Type of survey) + s(Escarpment area)* + s(Maximum depth)* + s(Distance to escarpment)* + s(Year)* + s(Effort)*	31.20%	21.0	22
Balaenoptera physalus	15493	28	Groups	factor(Type of survey) +s(Distance to 2000 isobath)* + s(Month)* + offset(log(Effort))	29.82%	10.7	26

Table 4.9 – Summary table of the observed and predicted (when applicable) encounter rates (ER) of groups and individuals per kilometre, as well as observed mean group size, of Bryde's and fin whales. The observed ER of individuals =observed ER group * observed mean group size; predicted ER of individuals = predicted ER of groups * observed mean group size (fin whales) or obtained from the model (Bryde's whale). The CV was calculated from the models' variance estimated by posterior simulation.

Species	Nº of observ.	ER groups		Group size		ER individuals		
		Observed	Predicted	Observed	Predicted	Observed	Predicted	CV
Balaenoptera edeni	122	0.0029	-	1.72	-	0.0050	0.0020	1.71
Balaenoptera physalus	28	0.00050	0.00017	2.14	-	0.0011	0.0004	0.76

Effort was also among the covariates selected in the model of Bryde's whale but not "Beaufort", probably because of the high detectability of the species in different weather conditions (highly visible spout) and to the species presence in the archipelago when weather conditions are on average better (late spring to early autumn). Neither covariate was selected in the fin whale model, primarily because of the low number of observations (28).

Balaenoptera edeni

The environmental covariate with the strongest effect on the ER of individuals was "Distance to escarpment", followed by "Escarpment area" (Figure 4.38). These covariates' smooth shape, indicate an increase in relative abundance of individuals as distance to the islands' escarpment decreases and, in apparent contradiction, an increasing preference for waters where the percentage of sea floor is not classified as escarpment. The other covariate selected was "Maximum depth" and the relationship with the response indicates a preference of these animals for shallower waters in the study area. The model explained 31.20 % of the deviance in the data (Table 4.8).

The covariate "Year" also had a strong effect on the response. The shape of the covariate's smooth indicates cyclic changes in the ER of individuals, with peaks in 2006 and 2014, suggesting a periodicity of eight years in these relative abundance changes (Figure 4.38).

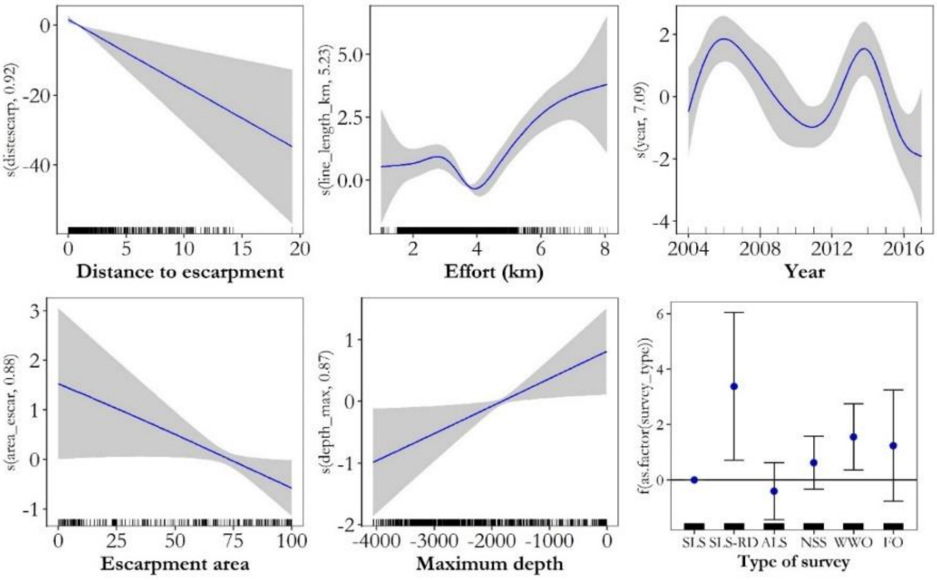


Figure 4.38. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Bryde's whales (relative abundance) in the Madeira inshore waters for the period 2001 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – fisheries observers program.

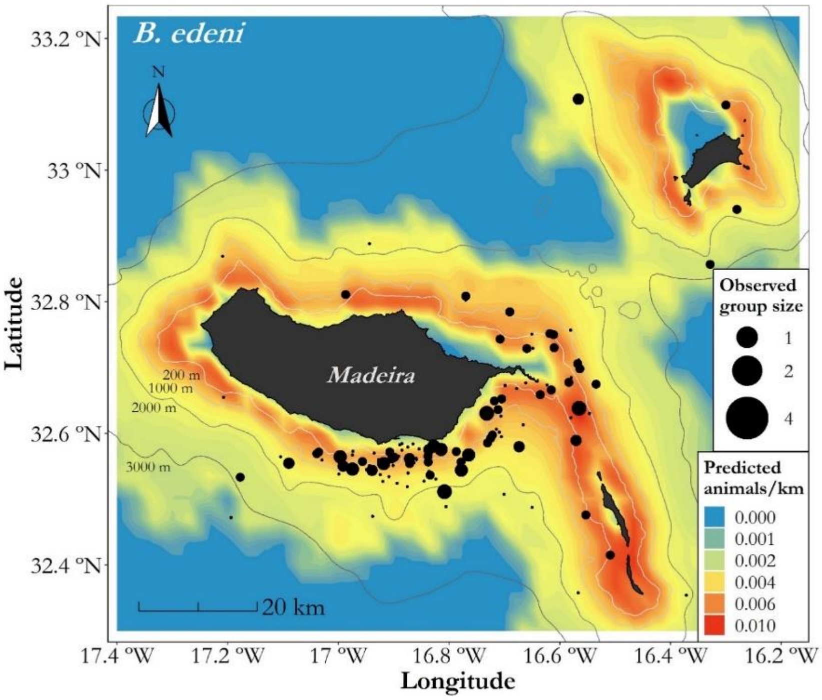


Figure 4.39. Predicted distribution of relative abundance (animals per km of transect line) of Bryde's whales in the Madeira inshore waters for the period 2004 – 2017.

These results suggest that Bryde's whales have a preference for shallower waters close to the islands' escarpment, mostly in the transition to insular shelf waters and over it, as suggested by the covariates and expressed in the predicted distribution (Figure 4.39).

Balaenoptera physalus

There is a strong relationship between the fin whale's occurrence in the Madeira archipelago inshore waters and bathymetry as expressed by the covariate "Distance to 2000m isobath" (Figure 4.40). The low number of observations of fin whales limited the number of covariates selected. Nevertheless, the selected model explained 29.82 % of the deviance in the data (Table 4.8), with a single environmental covariate. The other relevant covariate is "Month" which reflects the seasonal presence of the species in the archipelago, with a clear peak at the end of winter (March).

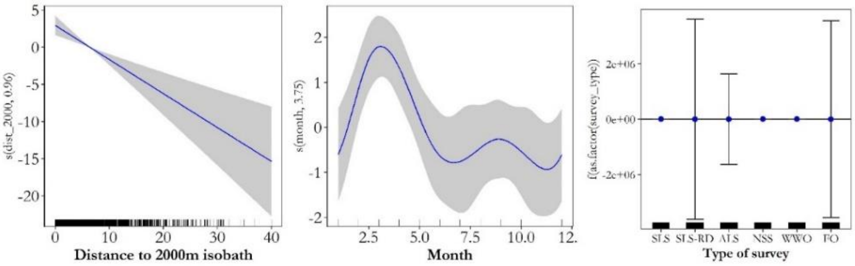


Figure 4.40. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of fin whales (relative abundance) in the Madeira inshore waters for the period 2001 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – fisheries observers program.

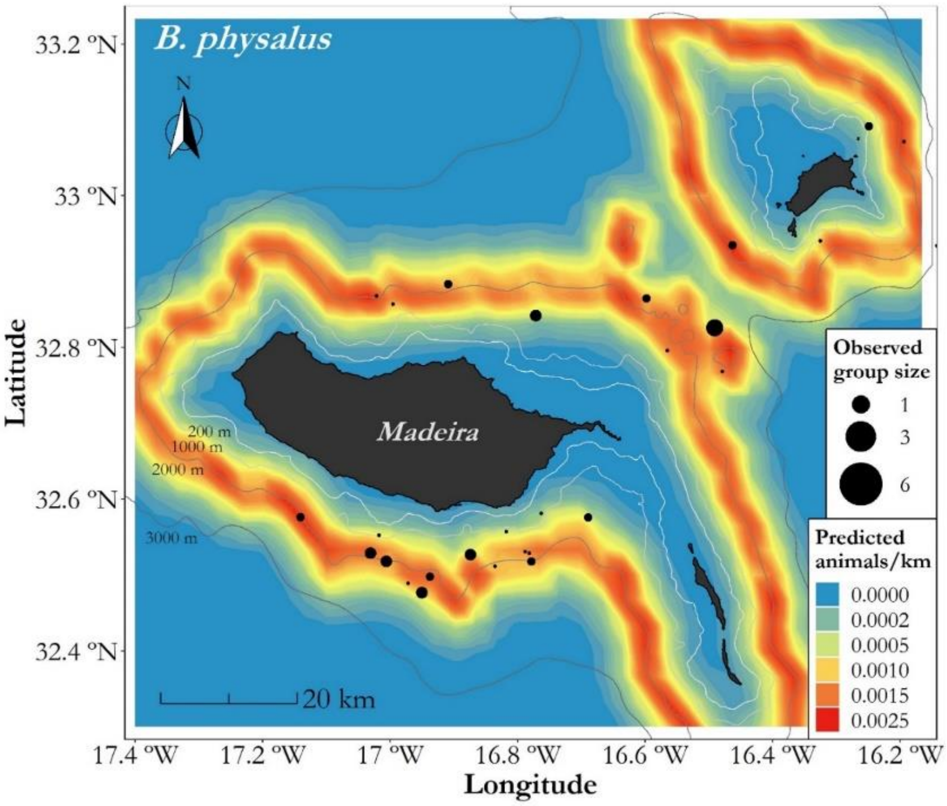


Figure 4.41. Predicted distribution of relative abundance (animals per km of transect line) of Bryde's whales in the Madeira inshore waters for the period 2001 – 2017, as a result of the combination of predicted relative abundance of groups and observed mean group size.

Overall, the fin whale has further offshore distribution than the Bryde's whale, primarily associated with the 2 000 m water depth (Figure 4.41). Its present in Madeira inshore waters seasonally, mostly in winter, when the Bryde's whale is usually absent from the archipelago.

4.3.5 Modelling the seasonal use of the habitat and predicting its distribution of relative abundance

Habitat use modelling by season (winter, spring, summer and autumn) was attempted for species or families which had a sufficient number of observations per season. This resulted in the exclusion of the striped dolphin, sperm whale, fin whale *Mesoplodon sp.* and Ziphiidae from the analysis. The habitat use modelling analysis covered the period 2001 – 2017 for all taxa, except Bryde's whale that covered the period 2004 – 2017 (Section 4.2.5.3).

The results of the habitat use modelling by season are also presented by groups of species (oceanic dolphins, deep divers and baleen whales), following the same rationale for the organization and presentation of data (tables, prediction maps and smooth plots) of Section 4.3.4. In Appendix V.2 are given the tables with the parametric and smooth terms values, diagnostic plots and uncertainty plots of the selected models. For all taxa, except Bryde's whales, the relative abundance of groups was modelled rather than the relative abundance of individuals, and no group size models fulfilled the model selection criteria (Section 4.2.5.5) for the species analysed. The calculation of the predicted ER of individuals and corresponding CV for each species model, given in the summary tables, is explained in Section 4.3.4.

The covariates "Effort", "Month", "Year" and "Beaufort" were considered in the modelling exercise for all species.

4.3.5.1 Oceanic dolphins

Tursiops truncatus

The selected models of habitat use by season for the bottlenose dolphin are presented in Table 4.10, and the respective observed and predicted relative abundance in Table 4.11.

The physiographic explanatory variables "Distance to slope" and "Maximum depth" showed the strongest effect on the response in autumn and winter, respectively, while the dynamic explanatory variables "Primary Productivity" and "Sst-a 2001-17 Summer" had the strongest effect on the response in spring and summer, respectively. However, in these seasons the physiographic covariates "Distance to 2500m isobath" and "Distance to 500m isobath" had also a strong effect on the response. Dynamic covariates were only selected in the spring and summer models, with mixed layer depth being selected in both. The final models explained from 15.66 % to 25.17 % of the deviance in the data (Table 4.10).

Table 4.10 – Summary table of the selected habitat use models of relative abundance of groups of bottlenose dolphin by season, and respective main model parameters; * - significant relationship between covariate and response (p<0.05).

Species	Season	Nº of segment	Nº of observ.	Response variable	model selected	edf model	% Dev. Explained	AIC	Nº models
Tursiops truncatus	*Winter*	2993	54	Groups	factor(Type of survey) + s(Maximum depth)* + s(Distance to slope)* + s(Year)* + s(Effort)*	15.5	24.08%	2996.43	4
	Spring	4764	115	Groups	factor(Type of survey) + s(Pp 2001-17 Spring)* + s(Maximum slope)* + s(Distance to 2500m isobath)* + s(Mld 2001-17 Spring)* + s(Year)* + s(Effort)*	16.7	23.20%	4711.85	53
	Summer	4626	144	Groups	factor(Type of survey) +s(Distance to 500m isobath)* + s(Mld 2001-17 Summer)* + s(Sst-a 2001-17 Summer)* + s(Beaufort)* + s(Month)* + s(Year) + s(Effort)*	19.1	25.17%	4586.22	24
	Autumn	3110	82	Groups	factor(Type of survey) + s(Maximum depth)* + s(Beaufort)* + s(Effort)*	12.4	15.66%	3075.91	6

Table 4.11 – Summary table of the observed and predicted encounter rates (ER) of groups and individuals per kilometre, as well as observed mean group size, of bottlenose dolphin by season. The observed ER of individuals = observed ER group * observed mean group size; predicted ER of individuals = predicted ER of groups * observed mean group size (no final group size models were selected). The CV was calculated from the models' variance estimated by posterior simulation.

Species	Season	N° of observ.	ER groups		Group size		ER individuals		
			Observed	Predicted	Observed	Predicted	Observed	Predicted	CV
Tursiops truncatus	*Winter*	54	0.0050	0.0041	14.09	-	0.070	0.058	3.679
	Spring	115	0.0067	0.0460	13.05	-	0.088	0.600	1.318
	Summer	144	0.0086	0.0020	18.86	-	0.162	0.038	2.257
	Autumn	82	0.0073	0.0220	16.00	-	0.117	0.353	0.916

The environmental covariates selected in the winter model were "Distance to slope" and "Maximum depth", with the first covariate showing a negative linear relationship and very strong effect on the response (Figure 4.42). The covariate "Year" was also selected in the final model with a smooth curve describing a positive increase in relative abundance of groups in winter between 2002 and 2008, followed by a plateau until 2012 and then a steep decrease until 2016.

In the spring model, the dynamic covariates were more important with primary productivity ("Pp 2001-17, Spring") having the greatest effect on the response, followed by "Distance to 2500m isobath", "Mld 2001-17, Spring" and "Maximum slope" (Figure 4.43). The shape of the smooths indicates the use of areas with intermediate primary productivity by bottlenose dolphin, away from deep waters (2500m isobath), over steeper slopes and where the mixed layer depth is shallower. The model also predicted an increase in relative abundance of groups in spring during the study period.

The explanatory variable with the strongest effect on the response in the summer model was "Sst-a 2001-17, Summer" followed by "Distance to 500m isobath", suggesting use by the bottlenose dolphin of relatively shallow areas with colder waters than average over the islands' slope (Figure 4.44). An increase in relative abundance of groups over the summer was indicated by the selection of the covariate "Month", with a positive slope smooth.

In Autumn, "Maximum depth" was the only environmental variable selected, with a moderate effect on the response (Figure 4.45). The smooth curve of this covariate suggests a use by bottlenose dolphins of waters between 1 000 m and 2 000 m depth.

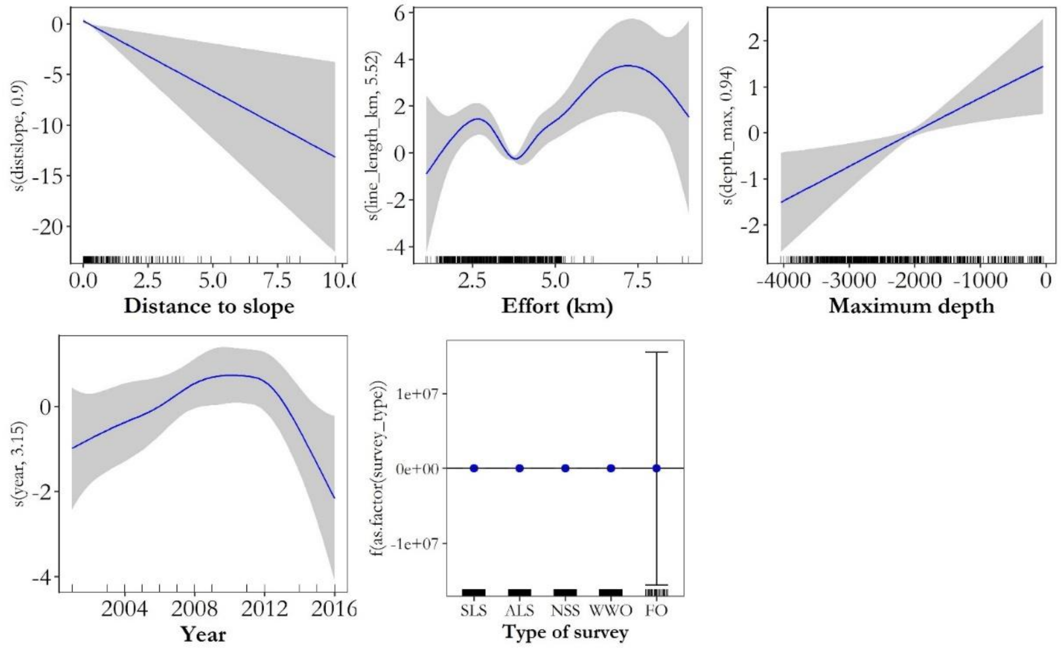


Figure 4.42. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of bottlenose dolphin groups (relative abundance) in the Madeira inshore waters in winter (January – March), for the period 2001 – 2017. SLS – shipboard line-transect surveys; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – fisheries observers program.

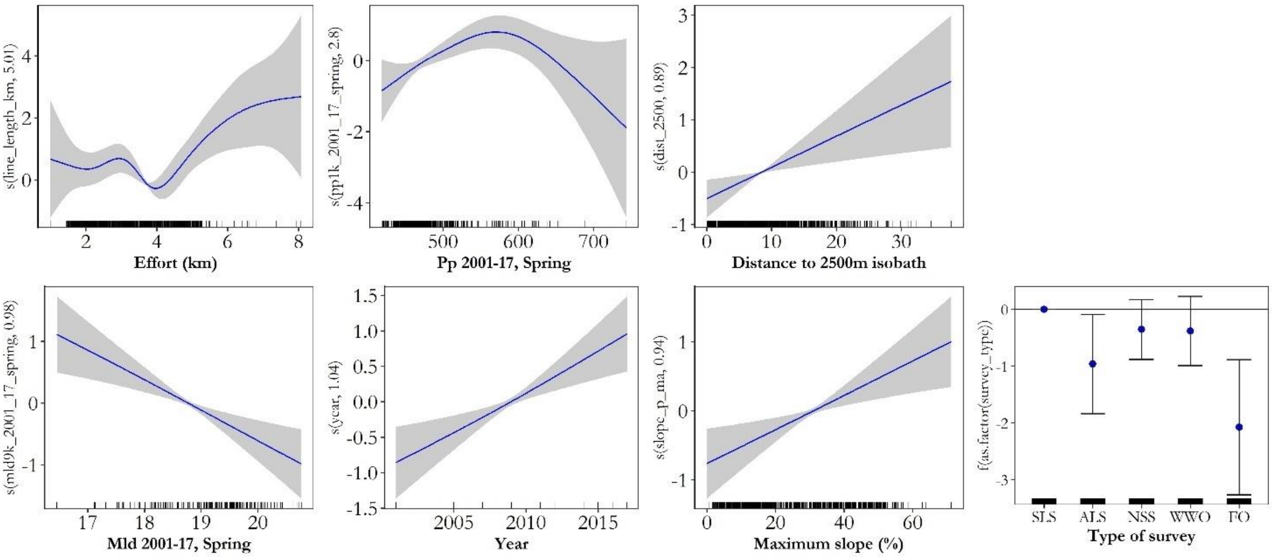


Figure 4.43. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of bottlenose dolphin groups (relative abundance) in the Madeira inshore waters in spring (April – June), for the period 2001 – 2017. SLS – shipboard line-transect surveys; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – fisheries observers program.

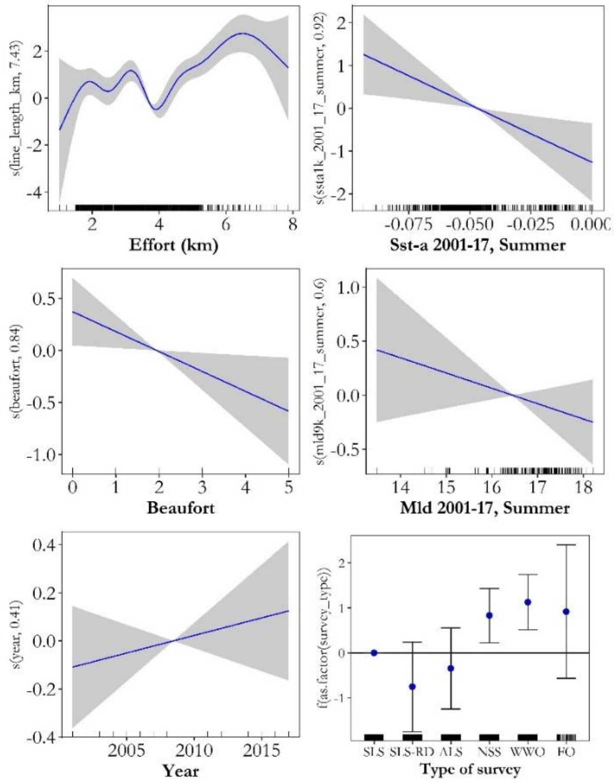


Figure 4.44. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of bottlenose dolphin groups (relative abundance) in the Madeira inshore waters in summer (July – September), for the period 2001 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – Fisheries observer program.

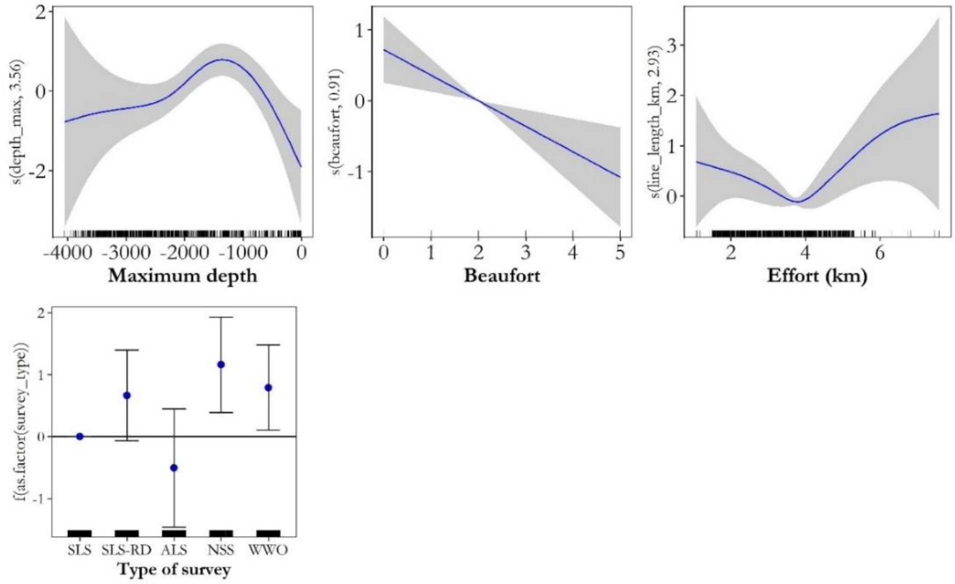


Figure 4.45. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of bottlenose dolphin groups (relative abundance) in the Madeira inshore waters in autumn (October – December), for the period 2001 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies and WWO – whale-watching observers program.

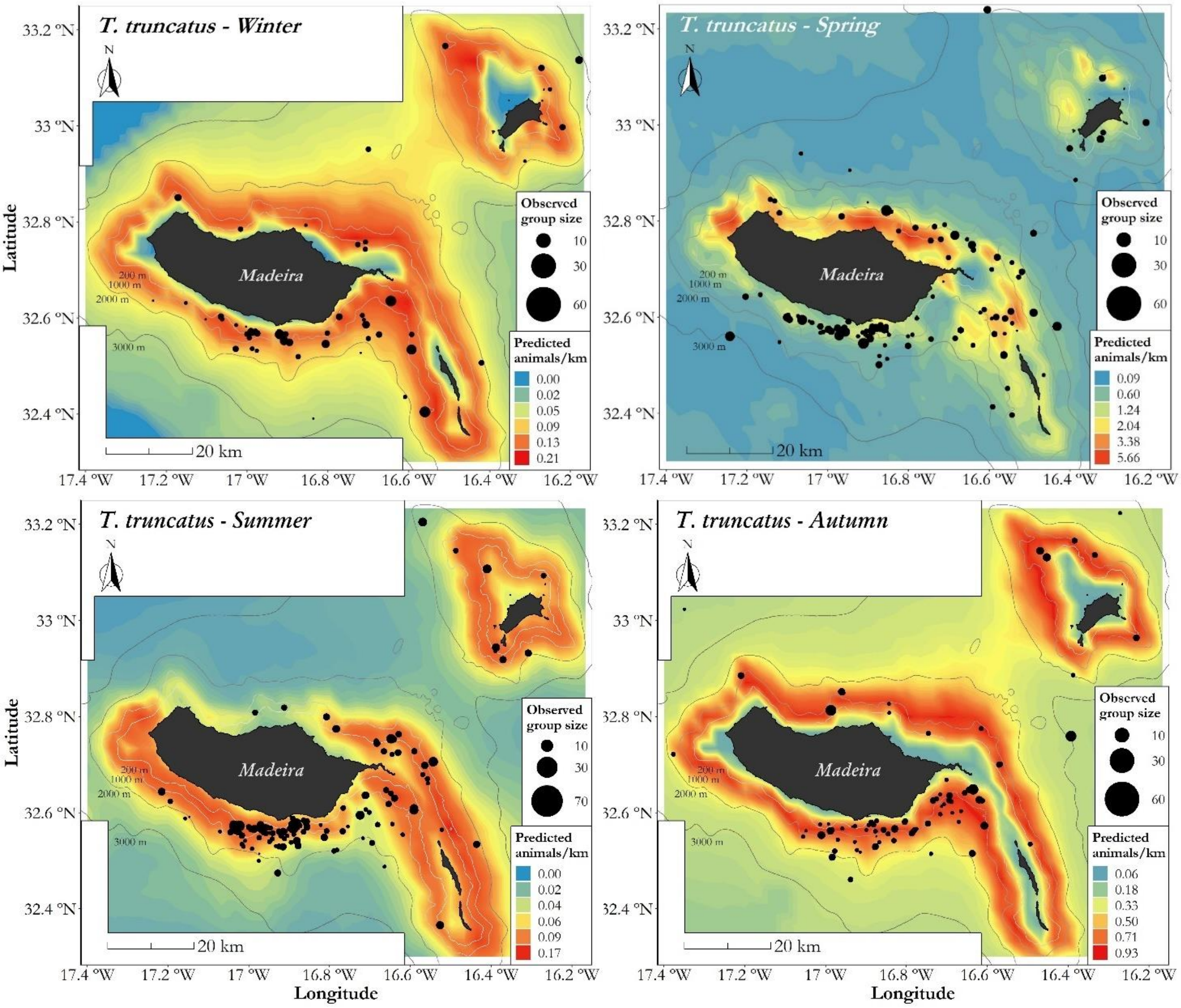


Figure 4.46. Predicted distribution of relative abundance (animals per km of transect line) of bottlenose dolphins by season in the Madeira inshore waters for the period 2001 – 2017, as a result of the combination of predicted relative abundance of groups and observed mean group size. The relative abundance scales are specific to each predicted distribution map and not directly comparable among each other. The comparison among the predicted distribution maps should be qualitative, i.e., comparison of the pattern of distribution of higher and lower relative abundance areas within the study area.

Figure 4.46 shows the prediction maps of the bottlenose dolphin for each season. The winter model predicted habitat use by the bottlenose dolphin of shallower depth waters on the slope areas around the islands and absence over the insular shelf. In spring there was a shift in the predicted distribution of the species with a higher presence to the north of Madeira and Porto Santo islands, relatively close to shore in the former, and in the channel between Madeira and Desertas Islands. In summer, the predicted distribution changed from the north to the south of Madeira Island, especially to the south-southwest, and around Desertas Islands, however, the species was predicted to continue to use the channel between Madeira and Desertas and the distribution around Porto Santo was more spread out compared with the spring. In autumn, the model predicted that relative abundance was higher around

Porto Santo, along the south coast of Madeira and, to lesser extent, along the north coast of this island and around Desertas, mostly between the 1 000 – 1 500 m depth contours (Figure 4.45).

The bottlenose dolphins seem to have used shallower waters over the islands' slope around the 1 000 m depth contour (200 – 2 000 m) throughout the year, although that preference was expressed by different physiographic covariates in the models of different seasons. They were mostly absent from the insular shelf and the waters further offshore. Furthermore, dynamic environmental variables such as primary productivity, sea surface temperature anomaly and mixed layer depth also seem to have influenced the bottlenose dolphin's distribution in spring and summer.

Stenella frontalis

In Table 4.12 and Table 4.13 are given the selected models of habitat use and predicted relative abundance, respectively, by season for the spotted dolphin.

Physiographic explanatory variables, mostly related with slope, were the most important to explain the habitat use of the spotted dolphin across the seasons, although in spring and autumn, sea temperature related dynamic covariates were equally important, especially in spring. The final models explained between 14 % and 29 % of the deviance in the data (Table 4.12).

The most important environmental covariates selected in the winter model were "Distance to 3000m isobath" and "Maximum slope". These covariates' positive relationship and moderate effect on the response, indicates a much lower presence in deep offshore waters and a use of areas with a steeper sea floor (Figure 4.47). The covariate "Year" was also selected in the final model, with a similarly shaped smooth curve as the corresponding smooth in the bottlenose dolphin winter model, including an increase in the relative abundance of groups in winter between 2002 and 2008, followed by a gentler decrease until 2016, but without the plateau between 2008 and 2012.

Table 4.12 – Summary table of the selected habitat use models of relative abundance of groups of spotted dolphin by season, and respective main model parameters; * - significant relationship between covariate and response (p<0.05).

Species	Season	Nº of segment	Nº of observ.	Response variable	model selected	edf model	% Dev. Explained	AIC	Nº models
Stenella frontalis	*Winter*	2993	40	Groups	factor(Type of survey) + s(Minimum aspect)* + s(Maximum slope)* + s(Distance to 3000m isobath)* + s(Mld 2001-17 Winter) + s(Month) + s(Year)* + offset(Effort)	11.3	14.29%	3000.99	12
	Spring	4764	119	Groups	factor(Type of survey) + s(Slope area)* + s(Chla 2001-17 Spring)* + s(Poc 2001-17 Spring)* + s(Sst 2001-17 Spring)* + s(Month)* + s(Effort)*	14.3	28.75%	4896.47	9
	Summer	4626	175	Groups	factor(Type of survey) +s(Average aspect)* + s(Contour index)* + s(Month)* + s(Beaufort)* + s(Effort)*	16.4	22.73%	4535.32	27
	Autumn	*3110*	50	Groups	factor(Type of survey) + s(Distance to Slope)* + s(Sst-a 2001-17 Autumn)* + offset(Effort)	6.8	10.01%	3094.08	17

Table 4.13 – Summary table of the observed and predicted encounter rates (ER) of groups and individuals per kilometre, as well as observed mean group size, of Atlantic spotted dolphin by season. The observed ER of individuals = observed ER group * observed mean group size; predicted ER of individuals = predicted ER of groups * observed mean group size (no final group size models were selected). The CV was calculated from the models' variance estimated by posterior simulation.

Species	Season	Nº of observ.	ER groups		Group size		ER individuals		
			Observed	Predicted	Observed	Predicted	Observed	Predicted	CV
Stenella frontalis	*Winter*	40	0.0037	0.0050	36.83	-	0.135	0.184	0.387
	Spring	119	0.0068	0.0353	26.45	-	0.181	0.184	0.917
	Summer	175	0.0105	0.0208	38.70	-	0.408	0.805	1.777
	Autumn	50	0.0045	0.0041	52.22	-	0.233	0.214	0.606

The distribution of spotted dolphins in spring was driven by dynamic and physiographic covariates. The covariate "Poc 2001-17, Spring" and "Chla-a 2001-17, Spring" had the strongest effect on the response, followed by "Slope area" and "Sst 2001-17, Spring", all with positive relationships with the response, except "Chl-a 2001-17, Spring" (Figure 4.48).

The shape of the smooths suggests an association of the spotted dolphin in spring with more turbid (more organic particles) but less productive warmer waters, mostly over slope areas. The model also reflects the known increase in relative abundance of groups in spring with the arrival of migratory animals to the study area, as shown by the shape of the smooth "Month" (Figure 4.48).

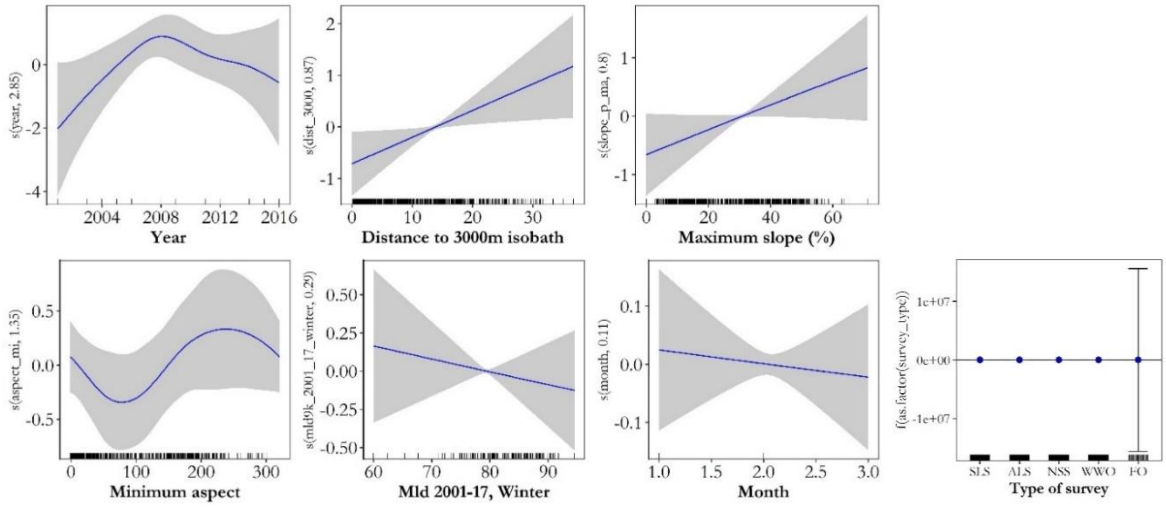


Figure 4.47. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Atlantic spotted dolphin groups (relative abundance) in the Madeira inshore waters in winter (January – March), for the period 2001 – 2017. SLS – shipboard line-transect surveys; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – Fisheries observer program.

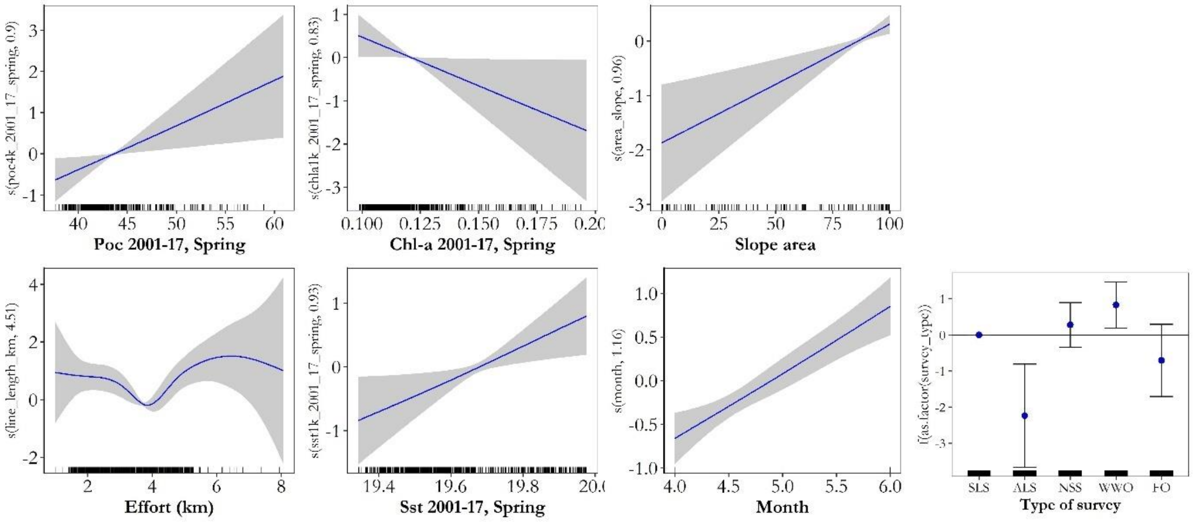


Figure 4.48. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Atlantic spotted dolphin groups (relative abundance) in the Madeira inshore waters in spring (April – June), for the period 2001 – 2017. SLS – shipboard line-transect surveys; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – Fisheries observer program.

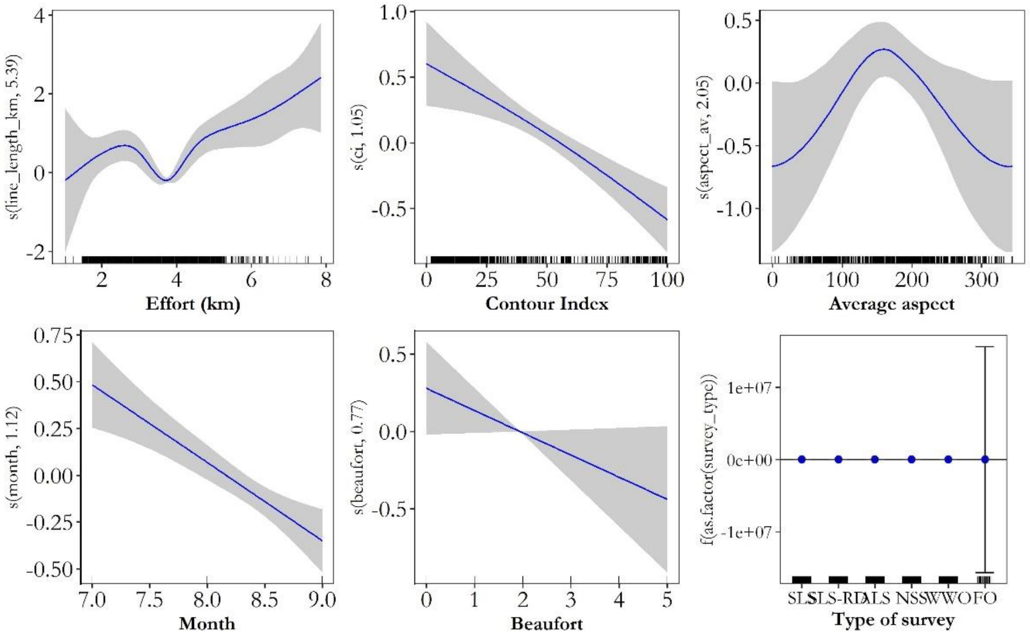


Figure 4.49. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Atlantic spotted dolphin groups (relative abundance) in the Madeira inshore waters in summer (July – September), for the period 2001 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies and WWO – whale-watching observers program; and FO – Fisheries observer program.

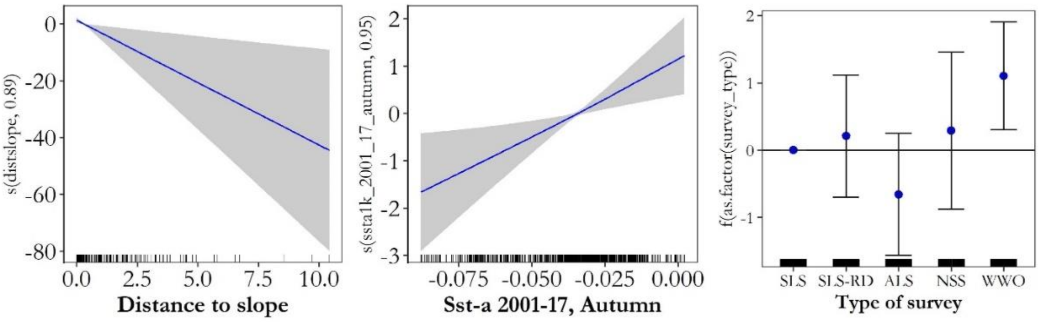


Figure 4.50. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Atlantic spotted dolphin groups (relative abundance) in the Madeira inshore waters in autumn (October – December), for the period 2001 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies and WWO – whale-watching observers program.

The summer habitat use model had environmental covariates with a weaker effect on the response, in spite of being the season with most observations (Figure 4.49 and Table 4.12). “Contour index” was the covariate with the strongest effect on the response followed by “Average aspect”. The relationships expressed by the smooth curves suggest a use by spotted dolphins of areas with a flatter bottom mostly facing south. However, the direct link between these bottom topographic characteristics and the species known ecological requirements is difficult to explain, and thus these covariates may be a proxy of other more ecologically meaningful variables for this species around Madeira and reflect a more offshore distribution of the species which, coincidentally, happens over flatter sea floor areas.

In autumn, the response showed a very strong negative relationship with “Distance to slope” and a strong positive relationship with “Sst-a 2001-17, Autumn”. The smooths suggest a use by the species of slope areas avoiding waters cooler than average (Figure 4.50).

The model predicted a distribution of the spotted dolphins in winter relatively close to shore, especially when compared with other seasons (Figure 4.51). The map shows a preference for the north coast of Madeira and Porto Santo islands, although the species was also predicted along the south coast of Madeira, especially in the southeast, and west of Desertas islands. The species predicted distribution changed in the spring, being mostly around Madeira, mainly in the south coast, and again in the summer when they were predicted to be more dispersed and further offshore. In autumn, the spotted dolphin predicted distribution was concentrated more in the channel between Madeira and Porto Santo islands and to lesser extent, northwest of Madeira, north of Porto Santo and west of Desertas. In all seasons except winter the prediction maps show a much lower presence or even absence from shallower waters.

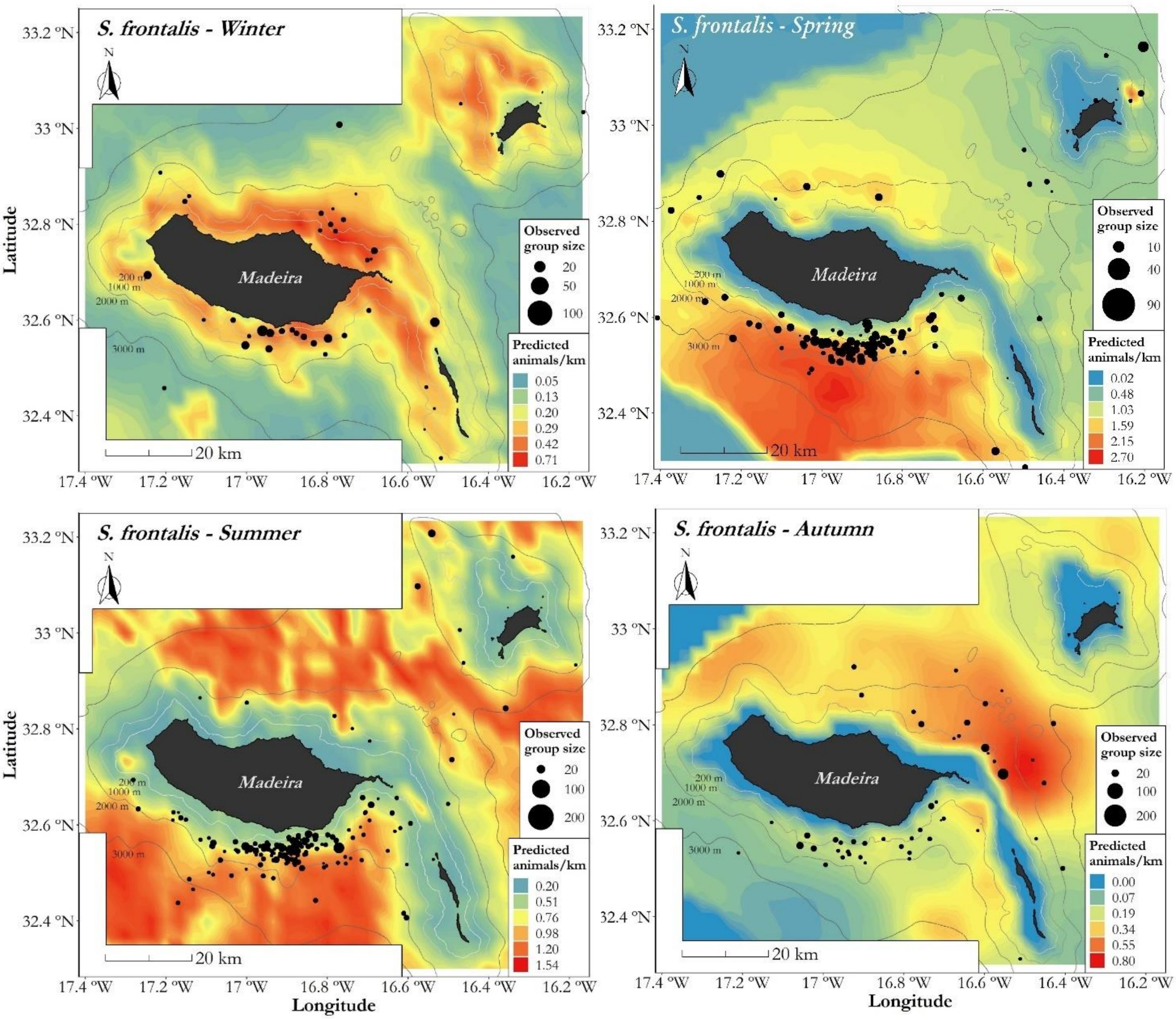


Figure 4.51. Predicted distribution of relative abundance (animals per km of transect line) of Atlantic spotted dolphins by season in the Madeira inshore waters for the period 2001 – 2017, as a result of the combination of predicted relative abundance of groups and observed mean group size. The relative abundance scales are specific to each predicted distribution map and not directly comparable among each other. The comparison among the predicted distribution maps should be qualitative, i.e., comparison of the pattern of distribution of higher and lower relative abundance areas within the study area.

Overall, the spotted dolphin had a preference for slope habitats, with generally a much lower presence in shallow waters over the insular shelf. However, in summer they were more dispersed to further offshore waters and in winter closer to shore, both in the north and south of Madeira. In spring they preferred the south of Madeira and in autumn the channel between Madeira and Porto Santo, with sea surface temperature related covariates having an important, direct or indirect, relation with the species' use of the local habitat.

Delphinus delphis

The common dolphin was mostly sighted in Madeira archipelago inshore waters from December to June (Figure 4.19 and Figure 4.20). As a result, there were only sufficient observations of the species to model its habitat use in winter and spring. Table 4.14 and Table 4.15 show the selected models of habitat use and predicted relative abundance, respectively, for the common dolphin for these seasons.

Although there was considerable effort and observations of common dolphin groups, the final models were simple (one or two environmental variables selected) and explained a relatively low percentage of deviance when compared with the models of the other delphinidae species by season (Table 4.14).

The winter habitat use model included only one environmental variable, "Sst 2001-17(Dd), Winter". The smooth has a negative slope, showing a preference of this species for cooler waters in the study area in this season (Figure 4.52). The known increase in ER of common dolphin groups in winter, as they move into the study area, is reflected in the model by the shape of the smooth for "Month".

In the spring model, the environmental covariate with the strongest effect on the response was "Maximum slope", followed by "Sst-a 2001-17 (Dd), Spring" and "Minimum aspect" (Figure 4.53). The shape of the smooths suggests an association of the common dolphin with areas of steeper slopes, mostly facing east/southeast and associated with warmer sea surface temperature than the average in the region. The model also reflects the known decrease in ER of groups in spring as animals leave the archipelago in their seasonal migration (negative slope of the smooth for "Month").

Table 4.14 – Summary table of the selected habitat use models of relative abundance of groups of common dolphin by season, and respective main model parameters; * - significant relationship between covariate and response (p<0.05).

Species	Season	Nº of segment	Nº of observ.	Response variable	model selected	edf model	% Dev. Explained	AIC	Nº models
Delphinus delphis	*Winter*	2993	130	Groups	factor(Type of survey) + s(Sst 2001-17 Winter)* + s(Month)* + s(Beaufort)* + s(Effort)*	11.1	11.94%	2923.59	38
	Spring	4764	205	Groups	factor(Type of survey) + s(Minimum aspect)* + s(Sst-a 2001-17 Spring)* +s(Maximum slope)* + s(Month)* + s(Effort)*	14.1	13.01%	4675.57	14

Table 4.15 – Summary table of the observed and predicted encounter rates (ER) of groups and individuals per kilometre, as well as observed mean group size, of common dolphin by season. The observed ER of individuals = observed ER group * observed mean group size; predicted ER of individuals = predicted ER of groups * observed mean group size (no final group size models were selected). The CV was calculated from the models' variance estimated by posterior simulation.

Season	Nº of observ.	ER groups		Group size		ER individuals		
		Observed	Predicted	Observed	Predicted	Observed	Predicted	CV
Winter	130	0.0120	0.0869	20.44	-	0.244	1.776	3.520
Spring	205	0.0119	0.0150	18.31	-	0.217	0.275	1.042

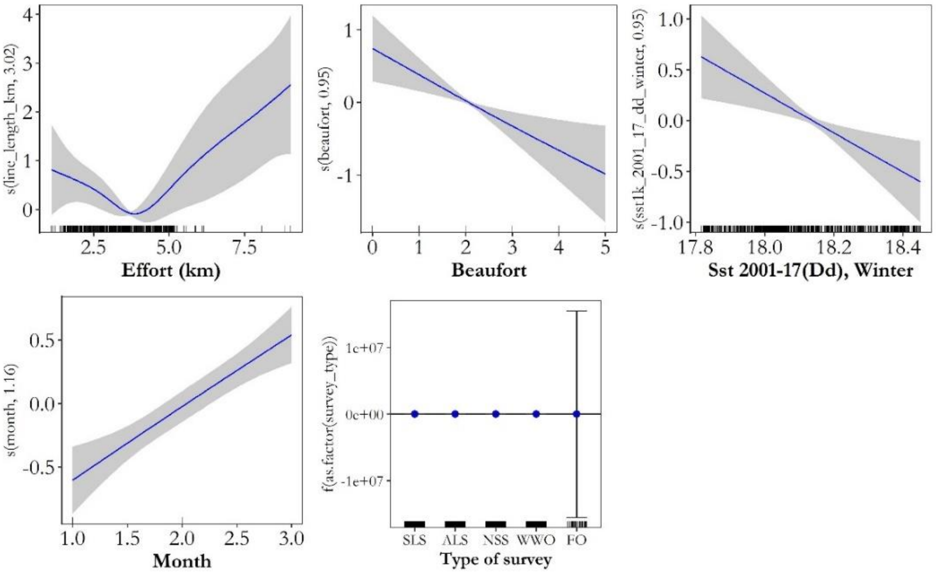


Figure 4.52. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Atlantic spotted dolphin groups (relative abundance) in the Madeira inshore waters in winter (January – March), for the period 2001 – 2017. SLS – shipboard line-transect surveys; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – Fisheries observer program.

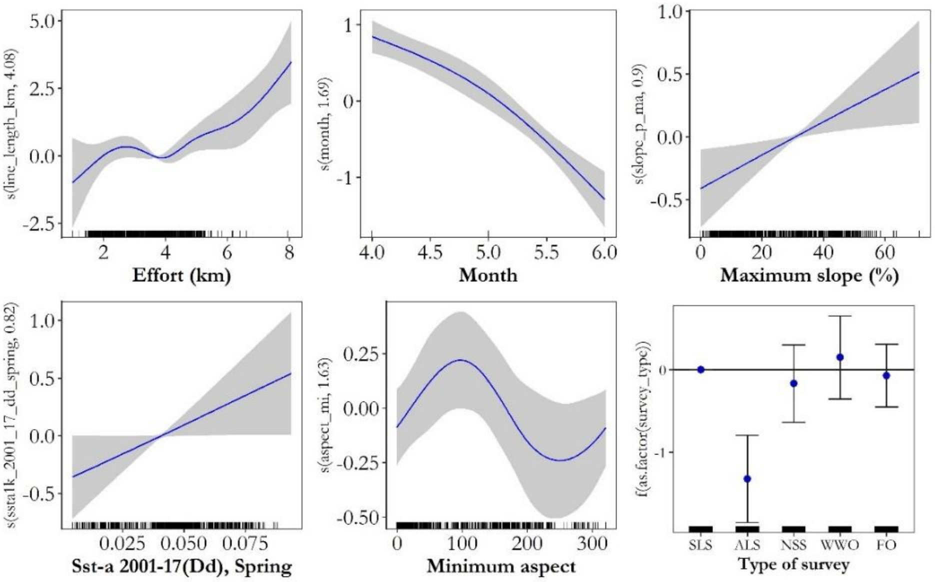


Figure 4.53. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Atlantic spotted dolphin groups (relative abundance) in the Madeira inshore waters in spring (April – June), for the period 2001 – 2017. SLS – shipboard line-transect surveys; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – Fisheries observer program.

Figure 4.54 shows the predicted distribution of common dolphin in winter and spring in the study area. In winter the predicted distribution of common dolphins followed a gradient from the northeast (around Porto Santo) to the southwest of the study area (Figure 4.54). In spring, their predicted distribution was concentrated in the northeast, east and southeast of Porto Santo, on the southeast of Madeira and on the slopes of the north coast of Madeira and east of Madeira and Desertas Islands (Figure 4.54). Conversely, the predicted ER southwest of Madeira was low, following the same pattern as in winter.

The common dolphin had a more dispersed distribution in the study area than the other dolphin species, with its presence observed and predicted both close to shore and in offshore waters. However, its habitat use was associated with sea surface temperature and slope areas. In general, there was a gradient in distribution, with higher values of predicted ER in the northeast of the study area and lower values in the southwest. However, in spring there was a clear relationship between distribution and slope areas, especially to the north and eastern side of the islands.

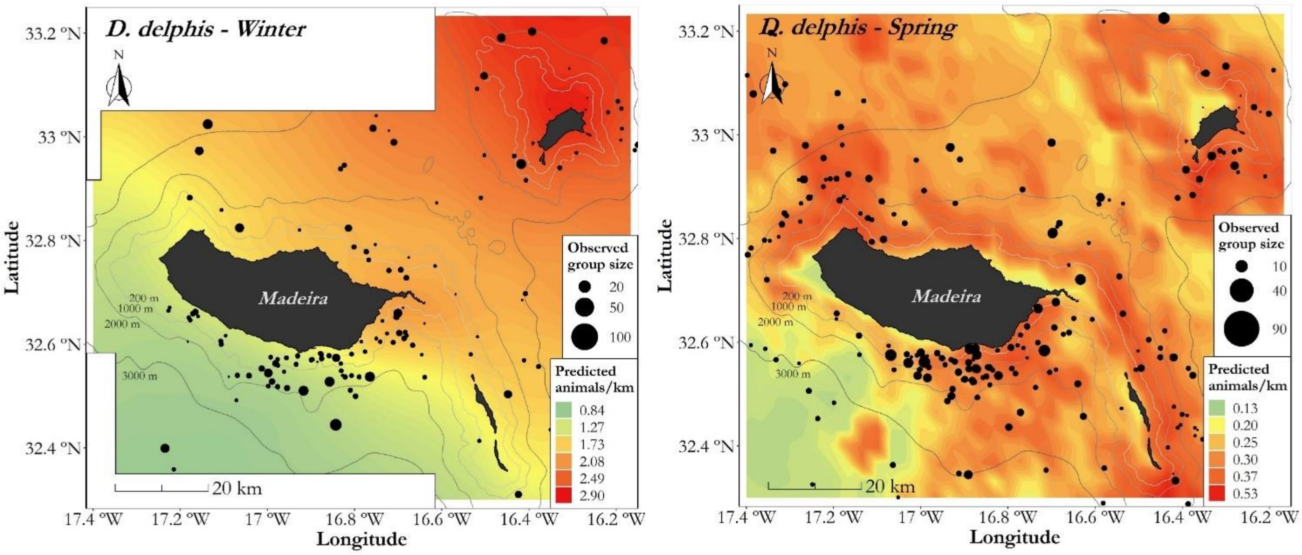


Figure 4.54. Predicted distribution of relative abundance (animals per km of transect line) of bottlenose dolphins by season in the Madeira inshore waters for the period 2001 – 2017, as a result of the combination of predicted relative abundance of groups and observed mean group size. The relative abundance scales are specific to each predicted distribution map and not directly comparable among each other. The comparison among the predicted distribution maps should be qualitative, i.e., comparison of the pattern of distribution of higher and lower relative abundance areas within the study area.

4.3.5.2 *Deep divers*

Globicephala macrorhynchus

Pilot whales were seen in Madeira archipelago inshore waters throughout the year, although with fluctuations in ER, as shown in Section 4.3.3. As a result, there were fewer observations to model habitat use in winter and spring when compared to summer and autumn. The covariates with the strongest effect on the response in all models were static explanatory variables and the percentage deviance explained by the models ranged from 14.10 % to 38.80 % (Table 4.16). The selected habitat use models by season for this species are presented in Table 4.16, and the respective observed and predicted relative abundance in Table 4.17.

The environmental covariates “Slope area”, “Maximum aspect” and “Distance to 3000m isobath” were selected in the winter model, however only for “Maximum aspect” did the smooth curve had a narrow confidence band (Figure 4.55). The model also included the temporal covariates “Year” and “Month”, but only the former had a strong relationship with the response, indicating an increase in relative abundance of the species groups in winter during the study period.

The spring model included the environmental covariates “Distance to 1500m isobath” and “Minimum slope”, both with a strong effect on the response, indicating a preference of pilot whale groups for waters with depths closer to -1 500 m and with flatter sea floor (Figure 4.56).

Table 4.16 – Summary table of the selected habitat use models of relative abundance of groups of short-finned pilot whale by season, and respective main model parameters; * - significant relationship between covariate and response ($p<0.05$).

Species	Season	Nº of segment	Nº of observ.	Response variable	model selected	edf model	% Dev. Explained	AIC	Nº models
Globicephala macrorhynchus	*Winter*	2993	36	Groups	factor(Type of survey) + s(Slope area) + s(Maximum aspect)* + s(Distance to 3000m isobath) + s(Month)* + s(Year)* + s(Effort)	12.2	36.52%	2996.58	7
	Spring	4764	29	Groups	factor(Type of survey) + s(Distance to 1500m isobath)* + s(Minimum slope)* + s(Beaufort)* + offset(Effort)	7.8	14.06%	4754.07	13
	Summer	4626	78	Groups	factor(Type of survey) + s(Distance to slope)* + s(Average aspect)* +s(Mld 2001-17 Summer)* + s(Month)* + s(Effort)*	17.8	29.41%	4611.50	15
	Autumn	3110	93	Groups	factor(Type of survey) + s(Maximum aspect)* + s(Maximum depth)* + s(Year) + s(Beaufort)* + s(Effort)*	19.1	38.80%	3183.48	35

Table 4.17 – Summary table of the observed and predicted encounter rates (ER) of groups and individuals per kilometre, as well as observed mean group size, of short-finned pilot whale by season. The observed ER of individuals = observed ER group * observed mean group size; predicted ER of individuals = predicted ER of groups * observed mean group size (no final group size models were selected). The CV was calculated from the variance model(s) estimated by posterior simulation.

Species	Season	Nº of observ.	ER groups		Group size		ER individuals		
			Observed	Predicted	Observed	Predicted	Observed	Predicted	CV
Globicephala macrorhynchus	*Winter*	36	0.0033	0.0126	14.81	-	0.049	0.187	20.962
	Spring	29	0.0017	0.0011	18.59	-	0.031	0.021	0.436
	Summer	78	0.0046	0.0007	17.82	-	0.083	0.012	4.253
	Autumn	93	0.0083	0.0041	10.95	-	0.091	0.045	5.737

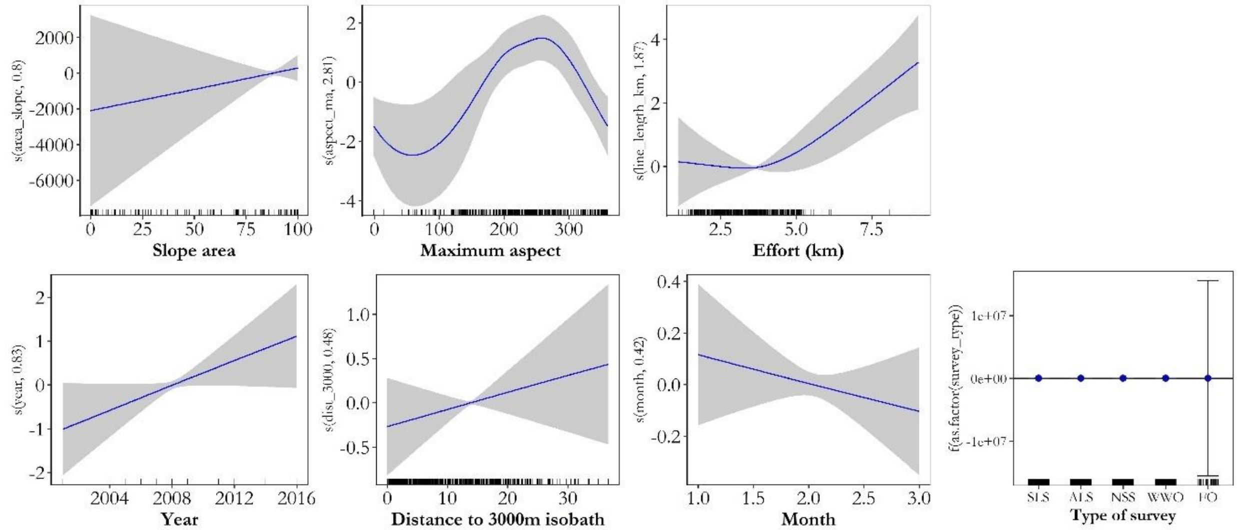


Figure 4.55. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of short-finned pilot whale groups (relative abundance) in the Madeira inshore waters in Winter (January – March), for the period 2001 – 2017. SLS – shipboard line-transect surveys; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – Fisheries observer program.

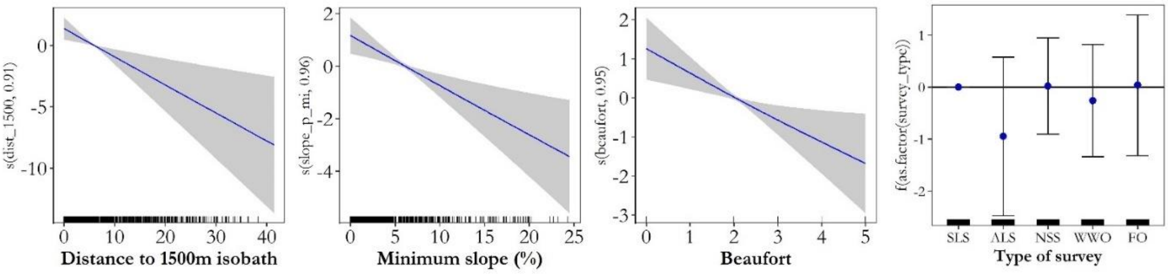


Figure 4.56. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of short-finned pilot whale groups (relative abundance) in the Madeira inshore waters in spring (April – June), for the period 2001 – 2017. SLS – shipboard line-transect surveys; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – Fisheries observer program.

The selected model for summer included the environmental covariates “Distance to slope”, “Average aspect” and “Mld 2001-17, Summer” (Figure 4.57), with “Distance to slope” having an especially strong and negative linear relationship with the response, indicating use of waters closer to the islands’ slope by pilot whale groups. The covariates “Average aspect” and “Mld 2001-17, Summer” had a moderate effect on the response, the former with a non-linear relationship and the latter with a negative linear relationship, suggesting a use of areas with an average sea floor aspect roughly between 100º and 270º and with waters with shallower mixed layer depth. The covariate “Month” was also included in the model, reflecting the increase in the relative abundance of groups in the study area during summer.

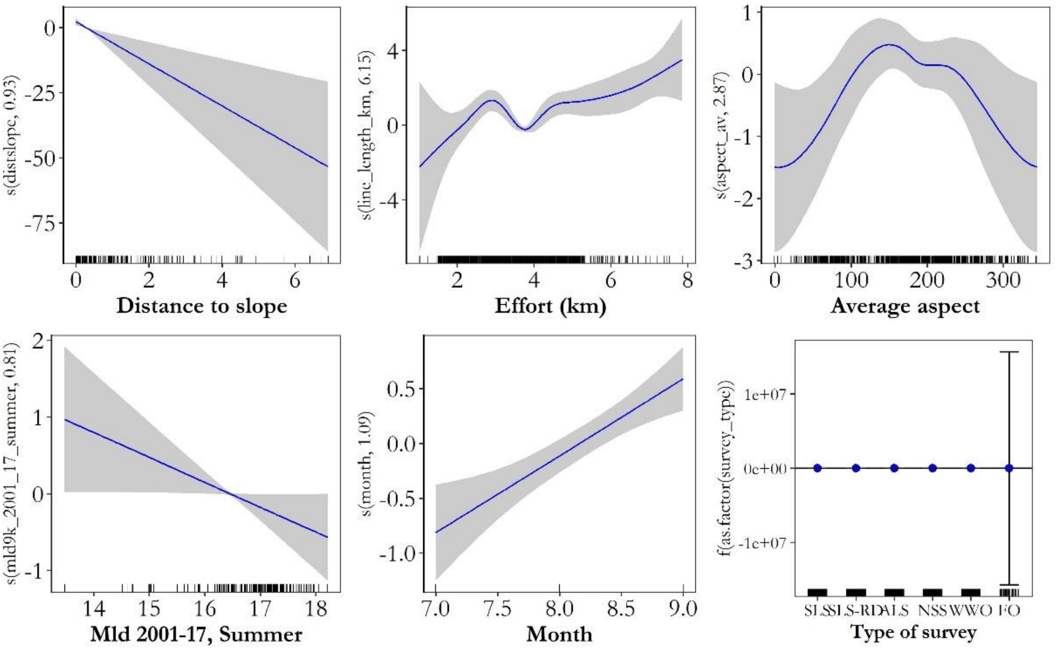


Figure 4.57. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of short-finned pilot whale groups (relative abundance) in the Madeira inshore waters in summer (July – September), for the period 2001 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – Fisheries observer program.

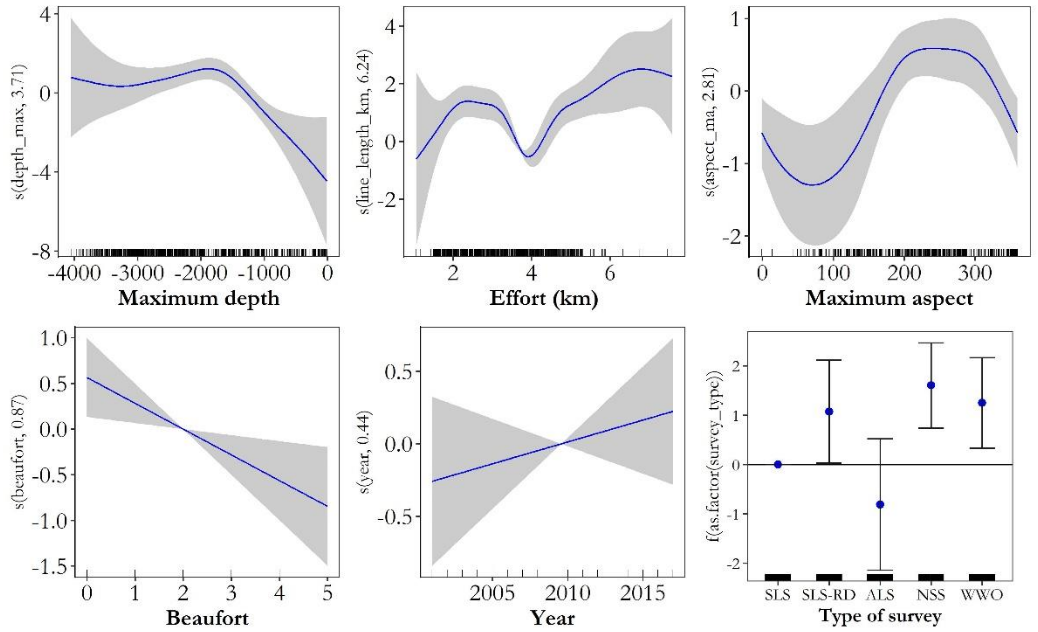


Figure 4.58. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of short-finned pilot whale groups (relative abundance) in the Madeira inshore waters in autumn (October – December), for the period 2001 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies and WWO – whale-watching observers program.

The environmental covariates “Maximum depth” and “Maximum aspect” were selected in the autumn model, both with non-linear relationships with the response and with a strong and moderate effect, respectively (Figure 4.58). The shape of the “Maximum depth” and “Maximum aspect” smooths, suggest pilot whale groups in autumn used waters preferably between 1 500 m and 2 000 m depth, and over areas with a sea floor maximum aspect roughly between 180º and 300º. The covariate “Year” was also included in the model, indicating a weak increase in the ER of group over the study period.

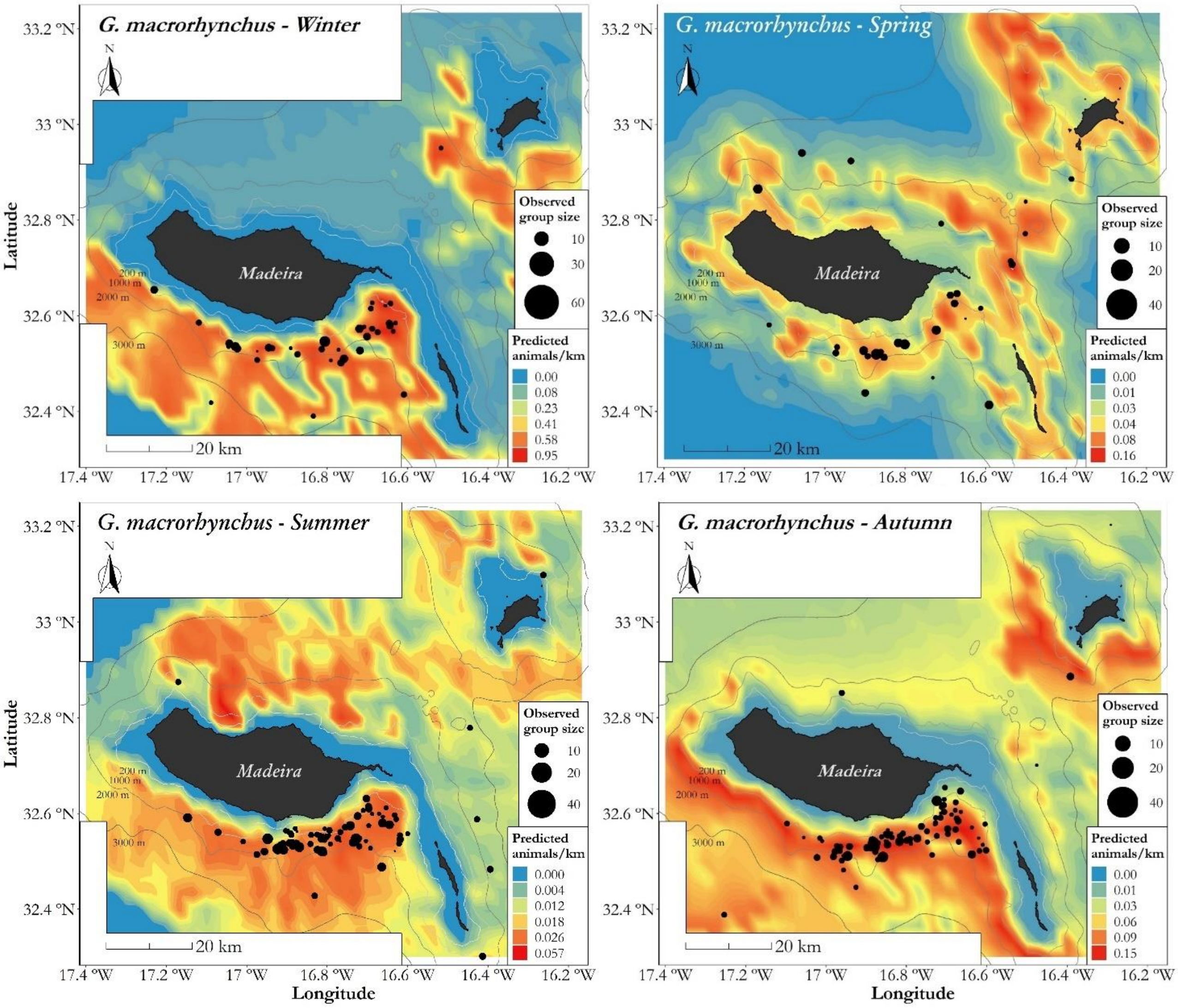


Figure 4.59. Predicted distribution of relative abundance (animals per km of transect line) of short-finned pilot whale by season in the Madeira inshore waters for the period 2001 – 2017, as a result of the combination of predicted relative abundance of groups and observed mean group size. The relative abundance scales are specific to each predicted distribution map and not directly comparable among each other. The comparison among the predicted distribution maps should be qualitative, i.e., comparison of the pattern of distribution of higher and lower relative abundance areas within the study area.

Figure 4.59 shows the predicted distribution of pilot whales for each season. In winter the predicted distribution included the waters south and southwest of Madeira and Porto Santo Islands, beyond the 1 000 m depth (Figure 4.55). In spring, the predicted distribution was dispersed around the islands in waters between 1 000 m and 2 000 m depth but including areas with shallow waters and close to shore. Although the prediction reflects the more dispersed sightings of pilot whales in spring when compared to winter, it also predicts the unrealistic presence of these animals in shallow waters in the west and north of Madeira, east of Desertas and southeast of Porto Santo. The low number of observations in both the winter and spring models may have limited the covariates selected in the models. In summer, the model predicted a distribution of pilot whale groups concentrated in the bay southeast of Madeira Island and to a lesser extent east and northeast of Desertas Islands and around Porto Santo. Conversely, pilot whale groups were not observed or predicted in shallow water over the insular shelf, and offshore waters southwest, west and northwest of Madeira. In autumn the predicted distribution indicates a use of waters beyond the 1000 m depth, especially in the south, southeast and west of the islands, and absence in waters over the insular shelf.

4.3.5.3 Baleen whales

Balaenoptera edeni

The seasonal presence of Bryde's whales in the study area meant that there were not enough sightings to model habitat use in winter. The selected habitat use models by season for this species are presented in Table 4.18, and the respective observed and predicted relative abundance in Table 4.19. The selected models explained between 20.59 % and 26.26 % of the deviance in the data (Table 4.18).

The spring model included the environmental covariate "Poc 2001-17, Spring", however its relationship with the response was weak, limiting any ecological inferences that might be made from the model (Figure 4.60).

The particulate organic carbon covariate ("Poc 2001-17, Summer") was also selected in summer model, but in an interaction with "Distance to escarpment" (Figure 4.61). The interaction plot indicates a use by the species of waters closer to the escarpment and with higher values of particulate organic carbon.

In autumn, the static covariate "Distance to 500m isobath" was the only one selected, unlike the previous seasons where a dynamic covariate was included (Figure 4.62). The relationship between the covariate and the response was linear with a negative slope, indicating a use by these animals of waters closer to -500 m water depth.

Table 4.18 – Summary table of the selected habitat use models of relative abundance of individuals of Bryde's whales by season, and respective main model parameters; * - significant relationship between covariate and response ($p<0.05$).

Species	Season	Nº of segment	Nº of observ.	Response variable	model selected	edf model	% Dev. Explained	AIC	Nº models
Balaenoptera edeni	*Spring*	2667	26	Individuals	factor(Type of survey) + s(Poc 2004-17 Spring) + s(Effort)*	7.8	26.26%	2696.65	26
	Summer	3617	61	Individuals	factor(Type of survey) +s(Distance to Escarpment, Poc 2004-17 Summer)* + s(Effort)*	12.1	20.59%	3724.76	16
	Autumn	2709	32	Individuals	factor(Type of survey) + s(Distance to 500m isobath)* + s(Effort)*	10.5	24.28%	2764.45	97

Table 4.19 – Summary table of the observed encounter rates (ER) of groups per kilometre, observed and predicted ER of individuals per kilometre, as well as observed mean group size, of Bryde's whale by season. The observed ER of individuals = observed ER group * observed mean group size; predicted ER of individuals is given by the model prediction. The CV was calculated from the variance model(s) estimated by posterior simulation.

Season	Nº of observ.	ER groups		Group size		ER individuals		
		Observed	Predicted	Observed	Predicted	Observed	Predicted	CV
Spring	26	0.0015	-	1.52	-	0.0023	0.0053	2.430
Summer	61	0.0036	-	1.77	-	0.006	0.006	2.792
Autumn	32	0.0029	-	1.75	-	0.005	0.001	4.963

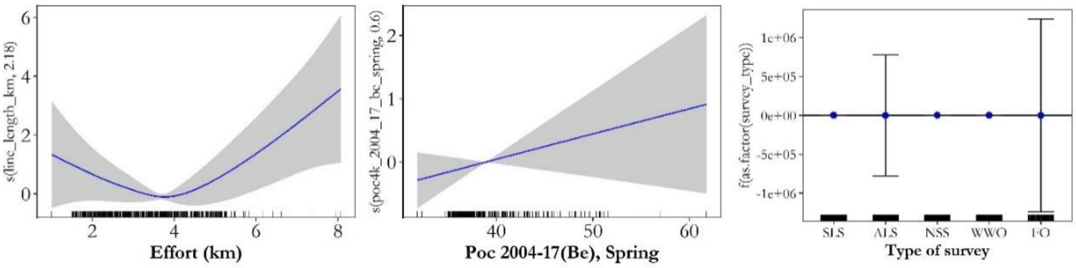


Figure 4.60. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Bryde's whale individuals (relative abundance) in the Madeira inshore waters in spring (April – June), for the period 2004 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies and WWO – whale-watching observers program.

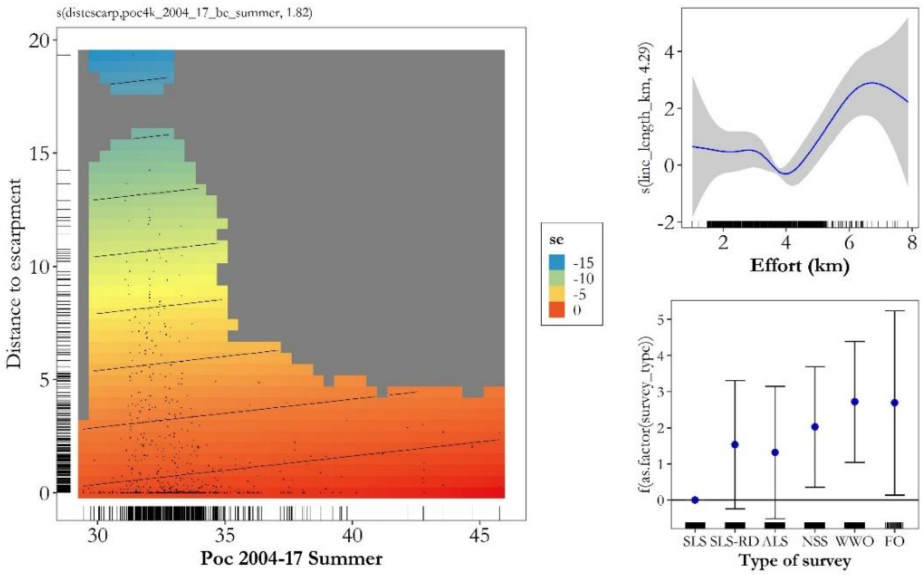


Figure 4.61. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Bryde's whale individuals (relative abundance) in the Madeira inshore waters in summer (July - September), for the period 2004 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies and WWO – whale-watching observers program.

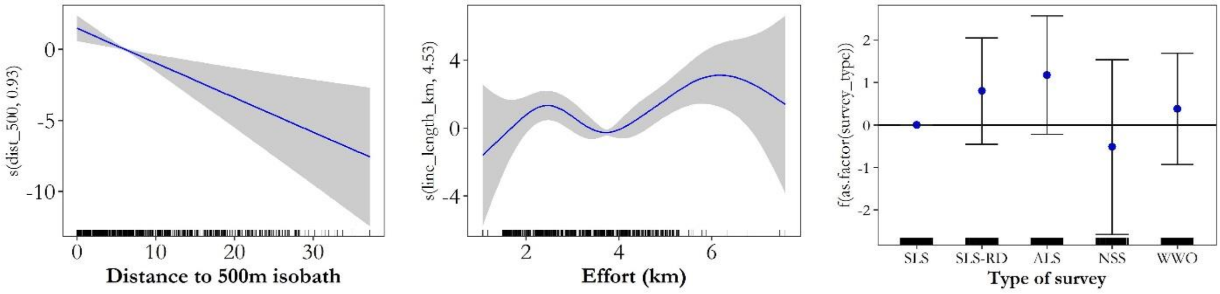


Figure 4.62. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Bryde's whale individuals (relative abundance) in the Madeira inshore waters in autumn (October - December), for the period 2004 – 2017. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies and WWO – whale-watching observers program.

The Bryde's whale in summer had highest predicted relative abundance closer to the islands' escarpment, especially in the areas around the channel between Madeira and Desertas Islands (Figure 4.63), with lower predicted relative abundance to the southwest of Madeira Island and to the north of Porto Santo. In autumn, the model predicted the species to occur closer to the coast and to be more evenly distributed around the islands (Figure 4.63).

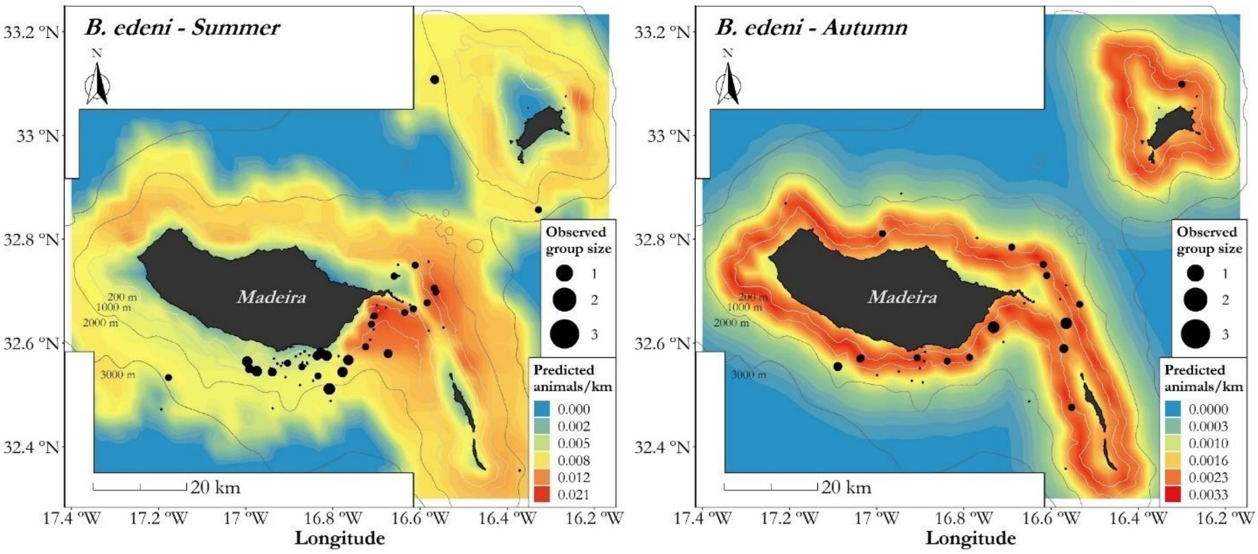


Figure 4.63. Predicted distribution of relative abundance (animals per km of transect line) of Bryde's whales in summer and autumn in the Madeira inshore waters for the period 2004 – 2017, as given by the model of relative abundance of individuals. The relative abundance scales are specific to each predicted distribution map and not directly comparable among each other. The comparison among the predicted distribution maps should be qualitative, i.e., comparison of the pattern of distribution of higher and lower relative abundance areas within the study area.

4.3.6 Bi-monthly with time-lagged covariates

The Bryde's whales, like other baleen whales, are known to feed at low trophic levels of the marine food chain. The relative abundance of individuals was modelled with time-lagged dynamic covariates to understand if and how primary productivity may drive the habitat use of this species throughout the year, taking into consideration the propagation of seasonal changes through the food web.

To have a more balanced distribution of the species observations, the datasets analysed were grouped bi-monthly (Table 4.20) rather than by season, as done in the previous seasonal models (Table 4.18). The bi-monthly selected habitat use models are given in Table 4.20, and the respective observed and predicted relative abundances in Table 4.21. To facilitate the comparison, in Table 4.22 are presented for each model the environmental covariates selected in decreasing order of their effect on the response, their level of significance, and the respective deviance explained and AIC values. The predicted distributions of relative abundance of Bryde's whales based on these models is presented in Figure 4.71.

For the period June-July, there are two best models (with no time lagged and two-months lagged covariates, respectively) with very similar values of AIC (2 284.18 and 2 284.41) and percent deviance explained (25.04 % and 25.26 %) (Table 4.22). The first model shows a moderate effect and linear positive relationships of the covariates "Sst-a 2004-17 Jun-Jul" and "Escarpment area" with the response, although marginally non-significant in the case of the latter (Figure 4.64).

Table 4.20 – Summary table of the selected habitat use models of the encounter rates of individuals by season, and respective main model parameters; * - significant relationship between covariate and response ($p<0.05$).

Nº of observ.	Lag information					model selected	edf model	% Dev. Explained	AIC	Nº models
	Nº of segments	Data month(s)	Covariates month(s)	Lag (month(s)	Prediction month(s)					
35	2225	*June - July*	*June - July*	0	*June - July*	factor(Type of survey) + s(Escarpment area) + s(Maximum slope) + s(Sst-a 2004-17 Jun-Jul)* + s(Year) + s(Beaufort) + s(Effort)*	7.5	25.04%	2284.18	62
		June - July	*May - June*	1		factor(Type of survey) + s(Escarpment area)* + s(Average aspect) + s(Chl-a 2004-17 May-Jun)* + s(Slope std dev)* + s(Effort)	8.9	25.38%	2288.08	25
		June - July	*Mar - Apr*	2		factor(Type of survey) + s(Escarpment area)* + s(Chl-a 2004-17 Mar-Apr)* + s(Year) + offset(Effort)	7.6	25.26%	2284.41	37
48	2739	*Aug - Sept*	*Aug - Sept*	0	*Aug - Sept*	factor(Type of survey) + s(Distance to escarpment)* + s(Mld 2004-27 Aug-sep) + s(Pp 2004-17 Aug-Sep)* + s(Effort)*	13.9	27.64%	2825.80	28
		Aug - Sept	*July - Aug*	1		factor(Type of survey) + s(Escarpment area) + s(Distance to escarpment)* + s(Minimum slope) + s(Poc 2004-17 Jul-Aug)* + s(Beaufort) + s(Effort)*	13.5	27.34%	2825.48	13
		Aug - Sept	*May - June*	2		factor(Type of survey) + s(Escarpment area)* + s(Distance to coast) + s(Mld 2004-17 May-Jun)* + s(Pp 2004-17 May-Jun)* + s(Beaufort) + s(Effort)*	14.4	25.48%	2829.21	10
31	2285	*Oct - Nov*	*Oct - Nov*	0	*Oct - Nov*	factor(Type of survey) + s(Distance to 200m isobath)* + s(Effort)*	10.5	24.71%	2343.40	29
		Oct - Nov	*Sept - Oct*	1		factor(Type of survey) + s(Distance to 200m isobath)* + s(Effort)*	10.5	24.71%	2343.40	13
		Oct - Nov	*Jul - Aug*	2		factor(Type of survey) + s(Distance to 200m isobath)* + s(Effort)*	10.5	24.71%	2343.40	27

Table 4.21 – Summary table of the observed and predicted encounter rates (ER) of individuals per kilometre and respective uncertainty, as well as observed group size, of Bryde's whale by season.

Nº of observ.	Lag information			ER groups	Group size	ER individuals		
	Lag (month(s)	Covariates month(s)	Data month(s)	Observed	Observed	Observed	Predicted	CV
35	0	*June - July*	*June - July*	0.0043	1.714	0.0075	0.0012	0.845
	1	*May - June*					0.0013	0.798
	2	*Mar - Apr*					0.0003	1.680
48	0	*Aug - Sept*	*Aug - Sept*	0.0048	1.708	0.0082	0.0077	3.526
	1	*July - Aug*					0.0074	2.346
	2	*May - June*					0.0090	1.490
31	0	*Oct - Nov*	*Oct - Nov*	0.0038	1.774	0.0067	0.0007	3.962
	1	*Sept - Oct*					0.0007	3.962
	2	*July - Aug*					0.0007	3.962

Table 4.22 – Summary table of the observed and predicted encounter rates (ER) of individuals per kilometre and respective uncertainty, as well as observed group size, of Bryde's whale by season.

Data month(s)	Covariates month(s)	Lag (month(s)	Environmental covariates by decreasing order of effect on the response *** - significant relationship between covariate and response (p <0.05)**	% Dev.	AIC
June - July	*June - July*	0	**Sst-a 2004-17 Jun-Jul*** ; Escarpment area ; Maximum slope	25.04%	2284.18
June - July	*May - June*	1	**Escarpment area* ; Slope std dev*** ; **Chl-a 2004-17 May-Jun*** Average aspect	25.38%	2288.08
June - July	*Mar - Apr*	2	**Chl-a 2004-17 Mar-Apr*** ; **Escarpment area***	25.26%	2284.41
Aug - Sept	*Aug - Sept*	0	**Distance to escarpment*** ; **Pp 2004-17 Aug-Sep*** ; Mld 2004-27 Aug-sep	27.64%	2825.80
Aug - Sept	*July - Aug*	1	**Distance to escarpment*** ; **Poc 2004-17 Jul-Aug*** Minimum slope ; Escarpment area	27.34%	2825.48
Aug - Sept	*May - June*	2	**Pp 2004-17 May-Jun*** ; **Mld 2004-17 May-Jun*** ; **Escarpment area*** Distance to coast	25.48%	2829.21
Oct - Nov	*Oct - Nov*	0	**Distance to 200m isobath***	24.71%	2343.40
Oct - Nov	*Sept - Oct*	1	**Distance to 200m isobath***	24.71%	2343.40
Oct - Nov	*Jul - Aug*	2	**Distance to 200m isobath***	24.71%	2343.40

In the second model there is a stronger effect and significant linear positive relationships between the response and the covariates "Chl-a 2004-17 Mar-Apr" and "Escarpment area" (Figure 4.66). The "Chl-a 2004-17 May-Jun" covariate was also selected in the one-month lagged covariates' model, although with less effect on the response than the two-month lagged covariates' model (Figure 4.65). The chlorophyll-a concentration seems to influence the distribution of Bryde's whales in the study area during the end of spring and early summer, with one to two months' time lag.

For the period August-September, there are also two equivalent best models: no time lagged and one-month lagged covariates. These models have similar values of AIC (2 825.80 and 2 825.48, respectively) and of percentage of deviance explained (27.64 % and 27.34 %, respectively) (Table 4.22). In both models the "Distance to escarpment" is the covariate with the strongest effect and a negative linear relationship with the response. In the first model, the covariate with the next strongest effect on the response is "Pp 2004-17 Aug-Sep" with a significant linear positive relationship. This smooth indicates use by the species of areas with higher productivity in the study area (Figure 4.67). In the second model, the covariate with the next strongest effect on the response is "Poc 2004-17 Jul-Aug" also with a significant linear positive relationship, suggesting a use of areas with higher concentration of particulate organic carbon in the previous month (Figure 4.68). The next best model for this period included the covariate "Pp 2004-17 May-Jun", with the strongest effect, followed by "Mld 2004-17 May Jun" and finally "Escarpment area" (Figure 4.69).

For the period October – November, the covariate "Distance to 200m isobath" was the only covariate consistently selected in the best models regardless of trying different time-lagged dynamic covariates (Figure 4.70).

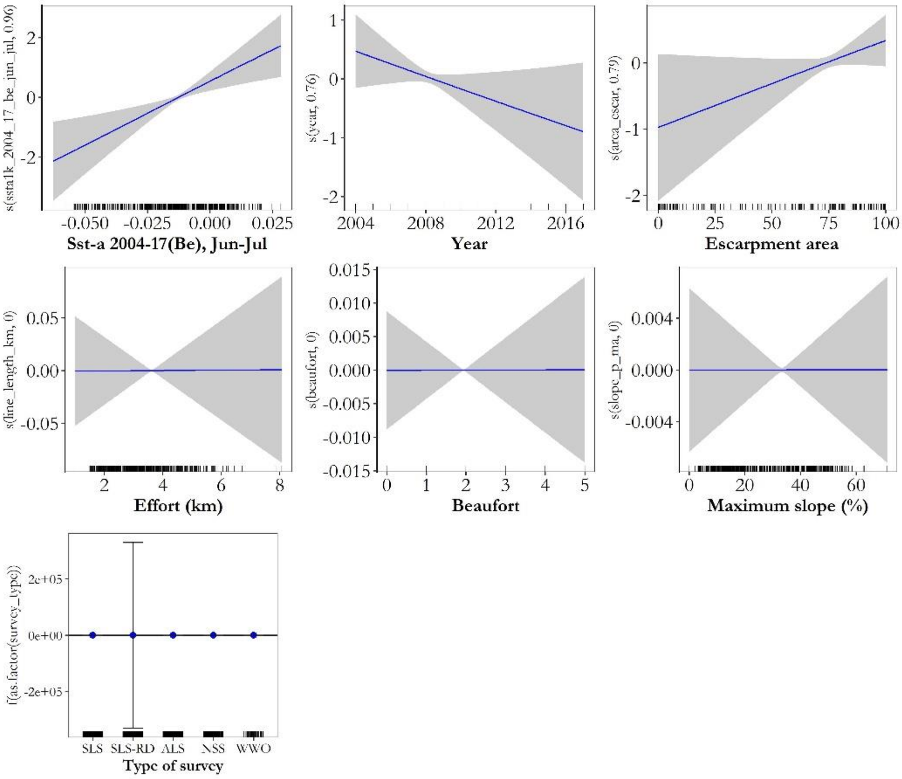


Figure 4.64. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Bryde's whale individuals (relative abundance) in Madeira inshore waters in June/July for the period 2004 – 2017, without time-lag dynamic covariates (June/July). SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; and WWO – whale-watching observers program.

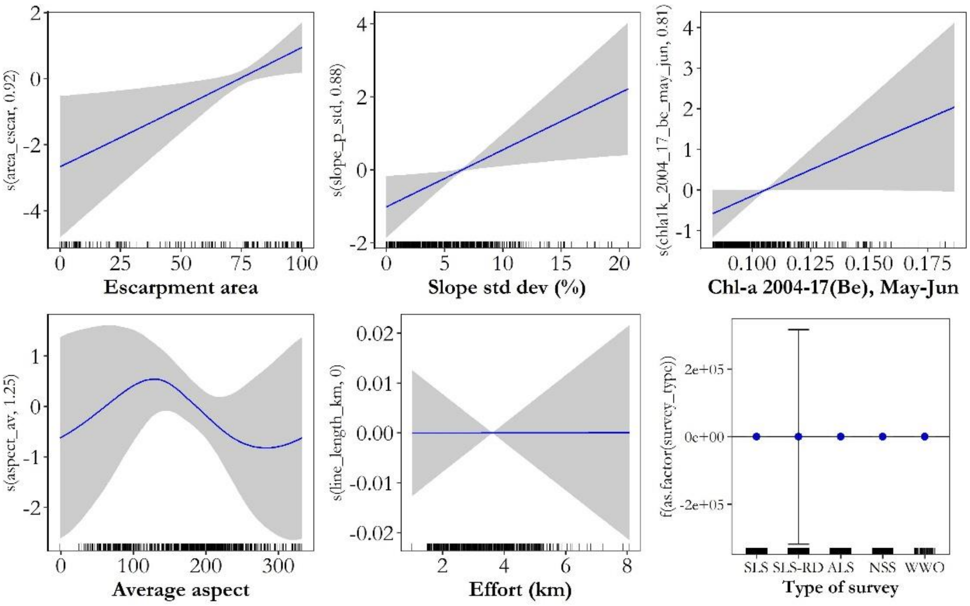


Figure 4.65. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Bryde's whale individuals (relative abundance) in Madeira inshore waters in June/July for the period 2004 – 2017 with one-month time-lag dynamic covariates (May/June). SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; and WWO – whale-watching observers program.

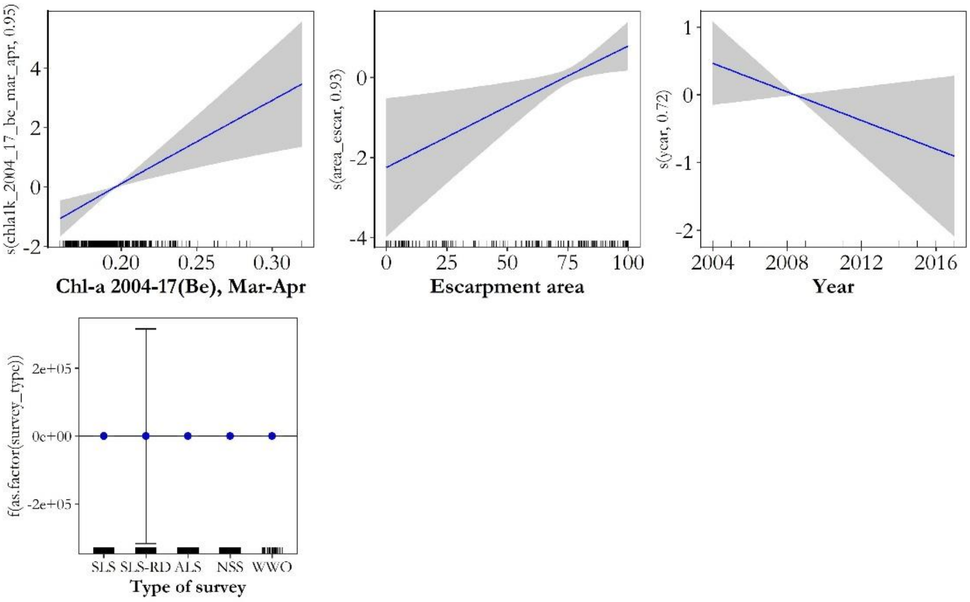


Figure 4.66. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Bryde's whale individuals (relative abundance) in Madeira inshore waters in June/July for the period 2004 – 2017, with two-month time-lag dynamic covariates (March/April). SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; and WWO – whale-watching observers program.

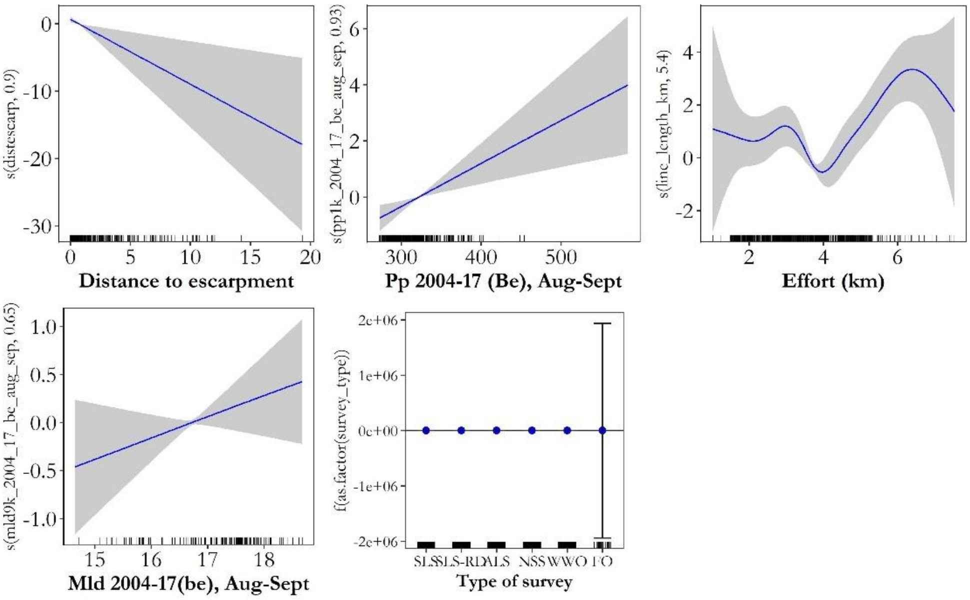


Figure 4.67. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Bryde's whale individuals (relative abundance) in Madeira inshore waters in August/September for the period 2004 – 2017, without time-lag dynamic covariates (August/September). SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; and WWO – whale-watching observers program; and FO – Fisheries observer program.

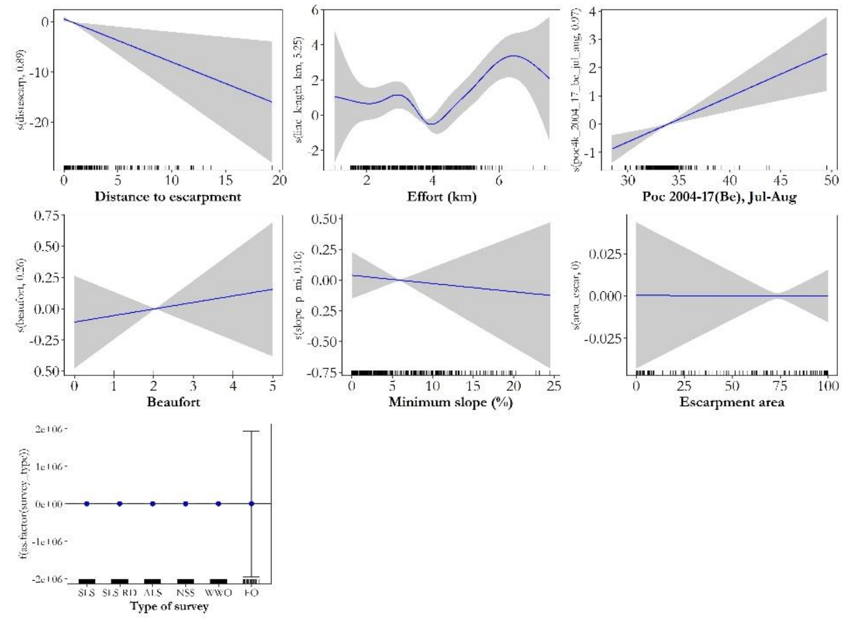


Figure 4.68. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Bryde's whale individuals (relative abundance) in Madeira inshore waters in August/September for the period 2004 – 2017 with one-month time-lag dynamic covariates (July/August). SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – Fisheries observer program.

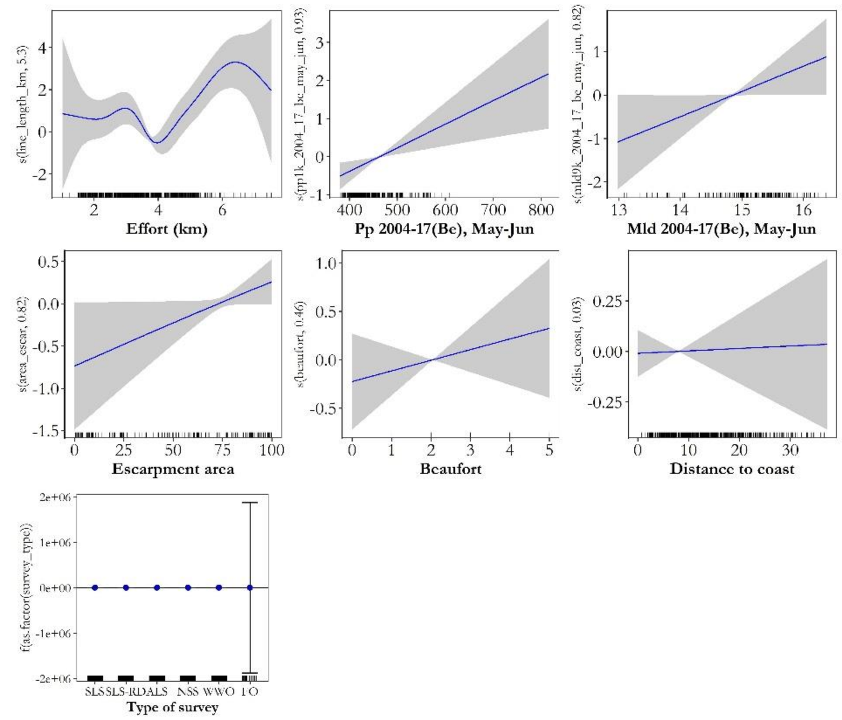


Figure 4.69. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Bryde's whale individuals (relative abundance) in Madeira inshore waters in August/September for the period 2004 – 2017 with two-month time-lag dynamic covariates (May/June). SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – Fisheries observer program.

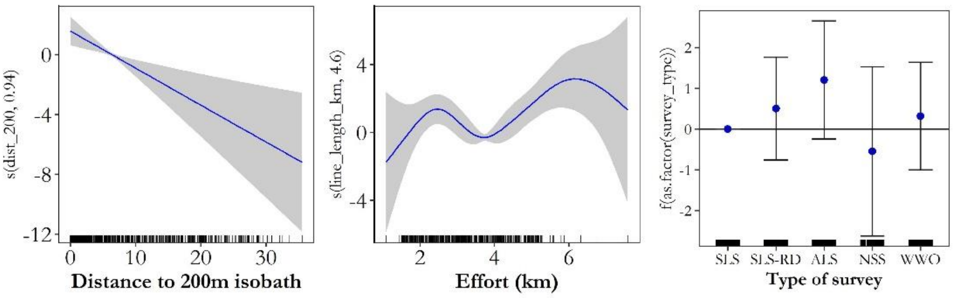


Figure 4.70. Plot of the factor covariate (Type of survey) and smooths of the predictors of the model selected that best explains the habitat use of Bryde's whale individuals (relative abundance) in Madeira inshore waters in October/November for the period 2004 – 2017 without time-lag dynamic covariates (October/November). This was also the final model selected when analysis with one-month (September/October) and two-month (June/July) time-lagged covariates were tested for the October/November dataset. SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; and WWO – whale-watching observers program.

In summary, the results show the decreasing importance of dynamic covariates and the increasing importance of physiographic covariates in explaining the habitat use of Bryde's whales as the bi-monthly models progress from spring to autumn. There is a consistent use by Bryde's whales of waters over the islands' escarpment or nearby depths, as expressed by the selection in most bi-monthly models of the covariates "Escarpment area", "Distance to Escarpment" and "Distance to 200m isobath". These or similar covariates (e.g. "Distance to 500m isobath") were also selected in the best habitat use models of Bryde's whales for the period 2004 – 2017 (Table 4.8) and for two of the three seasons modelled (Table 4.18). However, the local habitat use of Bryde's whales is also strongly related with one to two months' time-lagged chlorophyll-a concentration in the period June-July and with primary productivity and particulate organic carbon concentrations in the period August-September.

The two best models predicting the use of the study area by the Bryde's whales during June – July (no lag and two-month lag), consistently had higher relative abundance in the bay between Madeira and Desertas Islands and east of Desertas, although the model with no time-lag also predicted higher relative abundance northwest of Madeira and north of Porto Santo (Figure 4.71, top row).

For August – September, the best models (no-lag and one-month lag) predicted the use by the Bryde's whales of all waters over the escarpment, but with higher relative abundances around the east end of Madeira island and in the channel between Madeira and Desertas Islands (Figure 4.71, centre row). The no-lag model also predicted higher relative abundances east of Desertas and Porto Santo islands for this period.

The predicted distribution of relative abundance of the species for October – November was consistently closer to shore and more spread around the islands than the two previous bi-monthly periods analysed (Figure 4.71, bottom row).

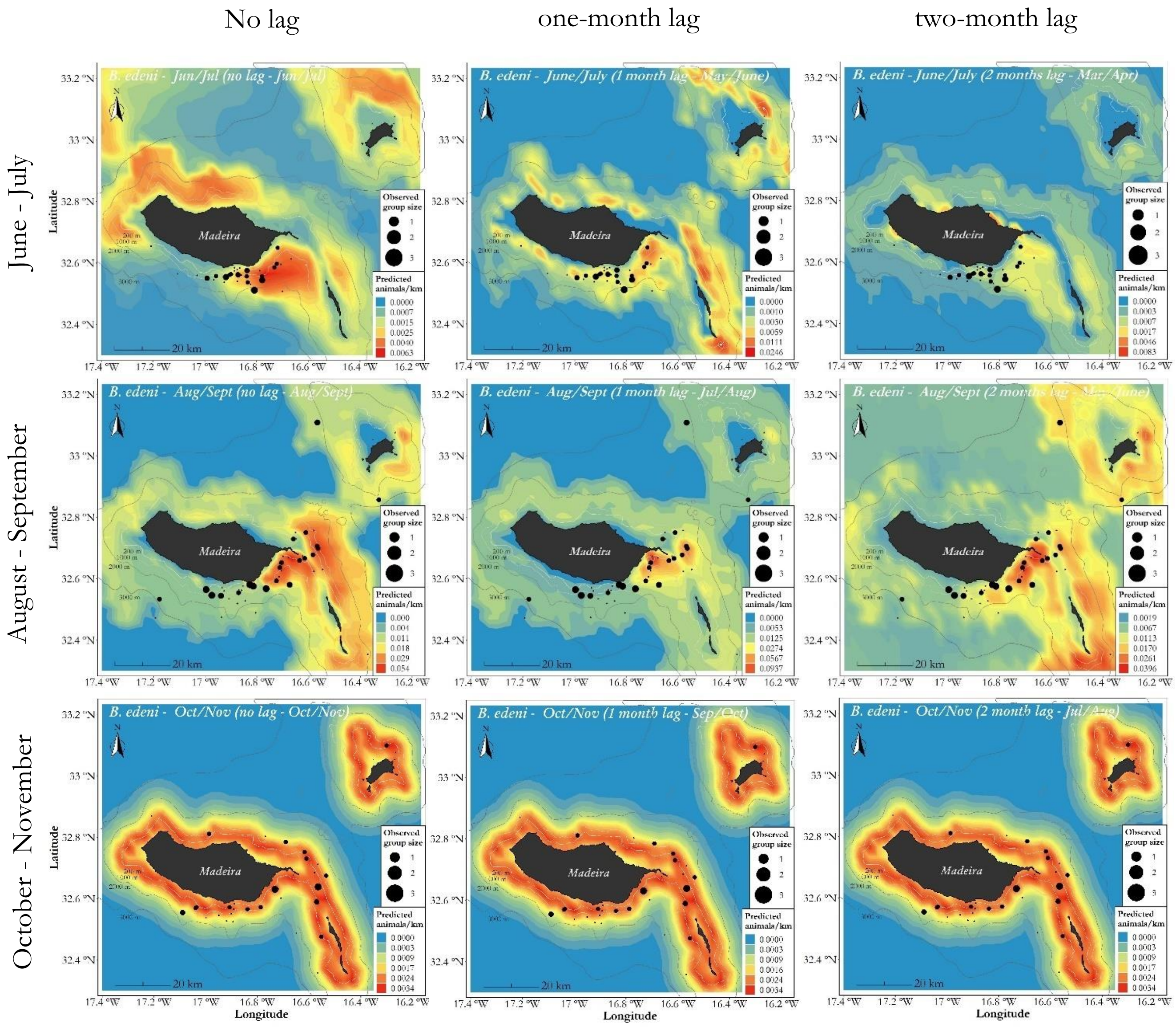


Figure 4.71. Predicted distribution of relative abundance (animals per km of transect line) of Bryde's whales for the months June-July (top row), August-September (centre row) and October-November (bottom row), without time-lagged covariates (left column), with one-month time-lagged covariates (centre column) and two-month time-lagged covariates (right column), for the period 2004 – 2017. The relative abundance scales are specific to each predicted distribution map and not directly comparable among each other. The comparison among the predicted distribution maps should be qualitative, i.e., comparison of the pattern of distribution of higher and lower relative abundance areas within the study area.

4.4 DISCUSSION

Open ocean islands marine environments are usually small but encompass a wide variety of local marine habitats such as coastal, insular shelf and slope, canyons, areas of local upwellings, areas with island induced eddies and nearby deep open ocean. This multitude of habitats provides a diversity of abiotic and biotic conditions and prey available to be explored by cetacean species, according to their characteristics and ecological needs. These small size insular marine habitats have limited productivity, especially in oligotrophic seas and, as a result, limited prey availability. Consequently, a limited density of animals of each cetacean species can be supported and dependent on these habitats, with expected local interspecific competition among sympatric species, especially among those with more similar ecological needs. As such, open ocean islands like Madeira archipelago can be ideal locations to study and understand how cetacean species (populations) share (or compete for) local resources (Thesis overarching question 2; Section 1.3).

To address this question, the most local ecologically relevant cetacean species were determined by combining encounter rates of multiple surveys to understand how frequently and when these species used the Madeira archipelago inshore waters. Species with very few sightings over the years used Madeira archipelago opportunistically and thus are of little local ecological relevance, with the possible exception of a few species of very low detectability such as the beaked whales, pygmy sperm whale or dwarf sperm whale. For the ecologically relevant species, GAMs were used to investigate the relationships between species sightings and environmental variables and predict their overall and seasonal habitat preferences. Moreover, temporal patterns in the species use of the study area were identified, which can be related with underlying local conditions driving their spatial and temporal distribution, including primary productivity and its impact, propagated with delays, through the food web (time lagged variables).

Habitat suitability predictions were made previously for several cetacean species in Madeira archipelago, using maximum entropy methods - Maxent (Fernandez *et al.*, 2021). This modelling exercise was based on presence-only opportunistic whale-watching data, with the limitations, bias and uncertainty associated with it (Phillips *et al.*, 2006; Fourcade *et al.*, 2014; Fernandez *et al.*, 2021), plus a very unbalanced coverage of the sampled area, with far more effort closer to the harbours of operation of the data collecting whale-watching boats. Although there are several approaches to minimize the heterogenous sampling effort, they have very different degrees of success and are very dependent on the species (Fourcade *et al.*, 2014). As pointed out by Booth and Hammond (2014), presence-only methods are subject to bias if effort is not distributed representatively across the area of interest and may generate misleading results in such cases. Furthermore, the data (sightings) in that study only covered a small portion (south of Madeira inshore waters) of the known area of general presence of cetacean species in the archipelago's inshore and nearby offshore waters. Nevertheless, the predictions were extrapolated to much larger area (similar to the area covered by the present study), encompassing different environmental contexts (e.g. inshore vs offshore; south vs north of Madeira; and Porto Santo Island), sometimes beyond the range of sampled covariates (e.g. depth) and, for some species, with a clear bias in the predictions towards inshore waters. Additionally, the predictions while considering temporal changes for every month of the year by rescaling relative habitat suitability estimates, did not reflected expected spatial changes. As such, the habitat suitability predictions made by Fernandez *et al.* (2021) for several cetacean species will not be compared with the results of the present study because of the limitations and likely biases mentioned before, and because equivalent models in each study represent approximations to different local realities.

4.4.1 Methodological considerations

To understand how cetacean populations use and share islands/archipelagos such as Madeira, it is important for the study to encompass an area that is, as much as possible, representative of the marine insular habitats locally available to those species. Furthermore, the study should cover a long enough period (several years) and all seasons of the year to reflect the species overall average habitat preferences (represented by the environmental predictors used in modelling) and species local seasonality, and not be so susceptible to abnormal years, temporary shifts in distribution, or represent very limited local areas and time periods. Mannocci *et al.* (2014b) showed that top predators may not primarily react to short term variations of their environment but may respond better to time-averaged oceanographic conditions, i.e., to persistent (highly predictable) compared to ephemeral (less predictable) environmental situations. As pointed out by those authors this behaviour is consistent with memory-based foraging strategy (Davoren *et al.*, 2003).

As such, this study combined in the analysis several types of surveys that gave a good spatial and temporal coverage of the local marine habitats and their context (e.g. insular shelf, slope, deep open waters; north and south of the islands) (Section 4.2.2). However, joining these different types of surveys brought challenges and potential biases, errors and uncertainty. To address these caveats several steps were taken. Although biases, error and uncertainty in data collection cannot be totally eliminated (e.g. estimation of group size or species identification) they were minimized as much as possible by implementing consistent field protocols and using trained and experienced observers. Although protocols were not strictly the same for all types of surveys because of their different purposes and platforms used, the basic sighting data (e.g. species and group size) and effort data (e.g.

track positions by GPS) were collected generally in the same way and, whenever possible electronically to minimize errors. The major differences were in the systematic (SLS; SLS-RD; and ALS) or non-systematic nature of each type of survey, their more localized or wider spatial coverage of Madeira waters and the existence for some types of surveys of incomplete track lines and/or missing information to identify sections within a transect when the survey platform was "with animals" or in "local activity" (effectively off effort engaging in activities unrelated to cetaceans) (Section 4.2.3). The caveats arising from these major differences among types of surveys were addressed either in data processing or in data analysis. All data were organized, processed, validated and selected following predefined criteria to minimize major inconsistencies among survey datasets (Section 4.2.3).

To address the differences in spatial and temporal coverage of the surveys, effort was explicitly included in the models, together with time related covariates that modelled changes in ER by year and by month of the year. However, the relationship between ER and sampling segment length (effort) was generally non-linear and thus its effect was considered in the models as a covariate rather than an offset. This non-linear relationship might be a consequence of the heterogenous and partially overlapping spatial coverage of the different surveys (especially SLS-RD with a very restricted and coastal coverage) in relation to the species local distribution that resulted in a much lower than expected ER for the most frequent segments lengths (closer to standard segment length - 3.704 km). Nevertheless, this effect was more pronounced for some species than others, with species like the common dolphin, the sperm whale and the striped dolphin, with a more offshore distribution, showing a more linear relationship between ER and segment length. The removal of SLS-RD surveys from the analysis would have minimized considerably this issue but would also result in less observation counts available to model.

Group size is important but always a challenge to estimate in the field, especially for large groups or for groups sighted from far away. As mentioned in Section 4.2.5.2, group size from FO surveys were not used in the calculation of group size statistics because the platforms of observation (fishing vessels) usually did not change their course to approach sighted groups and thus many group size estimates are expected to be negatively biased. However, the group size data collected during FO were used to model group size to have as many observations as possible, accepting the risk of some negative bias in group size estimates in further offshore waters, covered by the FO. To account for this effect "type of survey" was also considered in the group size models as a factor covariate. Nevertheless, no group size model fulfilled the model selection criteria (Section 4.2.5.5) for most species, except the pilot whale. The low number of sightings of this species recorded during FO surveys and the similar effect of FO on the response as other surveys in the factor covariate suggests that this survey's data did not have a negative impact on the estimation of group size.

The detection probability of an animal or group of animals is intrinsic to each species (e.g. size, cues, surfacing frequency and behaviour) and associated with the type of survey and platforms used, and the sighting conditions during the survey (Buckland *et al.*, 2001, 2015; Hammond *et al.*, 2021). The absence of perpendicular distance data for some types of surveys prevented the inclusion in the models of detection probability estimates (effective strip widths) for each species. To overcome this limitation, "type of survey" was considered in the analysis as a factor covariate to account for overall differences in detection probabilities of species among survey types. Although, this approach minimized biases in the surface estimates of relative abundance for a particular species within the study area (e.g. among cells of the prediction grid), the estimates obtained for different models are affected by the factor covariate results and thus are not directly comparable between species or between seasons for the same species. Detection of cetaceans on the surface was also affected by weather conditions. To account for this effect, sea conditions (Beaufort scale) was included in the models as a non-spatial variable.

Despite efforts to minimize biases and errors where possible, the relative abundance (ER) estimates presented here are an approximation of true abundance, primarily because of detection probability was not able to be estimated. One source of bias was perception bias, which results from animals being available at surface to be detected but being missed by the observer. Another source of bias was availability bias, which results from animals being submerged and thus unavailable to be detected. In line transect surveys that use perpendicular distance data to estimate detection probability, perception and availability bias relate to violation of the assumption that all animals are detected on the track line. In this study, however, they related to the whole area sampled, and estimates of ER thus estimate relative abundance. The inclusion of survey type and Beaufort in the models was intended to minimize bias, as far as possible, among prediction cells over the study area. However, this is dependent on the assumption that diving pattern and behaviour was similar throughout the study area for each species, which may not always be the case (e.g. if there were areas preferred for foraging at depth for deep diving species).

The ER calculated for each species is also expected to be underestimated because of errors or uncertainty in species identification. Not all sightings were identified to species level (Figure 4.13) and this varied depending on how easy those species were to identify and the conditions under which they were observed, e.g. distance, weather, etc. Furthermore, some species are less conspicuous than others (e.g. beaked whales) and thus their observed group ER is likely to underestimate relative abundance more than other species. Nevertheless, these biases are not expected to result in much variation in ER spatially, i.e. they should generally be similar across the study area, and thus not affect the predicted distribution of relative abundance.

Another constraint in this study was the limited number of observations for some species (e.g. beaked whale species), which did not allow their relative abundance to be modelled separately. The relationships between observations and environmental variables identified in the models of the pooled Ziphiidae and *Mesoplodon* species, reflect common habitat preferences among the species represented in those taxa and the weight given by the number of observations of each species used in the analysis, rather than the particular habitat preferences of each of those species. Nevertheless, they provide valuable insights to understand how these groups of species use insular marine environments.

A considerable number of environmental variables (40) were selected to represent the varied conditions and habitats that cetaceans may explore in Madeira archipelago waters. However, they do not cover all environmental influences that shape the species habitat preferences, namely prey distribution, which are possibly the most important to explain variability in the data. The selection of environmental variables, namely dynamic ones, was limited by their spatial and temporal coverage of the study area and period, respectively, as well as by their resolution. For some covariates it was necessary to make compromises (e.g. lower resolution) to have a wider number of covariates in the analysis (Section 4.2.4), with the risk of finding diluted effects of these environmental variables on the response as a result of the lower resolution of the covariate.

4.4.2 Relative importance of cetacean species

The annual average group ER of cetaceans in Madeira archipelago waters for the period 2001 – 2017 were dominated by four species (bottlenose dolphin, spotted dolphin, common dolphin and pilot whale), corresponding to 73 % of all sightings (Figure 4.13). Four other species (Bryde's whale, sperm whale, striped dolphin and fin whale) had intermediate ER and together represented 15.6 % of all sightings. These eight species represented the large majority of the sightings (~89%) recorded during the study. Beaked whales also seemed to be important, however, the high percentage of sightings identified only to the family level precludes a better understanding of the relative importance of each of these species. Nevertheless, beaked whales together represented 3.7 % of all sightings, with Cuvier's and Blainville's beaked whales being the most sighted species. Beaked whales, baleen whales, sperm whale and the most common Delphinidae species represented 98 % of all sightings and thus are likely to be locally the most ecologically relevant taxa, although with different degrees of importance depending on their seasonality, abundance of individuals, overall biomasses and roles in the local marine ecosystem. The remaining nine cetacean species represented together only 2 % of all sightings, indicating their marginal presence and thus expected minimal ecological relevance in the local marine ecosystem.

The group ER also showed that most species with an important presence in the archipelago had some seasonal patterns of relative abundance, even those with known year-round presence (bottlenose dolphin and pilot whale) (Figure 4.19 – Figure 4.20). Seasonal patterns in group size were also observed for some species (Figure 4.14 – Figure 4.18), although they were not nearly as marked as in the sightings ER (the effect of month over the response was small or non-existent)(Figure 4.18). These observed seasonal changes in group size may be real for some species but may also reflect better weather conditions that allow the detection of animals that otherwise would go unnoticed, especially in species with larger more dispersed groups (e.g. small dolphin species). However, the seasonal patterns revealed by the smooth of ER of individuals (combining seasonal changes in sightings ER and group size) are more relevant to understand how these cetacean species use Madeira archipelago waters.

The relative abundance of individuals of almost all species modelled changed seasonally in Madeira archipelago waters (Figure 4.21) and showed that these waters are for most, if not all individuals of these species, only part of a much wider distributional range, encompassing other habitats also important for their survival and fulfilment of their biological and ecological needs. Nevertheless, the seasonal return of these species, and many times the same animals (e.g. Chapter 3, Bryde's whales; Alves *et al.*, 2013, short-finned pilot whale; Dinis *et al.*, 2016b, bottlenose dolphin), to the Madeira archipelago is a testimony of its importance for their survival.

4.4.3 Habitat use by dolphin species

Bottlenose dolphin

Although bottlenose dolphins have mostly a coastal distribution, they are also present in pelagic waters, near oceanic islands, and over the continental shelf, especially along the shelf break (Wells and Scott, 2018). The more coastal distribution of the species in open ocean islands found in previous studies for other archipelagos (Dulau-Drouot *et al.*, 2008; Baird *et al.*, 2013a; Silva *et al.*, 2014) and for Madeira (Freitas *et al.*, 2004c; Dinis, 2014), is confirmed by this study for Madeira, but with a more robust dataset.

In spite of the wide number of physiographic, oceanographic and productivity variables tested, the selected group model only included "Distance to coast" to explain the overall mean distribution of the bottlenose dolphin throughout the year for the study period. This result indicate that the species has a wide distribution around all the archipelago islands, with a stronger preference for more coastal waters. However, the habitat preferences changed seasonally, with the distribution in autumn and winter spread further offshore, over the islands slopes and in deeper pelagic waters, in spite of maintaining an overall higher relative abundance closer to shore (Figure 4.42, Figure 4.45 and Figure 4.46). Usually slopes are associated with currents and high slopes induce prey aggregation or enhanced primary production (Virgili *et al.*, 2022). In spring and summer the species was closer to shore, where they may have taken advantage of the higher island associated productivity and prey aggregation effect (Fiedler, 2009; Virgili *et al.*, 2022). In spring, their more concentrated distribution in the north of Madeira island and in the channel between Madeira and Desertas Islands was associated with higher primary productivity and shallower mixed layer depths in shallower waters closer to shore, over the shelf break and slope (Figure 4.43 and Figure 4.46), probably associated with local upwellings and the increase in sun-light incidence (spring bloom)(Mann and Lazier, 1991; Caldeira *et al.*, 2002; Friedland *et al.*, 2016). In summer, the bottlenose dolphin distribution continued close to shore but spread out around Madeira, Desertas and Porto Santo, and possibly more associated with local upwelling areas, as suggested by the strong negative effect of the covariate "Sst-a 2001-17, Summer" on the response (Figure 4.45 and Figure 4.46).

To understand the local seasonal patterns of the bottlenose dolphin and other cetacean species, it is important to consider the seasonal patterns of primary productivity in Madeira archipelago's surrounding waters (Section 4.1) (Figure 1.2). In general, the primary productivity reaches is maximum during winter and spring decreasing in summer and reaching a minimum in autumn (Caldeira *et al.*, 2002; Martins *et al.*, 2007). A generally similar pattern is seen in the monthly average values of the productivity related dynamic environmental variables used in the study for the period 2001 – 2017 (Figure III.3-4, Appendix III).

Bottlenose dolphins are present year-round in Madeira inshore waters, with a small percentage (< 5%) classified as residents (Freitas *et al.*, 2004b; Dinis *et al.*, 2016b). Contrary to the results of Dinis *et al.* (2016b, 2016a), this study found a seasonal variation in relative abundance of groups and group size (Figure 4.18 – Figure 4.20 and Figure 4.44), manifested as an increase of the relative abundance of individuals from spring to summer (Figure 4.21), as a result of an influx of animals into the study area. This influx of animals coincides with the concentration of their distribution closer to the coast, driven probably by the increase in local island-associated coastal primary productivity in the previous seasons, and resulting in more prey available at higher trophic levels in the summer. Conversely, the overall relative abundance of individuals decreases in autumn and winter, indicating a net movement of animals away from the archipelago's waters. Simultaneously, the animals present in these seasons spread out in the study area possibly in an attempt to find prey in a wider area to compensate for the more coastal depletion of prey.

The estimated group size of bottlenose dolphins (median = 12; mean = 16) in this study was similar to the median value reported by Dinis *et al.* (2016b) and slightly lower than the mean group size (18) reported by Silva *et al.* (2014) for the Azores. Dinis *et al.* (2016b) proposed that the increase in group size in summer/autumn was a consequence of the arrival of larger transient pelagic groups. Those authors also reported that although groups with calves were recorded year-round, they were more common in spring and late summer/autumn, indicating a preferential period of the year for calving, possibly due to warmer conditions during those months. This study results suggest that the seasonal increase in local productivity provided the prey availability to not only attract animals to the area but possibly also for females to have enough prey in spring and summer to compensate for their gestation and lactation energy demands. Furthermore, the increase in group size might not only be a consequence of the arrival of larger offshore transient groups but also result from the aggregation of animals in larger groups for mating reasons, considering the 12.5 months gestation period (Wells and Scott, 2018), the late summer/autumn peak in birthing and this species dynamic and fluid social structure (Dinis *et al.*, 2018).

Bottlenose dolphins showed an increase in relative abundance over the study period (Figure 4.22). However, this increase was uneven among seasons. While in winter there was a steady increase followed by a quick reduction (Figure 4.42), in spring there was a constant positive trend throughout the study period (Figure 4.43). In summer and autumn, the relative abundance did not seem to change much from 2001 to 2017; the covariate “Year" was either non-significant or was not selected in those seasons’ models. These results suggest that the local habitats may have reached their maximum capacity to sustain the species in summer and autumn. However, the increase in relative abundance of animals in winter and spring, may have been supported by an increase in productivity locally (Figure III.3-4, Appendix III) and in the wider open ocean area around Madeira (Section 3.4.6) (Siemer *et al.*, 2021). In winter the smooth of the variable “Year” reached a plateau in 2008 that was maintained at least until 2012. This plateau may be an indication that the archipelago reached its maximum capacity to sustain bottlenose dolphins during that season under the productivity conditions at the time. The negative slope observed in winter after 2012 can be explained by a lack of effort in the north of Madeira and further offshore waters where the species spreads out in that season.

Spotted dolphin

The spotted dolphin is endemic to the tropical and warm temperate waters of the Atlantic Ocean, inhabiting continental waters (shelf, shelf break and slope) on both sides of the oceanic basin, as well as open ocean waters (Freitas *et al.*, 1998; Silva *et al.*, 2014; Herzing and Perrin, 2018). The smaller and less-spotted form inhabits more pelagic and offshore waters, including habitats around oceanic islands like Madeira and the Azores (e.g. Freitas *et al.*, 1998; Silva *et al.*, 2014), although their particular habitat preferences are less well known (Braulik and Jefferson, 2018).

The areas with higher relative abundance of spotted dolphins were further offshore than the bottlenose dolphin over the islands' slopes, in clearer deeper waters with a warmer water column, as suggested by the predicted distribution (Figure 4.25) and both the static ("Distance to escarpment" and "slope area") and dynamic variables ("Poc 2001-17" and "Ssh 2001-17") selected by the best model (Figure 4.24). This overall distribution shows a clear relation of the species with the pelagic habitats over the islands' slopes probably to take advantage of the islands' associated prey availability and aggregating effect (Fiedler, 2009; Virgili *et al.*, 2022), both epipelagic shoaling fish and mesopelagic prey (Dinis *et al.*, 2008; Quérouil *et al.*, 2013; Silva *et al.*, 2021). However, the overall habitat preferences in the study area also changed throughout the year, both in relative abundance and spatial distribution. In winter, the animals present in the study area were distributed closer to the islands with a preference for areas with steeper slopes (Figure 4.47 and Figure 4.51), possibly taking advantage of the islands prey aggregating effect (Fiedler, 2009; Virgili *et al.*, 2022). In spring, the distribution shifted to the south of Madeira still over the island slope but spread further offshore (Figure 4.51). In this season, these animals showed a preference for warmer waters with low chlorophyll-a concentrations but high concentration of particulate organic carbon (Figure 4.48). Chlorophyll-a is an indirect measure of phytoplankton concentration, while particulate organic carbon measures the concentration of living material (phytoplankton, zooplankton, bacteria, etc.) and detritus. The latter variable is often used as an indicator of productivity in the euphotic zone (Fingas, 2018). These variables' smooths (Figure 4.48) suggest that spotted dolphins preferred waters with lower concentrations of phytoplankton and higher concentrations of zooplankton in the spring. This apparent contradiction is probably the consequence of phytoplankton (growing over the slopes or nearby offshore waters or exported from the coastal waters) (Caldeira 2012) being grazed by zooplankton, thus keeping its concentration low. The day time prey of spotted dolphins (e.g. horse mackerel and other epipelagic fish) feed on zooplankton (Romero *et al.*, 2021; Silva *et al.*, 2021), possibly explaining the suspected presence of epipelagic fish and thus of spotted dolphins in these areas. *In situ* measurements of zooplankton in early spring, confirm high biomass of zooplankton in the south of Madeira (Alves and Kaufmann, 2003). In summer, spotted dolphins' distribution spread to offshore waters all around the archipelago (Figure 4.51), possibly to ease competition with bottlenose dolphins with a further inshore presence and to take advantage of prey availability in offshore waters. The wider distribution of spotted dolphins around Madeira archipelago may reflect a wider distribution of prey around the islands because of increased marine biological productivity and its export to further offshore waters. The increased marine biological productivity seems to be driven by the bloom happening in late winter and spring, by the occasional West Africa productive filaments reaching the archipelago, or by the intrusions of the Azores front, with associated meanders and eddies that stir the waters and contribute to an increase in productivity (Caldeira *et al.*, 2002, 2014; Campuzano *et al.*, 2010). Additionally, the anticyclonic eddies generated by the "islands mass effect" happen throughout the year, including the summer, and export part of the marine biological productivity to further offshore waters (Caldeira *et al.*, 2002, 2014; Caldeira and Sangrà, 2012). In autumn, the species distribution shifted to the slope areas north and northeast of Madeira island, possibly to take advantage of prey availability as a consequence of the increasing biological productivity along the north coast of Madeira when compared with the south in that season (Caldeira *et al.*, 2002; Martins *et al.*, 2007).

The spotted dolphins, like the bottlenose dolphins, were present year-round in Madeira archipelago, but with a more marked seasonality in relative abundance (Figure 4.19 – Figure 4.21 and Figure 4.24). Spotted dolphins' relative abundance of individuals reached its minimum at the beginning of spring (April), followed by a steep increase until a maximum in July. The rapid increase in the relative abundance of animals during spring is driven by the influx of new animals mostly to the south of Madeira Island, organized in smaller groups. This seasonal arrival of animals happens probably to take advantage of the wider prey availability resulting from the higher local primary productivity in winter and spring. In summer and autumn, the spotted dolphin relative abundance slowly decreases until the beginning of winter, apparently in response to the expected decrease in prey biomass availability closer to Madeira. Predation and lower primary productivity in these seasons are expected to contribute to the decrease in the local availability of prey biomass. However, at the same time, during those seasons the species expands its distribution to deeper offshore waters forming increasingly larger groups, possibly to enhance the chances of finding sparser prey agglomerations in open waters. The formation of larger groups increases foraging efficiency of shoaling fish and can be a response to minimize predation in open waters (Gowans *et al.*, 2007; Heithaus *et al.*, 2018). During winter, most of the animals leave the area, with those remaining coming closer to shore, organized in smaller groups, until the new influx of animals, in April. The differences between group ER seasonal fluctuations (Figure 4.19) and group size seasonal fluctuations (Figure 4.18) seem to be driven by group size dynamics associated with a more inshore or offshore distribution of the animals and differences in foraging strategies in those habitats (Gowans *et al.*, 2007; Heithaus *et al.*, 2018).

The spotted dolphin showed fluctuations in relative abundance of groups during the study period (Figure 4.24). The possible reasons for such patterns are discussed below together with the Bryde's whale, another tropical species that showed a similar pattern (Section 4.4.5, Bryde's whale). Nevertheless, in winter (Figure 4.47), the smooth of the variable "Year" had a relatively similar pattern as the bottlenose dolphin, suggesting an increase in the relative abundance of the species until 2008 possibly reaching the local maximum capacity to sustain spotted dolphins. After 2008, it is not clear if the levels of relative abundance of the species decreased as the variable smooth shows or reached a plateau, but the variable smooth curve changed to a negative slope for reasons already explained for the bottlenose dolphin.

Common dolphin

The common dolphin is present in tropical and warm-temperate oceanic waters of the world, from near shore to offshore waters (Hammond *et al.*, 2008; Perrin, 2018b). Their presence may be seasonal and changing according to fluctuations in sea-surface temperature (Henderson *et al.*, 2014; Campbell *et al.*, 2015). The common dolphin appears to have a preference for prominent bottom topographic features like escarpments, sea mounts and continental shelf areas, although it may also be associated with upwelling-modified habitats with less tropical characteristics than surrounding water masses (Evans, 1994; Perrin, 2018b). The seasonal presence of the common dolphin in Madeira archipelago is well known (Freitas *et al.*, 2004a), but not so much their local habitat preferences.

The common dolphins had a wide predicted distribution in Madeira archipelago both inshore and offshore, however with a much lower relative abundance of individuals in further offshore waters south and southwest of Madeira Island (Figure 4.27). This overall distribution shows a preference for both pelagic and coastal habitats that seem to be mostly driven by a preference for areas of higher concentration of phytoplankton, areas with waters warmer than average and, to a lesser extent, a preference for slope areas, as suggested by the environmental covariates of the selected model (Figure 4.26). As for the spotted dolphin, the wider distribution of common dolphins around Madeira archipelago may reflect the wider availability of prey around the islands, as a result of the increased marine biological productivity during winter and spring (Figure III.3-4 and Figure III.3.5, Appendix III) associated with the spring bloom, intrusions of the Azores front and the "islands mass effect" (Caldeira *et al.*, 2002, 2014; Campuzano *et al.*, 2010), including the export to offshore waters of coastal productive waters (Caldeira and Sangrà, 2012; Caldeira *et al.*, 2014).

Although primary productivity seems to be an important driver of the species overall local habitat preferences, its distributions in winter and spring were explained by sea-surface temperature related variables (Figure 4.49 and Figure 4.50) and, in the latter season, also by the preference for slope areas. In winter, the common dolphin's distribution seems to be mostly driven by the temperature gradient and temperature differences between the north and the south of Madeira.

The species known highly seasonal presence in winter and spring is confirmed by the much higher relative ER of groups (Figure 4.19) and predicted relative abundance of individuals, as shown by the smooth "Month" of the selected model (Figure 4.26). During all seasons, except summer, group size was around 20 animals (Figure 4.16 ,Table IV.2.2-1, Appendix IV). However, in summer, when the species was mostly absent from Madeira waters, the few groups seen were much larger than in the rest of the year (mean = 58; Figure 4.16 ,Table IV.2.2-1, Appendix IV), resulting in a smaller peak in the relative abundance of individuals in the study area in September (Figure 4.21). This increase in relative abundance of individuals (fewer but larger groups) in a single month in the middle of a period of low presence of the species in Madeira is surprising and not easily explained. It could be larger offshore groups passing by Madeira archipelago in seasonal migration or the beginning of the yearly seasonal arrival of common dolphins to the study area but staying further offshore (outside the study area) to minimize competition with the spotted dolphins and bottlenose dolphins while they are in higher numbers around Madeira archipelago. Actually, the increase in the relative abundance of common dolphins coincides with the decrease in relative abundance of spotted dolphins and, especially, of bottlenose dolphins, during autumn and winter.

Striped dolphin

The striped dolphin lives in the pelagic environment, usually over the continental slope and oceanic waters, frequently in areas influenced by upwelling, convergence zones and edges of currents (Archer, 2018). They have also been associated with temperatures ranging between 10 °C to 26 °C, although mostly 18 °C to 22 °C (Archer and Perrin, 1999).

Around Madeira archipelago, the striped dolphin had a higher predicted relative abundance of individuals further offshore than the previous dolphin species, in cooler waters with lower primary productivity (oligotrophic), as indicated by the predicted distribution and environmental variables ("Chl-a 2001-17", "Average depth" and "Sst 2001-17") of the selected model (Figure 4.28 and Figure 4.29). The predicted distribution also indicated a much lower presence or even absence from shallower inshore waters. The species preference for further offshore waters is in accordance with what is known for other open ocean archipelagos such as the Hawaiian Islands and the Azores (Section 4.3.3) (Baird *et al.*, 2013a; Silva *et al.*, 2014).

Although the species showed some seasonality in the relative abundance of groups (increase in late winter and early spring), the group size and the relative abundance of individuals showed no seasonal patterns (Figure 4.19 – Figure 4.21), indicating an apparent lack of association of the species with the seasonal variation in biological productivity around Madeira archipelago (Caldeira *et al.*, 2002; Martins *et al.*, 2007). However, the seasonal increase in relative abundance of groups may also mean that striped dolphins groups stay longer in the study area at the end of winter and beginning of spring to take advantage of the increased local biological productivity (Figure III.3.4, Appendix III; Figure 4.20).

The relatively low ER of groups (Figure 4.13), the lack of permanence or seasonality in the use of the study area (intermittent presence) (Freitas *et al.*, 2004b) and the habitat preferences of striped dolphins for deep offshore waters, suggest an overall lack of association or dependence of the species of the islands' more inshore marine habitats. Additionally, it can be inferred from the inclusion in the selected model of the physiographic variable "Average depth" and, mostly, of the dynamic variables "Chl-a

2001-17" and "Sst 2001-17" (Figure 4.28) that striped dolphins have a preference for the offshore open ocean habitats where their distribution may be more associated with dynamic oceanographic features, such as currents, fronts and the dynamic features associated with them (e.g. divergence and convergence zones, and front-generated meanders and eddies). It is also possible that island generated features (cyclonic and anticyclonic eddies) propagating to offshore waters are among this species habitats explored in offshore waters. The Azores current and the related Azores front (subtropical front), the islands' generated eddies (Caldeira *et al.*, 2002, 2014; Campuzano *et al.*, 2010) and the occasional intrusion of West Africa productive filaments (Caldeira and Sangrà, 2012) are probably among the open ocean habitats explored by this species in the vicinity of Madeira archipelago. Striped dolphins' presence closer to the archipelago's islands, especially in inshore waters, may be opportunistic as they pass by these waters or may be driven by the dynamics of the above-mentioned oceanographic features, including the formation and path of eddies generated by the islands or the intrusions near Madeira archipelago waters of the Azores front or West Africa productive filaments. Other cetacean species are known to take advantage of these offshore dynamic oceanographic features (Woodworth *et al.*, 2012; Rone *et al.*, 2015; Thorne *et al.*, 2017).

The negative relationship between relative abundance of striped dolphins and the concentration of chlorophyll-a (Figure 4.28) may be a proxy for the species preference for more oligotrophic waters, with lower productivity. Alternatively, that negative relationship may indicate a preferential association of the species with oceanographic features (e.g. eddies or fronts) to feed on higher trophic level prey, at a stage in time when the phytoplankton biomass (low chlorophyll-a signature) has subsided due to zooplankton grazing, which in turn increases the latter group's biomass and attracts fish and other predators. There is some evidence of community successions in fronts and eddies, although many factors enter into play that may affect the local productivity, community structure and succession, including the attraction or not of higher trophic level predators (Vinogradov and Shushkina, 1984; Bakun, 2006; Gruber *et al.*, 2011; Lévy *et al.*, 2018; Abdala *et al.*, 2022).

4.4.4 Habitat use by deep divers

Short-finned pilot whale

Pilot whales are usually found in tropical and subtropical waters of the world (Olson, 2018), being reported around many open ocean islands across their distributional range where they have been consistently reported having a preference for waters between 1 000 to 2 500 m (e.g. Dulau-Drouot *et al.*, 2008; Freitas *et al.*, 2014a; Prieto *et al.*, 2014; Servidio, 2014; Abecassis *et al.*, 2015; Hill *et al.*, 2019).

The species is known for its deep diving, with regular dives ranging between 600 m and 1 000 m and lasting around 20 minutes (Aguilar de Soto *et al.*, 2008; Wells *et al.*, 2013; Thorne *et al.*, 2017).

Overall, the areas with higher relative abundance of individuals were south-southeast of Madeira and west-northwest of Desertas Islands, mostly in waters around 1 500 m deep, with a smoother bottom (with less abrupt changes in depth), higher particular organic carbon and shallower mixed layer depths, as indicated by the predicted distribution (Figure 4.32) and the variables of the selected model (Figure 4.30). The distribution of the species sightings is explained by physiographic ("Distance to 1500m isobath" and "Contour index") and dynamic environmental variables ("Poc 2001-17" and "Mld 2001-17"), indicating a clear association with the islands, but also with areas of higher concentration of living matter, presumably plankton (Fingas, 2018). Some degree of spatio-temporal decoupling between areas of higher concentration of plankton and higher concentrations of higher trophic level predators like the pilot whale is expected in a dynamic marine environment. However, in this case the area with higher predicted relative abundance of pilot whales is near and downstream of a known upwelling area which usually has higher productivity than the surrounding areas (shallower waters in the channel between Madeira and Desertas Islands) in winter, spring and summer (Caldeira *et al.*, 2002). This suggests that the bay between southeast Madeira and Desertas slands benefits from the primary productivity generated in the channel between the islands and retains at least part of the subsequent biomass, generated at higher trophic levels, thus attracting the pilot whales. There is evidence of coastal convergence and downwelling processes taking place in the north of the bay, which help disperse and take zooplankton to deeper waters (Caldeira *et al.*, 2001).

Nevertheless, the species habitat preferences changed seasonally, maintaining however the bay southeast of Madeira as an important area (Figure 4.59). Regardless of season the species had an offshore distribution beyond the 1 000 m isobath, being mostly absent from the islands' shelves. In autumn and winter the species predicted distribution was mostly south-southwest of the islands, especially in winter. In spring and summer, the animals dispersed around the islands. The majority of the environmental variables explaining the distribution of pilot whale groups were related with physiographic features, such as slope and depth (Figure 4.55 – Figure 4.58). The only exception was mixed layer depth, "Mld 2001-17, Summer", probably reflecting the higher relative abundance of individuals in the south of Madeira (leeward side of the island) where warm water island wakes are formed in this season, with a stable vertical thermocline (Caldeira *et al.*, 2002; Caldeira and Tomé, 2013) and, consequently, a shallow mixed layer depth.

In comparison with surface dwelling species (dolphins and baleen whales), it is more difficult to associate and interpret the distribution of pilot whales and other deep diving species, in the context of productivity-related environmental variables and their seasonal changes. These variables (e.g. Chlorophyll-a or particulate organic carbon) are usually proxies of primary productivity measured on the sea surface, while deep diving species feed mostly on prey resources much higher in the trophic chain and located much deeper in the water column. As such the distribution of primary productivity and the distribution of deep diving species is spatio-temporally decoupled by their trophic level temporal gap and the spatial dynamics of the marine environment over time. Nevertheless, the changes in distribution of pilot whales may be captured by the relationships with physiographic variables if the distribution of prey positioned higher in the food chain (usually larger prey with more independent mobility from the surrounding medium) is less and less determined by the distribution of primary productivity and more influenced by other factors, such as predictability of resources (Baird *et al.*, 2008; Mannocci *et al.*, 2014b) and the prey aggregating effect of physiographic features such as islands and seamounts and their slopes (Genin, 2004; Morato *et al.*, 2008; Fiedler, 2009; Virgili *et al.*, 2022).

Pilot whales are present year-round in Madeira inshore waters, with a small percentage (11.4%) classified as residents (Freitas *et al.*, 2004b; Alves *et al.*, 2013). This study found a significant seasonal variation in relative abundance of groups and group size (Figure 4.18 – Figure 4.20 and Figure 4.30), translated into an increase of the relative abundance of individuals from summer to autumn (Figure 4.21), like the bottlenose dolphin. This influx of animals coincided with a gradual concentration of their distribution in the bay southeast of Madeira in autumn, possibly driven by prey availability in the area as a result of higher productivity in the bay and in the local upwelling in the channel between Madeira and Desertas Islands, in the previous seasons (Caldeira *et al.*, 2002). Additionally, animals of different residency patterns may aggregate in the area to breed at the end of summer and beginning of autumn, as proposed by Alves *et al.* (2013), and supported by the observed increase in number of visitors and the statistically significant higher proportion of groups composed of animals of different residency patterns. The relative abundance of pilot whales decreases in winter, after the peak in October, with a net emigration of animals away from the study area, while the remaining animals continue to have preference for the same areas used in the previous season. The minimum relative abundance of animals was reached in spring, coinciding with an expansion around the islands of the species distribution in the archipelago. The seasonal fluctuations in the relative abundance of pilot whales around Madeira possibly reflects the time delay between the increase in primary productivity at the beginning of the year and the increase of the higher trophic level prey species biomass, on which the pilot whales depend to feed.

The estimated group size of pilot whales (median = 12; mean = 14.7) in this study was lower than the value reported by Alves *et al.* (2013) and larger than the mean group size (9.4) reported by Silva *et al.* (2014) for the Azores. Contrary to the results of Alves *et al.* (2013), this study showed a significant variation in group size over the year, increasing during spring and summer and decreasing in autumn and winter, although large groups were observed in all seasons (Figure 4.16 and Figure 4.18; Table IV.2.2-1, Appendix IV). Larger group sizes tended to be recorded further offshore, at depths closer to the 2 000 m isobath, while more groups were found closer to shore at the 1 500 m isobath (Figure 4.30 and Figure 4.31). Additionally, larger groups were recorded along the south and southeast coast of Madeira (Figure 4.32), suggesting that either larger groups used that area or, more likely, groups came together to breed and socialize in that core area.

Pilot whales, like the bottlenose dolphins showed an increase in relative abundance over the study period (Figure 4.30), mostly in winter (Figure 4.55). In the remaining seasons, the covariate "Year" was either non-significant or was not selected in those seasons' models, suggesting that the local habitats may have reached their maximum capacity to sustain animals or the animals have preference for other habitats outside the study area. The increase in relative abundance of animals in winter, may have been supported by the increase in biomass at higher trophic levels later in the year as a consequence of the increase in local productivity (Figure III.3-2 and Figure III.3-4, Appendix III) and in the wider open ocean area around Madeira over recent years (Siemer *et al.*, 2021), as mentioned previously.

Sperm whale

The sperm whale is one of the cetacean species with the widest worldwide distribution, ranging from the equator to close to ice-edge high latitude waters, in both hemispheres. Sperm whales are deep divers with preference for waters usually far from land, over and beyond the continental slope deeper than 1 000 m, except for oceanic islands. The species habitat preferences include areas of higher primary productivity (e.g. upwelling areas) than the surrounding waters (Whitehead, 2018). Sperm whales are known to have a year-round presence in Madeira (Freitas *et al.*, 2004b), which seems to be intermittent and consistent with nomadic behaviour also observed in the Pacific (Mizroch and Rice, 2013).

No seasonal pattern was identified in relative abundance of groups (Figure 4.20) or in group size (Figure 4.18). The sperm whale's use of Madeira archipelago waters does not seem to be driven by the seasonal increase in local productivity, as in other cetacean species (e.g. most delphinidae and Bryde's whale). Their presence is either opportunistic or, possibly, driven by factors outside the study area. The very low site fidelity and short permanence periods on average around Madeira archipelago (0.8 days) found by a photo-identification study (Ferreira *et al.*, 2022), give support to this interpretation. Nevertheless, it would be expected that sperm whales coming to Madeira would at least stay longer around the archipelago's islands to take advantage of local prey resources when more prey biomass was available as a result of the seasonal increase in primary productivity and the subsequent cascade increase in biomass at higher trophic levels. This hypothesis is supported by the increase in relative abundance of sperm whales (Figure 4.21) from summer to autumn, albeit not statistically significant.

Although, in general, sperm whales do not seem particularly attracted to open ocean islands (Section 2.3, Deep divers), when around Madeira archipelago they showed a preference for certain habitat characteristics. Their distribution of relative abundance was mostly concentrated in slope areas of the northern side of the islands, although their presence was also predicted and observed over the southern facing slopes of the islands (Figure 4.34). They were absent from shallow waters over the insular shelf and had a very low predicted relative abundance further offshore waters over the abyssal plain. The species preference for slope areas with a particular orientation is in accordance with studies in other areas (Waring *et al.*, 2001; Pirotta *et al.*, 2011; Rogan *et al.*, 2017). Slopes are known to induce prey aggregation (Virgili *et al.*, 2022), including mesopelagic fish and cephalopods (Röpke *et al.*, 1993; Boyle and Boletzky, 1996; Quetglas *et al.*, 2000).

The sperm whale, like the striped dolphin, did not show a seasonal trend or dependency on the archipelago, using mostly offshore habitats outside the study area. Both species, unlike most others, did not show an increase in relative abundance of individuals over the study period, which supports the interpretation that the presence and abundance of these species is not driven by local conditions, such as an increase in productivity during the study period in the study area reported by Siemer *et al.* (2021).

Beaked whales

Beaked whales are oceanic species with a preference for deep offshore waters, usually over 200 m deep (beyond the continental shelf), coming closer to land around oceanic islands. This group of species is associated with areas of complex seabed topography where deep-water currents interact with the seabed (MacLeod, 2018). Five beaked whale species have been recorded in Madeira archipelago, namely Cuvier's beaked whale, Blainville's beaked whale, Sowerby's beaked whale, Gervais' beaked whale and northern bottlenose whale (Freitas *et al.*, 2012; Ferreira *et al.*, 2017), with the first two species being probably the most common in the area (Section 4.3). These species are expected to have specific habitat preferences within the overall habitat preferences shown by the Ziphiidae family.

The predicted distribution of relative abundance of individuals showed a clear preference of *Mesoplodon* species and beaked whales as a whole for offshore waters with deeper mixed layer depth (Figure 4.35 – Figure 4.37). The physiographic variable "Aspect std dev" was also selected in the models of both taxa, albeit not significant for *Mesoplodon*. This variable negative relationship with the response suggests an overall preference of these taxa for flatter or a less rugged sea floor (less changes in the orientation of the sea floor). However, the covariates tested in the models probably do not reflect directly (i.e. they are proxies) the ecological factors driving beaked whale distribution, especially the dynamic covariates, which represent habitat features closer to the sea surface (e.g. sea surface temperature, mixed layer depth). For example, the depth of the mixed layer depth is driven by processes at the surface (wind, surface currents and waves), which apparently have no direct influence on the deep-sea habitats relevant for the beaked whales. Furthermore, the very limited number of observations of each beaked whale species (Table 4.7), forced the grouping of sightings by genus (*Mesoplodon*) and family (Ziphiidae) to reach an acceptable number of observations for modelling. However, these beaked whale species probably have specific and different habitat requirements. Pooling together observations of different species may result in non-significant relationships with some covariates that otherwise could be relevant. It also prevents the investigation and understanding of the ecological requirements and drivers of each species local habitat use and distribution. For example, in general, Blainville's beaked whales prefer relatively shallow waters with a steeper seabed, especially around oceanic islands, while other beaked whale species prefer areas with deeper waters and gentler seafloor gradients (MacLeod, 2005).

These results are in line with the known preference of beaked whales for offshore waters (Section 2.3, Deep divers), but contradicts current knowledge that they associate with areas of complex seabed topography (MacLeod, 2018). Both mixed layer depth ("Mld 2001-17") and the standard deviation of aspect ("Aspect std dev") are probably proxies for further offshore waters. The mixed layer depth is generally deeper in offshore waters (variable plots not presented) more subject to wind-induced surface mixing, while the standard deviation of aspect represents the flatter sea floor at the base of the islands slopes and the abyssal plain, both located further offshore in the study area.

Although beaked whales, including *Mesoplodon* species, have a year-round presence in Madeira archipelago (Figure 4.19), there is a seasonal increase in relative abundance of individuals in summer as a result of an increase in relative abundance of groups and group size (Figure 4.18, Figure 4.20 and Figure 4.21). This seasonal increase seems to be real and in line with the seasonal increase of most of the other cetacean species using the study area. However, due to the difficulty to detect beaked whales at sea, especially in worst weather conditions, some influence of bad weather expected to be more frequent in winter cannot be totally ruled out. The absence of the covariate "Beaufort" from these taxa models is likely a consequence of the limited number of sightings available for modelling rather than the absence of a relationship with the response. The seasonal variation in relative abundance of these taxa reflects inshore/offshore displacements of beaked whales or seasonal immigration of animals from elsewhere, attesting to their attraction/dependence on the habitats around Madeira archipelago. The peak in relative abundance of beaked whales in summer possibly reflects the time delay between the increase in primary productivity at the beginning of the year and the increase of higher trophic level prey biomass, on which these species feed. Additionally, it would not be surprising that beaked whales took advantage of the increase in food availability during late spring and summer to breed and give birth to their young (for energetic reasons), as suggested by the increase in group size.

4.4.5 Habitat use by baleen whales

Bryde's whale

Bryde's whales have a worldwide distribution in inshore and offshore tropical and warm-temperate waters, associated with water temperature (Kato and Perrin, 2018). Knowledge about the habitat preferences of the offshore larger form of Bryde's whale using Madeira waters is scarce. However, the higher occurrence of Bryde's whales has been associated elsewhere with areas of higher productivity, such as oceanic convergence areas, fronts, temporary or seasonal upwelling areas or the presence of islands (Freitas and Penry, 2021). The species has a seasonal presence (from late spring to autumn) in Madeira archipelago, where the animals feed close to shore, both at the surface on schooling fish and lunge feeding at depth, possibly on zooplankton (Freitas and Penry, 2021).

The overall distribution of Bryde's whales' relative abundance around Madeira archipelago seems to be driven directly or indirectly by physiographic features, such as escarpment and depth (Figure 4.38). The species general habitat preferences are for shallower waters over the steeper slope areas around the islands (the escarpment), but especially over the shelf break, as suggested by the combination of physiographic variables ("Distance to escarpment", "Escarpment area" and "Maximum depth") and their relationship with the response, and the respective predicted distribution (Figure 4.38 and Figure 4.39). However, when looking at a finer temporal scale (by season), the dynamic environmental variable "Poc 2004-17(Be)" emerged as important to explain the species habitat use in summer (Table 4.18; Figure 4.60 and Figure 4.61). In that season, the predicted higher relative abundance of animals is in the areas close to the channel between Madeira and the Desertas Islands, known for its higher biological productivity driven by local upwelling processes, happening also in the summer (Caldeira *et al.*, 2002). The interaction between "Distance to escarpment" and "Poc 2004-17, Summer" (Figure 4.62), indicates the preference of the species for areas with higher concentrations of particulate organic carbon, presumably zooplankton, closer to the escarpment. These results are in line with the dive profile data of two tagged Bryde's whales on the southeast of Madeira at the end of June, showing synchronized dives that suggest lunge feeding at depth, presumably on zooplankton or other prey, following the deep scattering layer diel migrations (Alves *et al.*, 2009). In autumn, the Bryde's whales spread around the islands more concentrated around the 500 m depth contour, i.e. over higher slope areas and the shelf break (Figure 4.63, right), possibly to take advantage of the prey aggregating effect of the islands (Fiedler, 2009; Virgili *et al.*, 2022), including the deep scattering layer diel migrating prey, in the season with the lowest primary productivity (Figure III.3-4, Appendix III) (Caldeira *et al.*, 2002; Martins *et al.*, 2007).

When modelling the habitat use at an even finer temporal scale (two months), and using time-lagged dynamic variables, new relevant dynamic variables and new combinations of those variables (models) emerged, bringing insights into the possible drivers behind the changes in the habitat preferences of the species during their seasonal presence in Madeira archipelago. The distribution of Bryde's whales in June-July had two equivalent models ($\Delta AIC \leq 2$), one with no time lagged covariates and the other with two-month time lagged covariates (Figure 4.64 and Figure 4.66). In both models the variable "Escarpment area" was selected, while the dynamic variables were different. Chlorophyll-a was important in the model with two-month lagged covariates, indicating that the distribution in June-July of the species was positively related with the phytoplankton distribution two month before (March-April). This time-lagged relationship with chlorophyll-a makes sense, as it reflects the time delay necessary for the increase on phytoplankton to be felt on the higher trophic levels' biomass, namely zooplankton on which the Bryde's whales feed. The increase in zooplankton abundance and biomass in late spring-summer is confirmed by *in situ* measurements of zooplankton in the south of Madeira (Alves and Kaufmann, 2003). The model without time-lagged dynamic variables, only included "Sst-a 2004-17, Jun-Jul". The selection of this model may indicate that areas with higher primary productivity two months before had higher than average sea surface temperature, namely on the southeast of Madeira, used preferentially by the Bryde's whale (Figure 4.71). These pockets of warmer surface waters may also reflect a more vertically structured water column (Figure III.3-5, Appendix III), where the plankton biomass produced in previous months is maintained closer to the surface (prevented from sinking) by the pycnocline, and thus more accessible to the whales.

Similarly, August-September had two equivalent models selected, one with no time lagged covariates and another with one-month time lagged covariates (Figure 4.67 and Figure 4.68). In both models "Distance to the escarpment" was the most important variable. The distribution of the Bryde's whales in this period was strongly related with the distribution of particulate organic carbon in the previous month, a proxy for zooplankton and other living material in the euphotic zone (Fingas, 2018). However, the species distribution was also related with the primary productivity and mixed layer depth in August-September, i.e. the same period of the whales' observations. In both models, the predicted area of higher relative abundance of Bryde's whales was in the vicinity of the channel between Madeira and Desertas Islands, as in June-July (Figure 4.71). The combined interpretation of both models suggests that Bryde's whales have preference for this area in August-September because of the presence of zooplankton and probably other higher trophic level prey (e.g. schooling fish like horse mackerel), which in turn are attracted to or stay in the area throughout the summer because of the increased primary productivity supported by a local upwelling at this time of the year (Caldeira *et al.*, 2002). This interpretation is corroborated by the positive relationship between primary productivity (and mixed layer depth) and the response in the model with no time-lagged covariates (Figure 4.67). Nevertheless, the models also predict an expansion of the distribution around the islands, over the escarpments. This expansion suggests that the channel between Madeira and the Desertas Islands in August-September does not provide enough prey for the Bryde's whales.

For the period October-November, the habitat preferences of Bryde's whales were exclusively explained by a static covariate ("Distance to 200m isobath"), regardless of whether or not the models considered time-lagged dynamic environmental variables (Table 4.22 and Figure 4.70). Like the autumn model (Figure 4.62), the predicted Bryde's whales distribution is around the islands, more concentrated over the insular shelf and the shelf break (Figure 4.71), presumably to take advantage of the prey aggregating effect of the islands (Fiedler, 2009; Virgili *et al.*, 2022).

There is a clear progression in the habitat preferences of Bryde's whales during the months they are in Madeira archipelago. In June-July the distribution is mostly shaped by the increase in primary productivity that took place in the previous months and probably mostly focused on an area (southeast of Madeira) with higher prey availability. In August-September, with the decreasing primary productivity the species distribution expands around the islands (shelf break and escarpment) to presumably take advantage of islands' prey aggregating effect, although the channel between Madeira and Desertas continues to be important because of the local upwelling. In October-November, with primary productivity at its minimum the animals spread equally around the islands mostly over the insular shelf and shelf-break, where the remaining prey probably aggregate.

Bryde's whales, like the spotted dolphins, have a more tropical distribution among the main species using Madeira archipelago waters. Both have a marked seasonal presence in Madeira archipelago, at the same time of the year, although in winter Bryde's whales tend to be absent while the spotted dolphins have a minor presence in the archipelago (Figure 4.21). Both species have a steep increase in relative abundance of individuals during spring, reaching a maximum in July. The influx of animals of both species to the study area happens at the same time of the year, allowing them to benefit from the prey availability resulting from the winter and spring increase in local biological productivity (Figure III.3-4, Appendix III). However, while spotted dolphins start gradually leaving the archipelago from summer onwards, probably driven by the decrease in prey availability, Bryde's whales have a similar relative abundance throughout summer and most of autumn, only decreasing markedly from December onwards. This is possible because Madeira archipelago is part of a wider range of habitats (e.g. sea mounts, offshore waters) explored by the Bryde's whales during summer and winter at these latitudes in the wider Eastern Atlantic basin. In chapter 3 (Section 3.3.2), photo-identification and satellite telemetry data showed that Bryde's whales moved in and out of the study area during the seasons they were present in Madeira.

The spotted dolphin (Figure 4.24) and the Bryde's whale (Figure 4.38) showed fluctuations in relative abundance of groups during the study period. These fluctuations may reflect cyclic changes in the number of animals migrating into the study area or changes in relative abundance of animals around Madeira archipelago, with animals alternating between the study area in peak years and further offshore waters in trough years. The ocean heat content (OHC) in the Northern Hemisphere showed generally a similar cyclic pattern (Llovel and Terray, 2016), although it is not possible to say if that Northern Hemisphere pattern reflects well what happened in the region of relevance for the spotted dolphins and Bryde's whales coming to Madeira, or even if these animals would respond to changes in OHC. If that was the case, the warming and cooling of the water column during those years could explain the cyclic expansion and contraction in the distribution of these species, with a more tropical distribution. However, in the case of the Bryde's whale, the abundance estimates (Section 3.3.4.2) show a consistent increase in the number of animals using Madeira archipelago's inshore waters throughout the period, contradicting a cyclic fluctuation in the immigration rate to the study area. Another possibility could be the cyclic change of local environmental conditions (either inside or outside the study area, or both) that would influence the further inshore or offshore distribution of the species around Madeira archipelago. The only environmental variable showing a relatively similar cyclic pattern in the study area was the mixed layer depth (Figure III.3-3, Appendix III), however there is no obvious explanation of how those changes may drive an inshore/offshore local distribution of these species.

Fin whale

Fin whales have mostly an offshore distribution, outside the continental slope, but can also be seen over the continental shelf (Aguilar, 2009). This offshore distribution means that sometimes animals come close to open ocean islands like Madeira and the Azores (Freitas *et al.*, 2012; Silva *et al.*, 2014), while migrating, for example, between winter and summer grounds (Silva *et al.*, 2013).

The predicted distribution of relative abundance of individuals showed a clear preference of the fin whales for offshore waters at depths around 2 000 m (Figure 4.40 and Figure 4.41). The species also showed a highly seasonal presence in Madeira archipelago, with a clear peak in winter (March) (Figure 4.19 – Figure 4.21), in line with their expected seasonal migratory pattern (Aguilar and García-Vernet, 2018). Although the seasonal passage of some fin whales (relatively low ER of groups; Figure 4.13) through the archipelago may be driven by their migration to higher latitude feeding grounds, nevertheless animals seem to take advantage of the increased local productivity during winter and spring by foraging in these waters when the opportunity arises, as shown by observations of animals feeding on small crustaceans (*Meganyctiphanes norvegica*) north of Madeira in May (Gordon *et al.* 1995). In spite of these episodic feeding events, the short periods fin whales stay in these waters while migrating attest to the probably small relevance of local habitats in the lives of these animals.

4.4.6 Sharing Madeira archipelago's habitats

The fluctuations in relative abundance of most cetacean species using Madeira archipelago, suggest that these seasonal patterns are driven by the variation in local primary productivity and its impact at higher trophic levels. There was a sequence in the peaks of relative abundance of individuals (Figure 4.21 and Table 5.7) of the species using the study area (fin whale – March to April ; common dolphin – March to May; spotted dolphin – June to August; Bryde's whale – July to November; *Mesoplodon* species – July to August; Ziphiidae – July to September; bottlenose dolphin – August to September; pilot whale – October; sperm whale – November), some more marked than others. In general, the sequence of the seasonal peaks of relative abundance is in accordance with the information available on the trophic positions of these species in Macaronesia (Bode *et al.*, 2022), with the exception of the bottlenose dolphin, the Bryde's whale and the beaked whales. If the seasonal cascade effect on the local prey biomass at different trophic levels was linear and drove exclusively the relative abundance of cetacean species, it would be expected that the Bryde's whale and bottlenose dolphin peaks be earlier in the year and the beaked whales peak later in the year; however, that is not the case (Figure 4.21). It may be that the cascade effect propagates in the epipelagic zone (< 200 m) differently from deeper ocean layers, as suggested by the differences in the water flow regimes between those layers (Caldeira and Sangrà, 2012), with the expected differences in biomass retention around the archipelago, or, more likely but not mutually exclusive, that the timing of the arrival of new animals to the area is determined by factors outside the study area.

The decision made by these animals to immigrate to Madeira archipelago must not be completely random, as supported by evidence of species with animals showing different patterns of site fidelity (Section 3.3.3) (Alves *et al.*, 2013; Dinis *et al.*, 2016b). These animals might return to the archipelago based on the foraging success (or positive energetic budget) of previous year(s), which would be consistent with the memory-based foraging strategy proposed for sea birds (Davoren *et al.*, 2003). The fixed location of the archipelago, its seasonal higher productivity, when compared with surrounding offshore waters, gives immigrating animals the predictable conditions to maintain a balanced energy budget and, possibly, fulfil important aspects of their life cycles, such as breeding.

As the number of predators increases, and with them the levels of predation, the primary productivity reaches its minimum (summer) in Madeira archipelago. As a result, the ability of the local marine ecosystems to sustain these animals decreases as a consequence of low primary productivity and prey depletion. Most animals may be forced to leave the area in autumn and winter to complement their energy needs in other habitats (e.g. nearby islands, neighbouring archipelagos or sea mounts, offshore open ocean waters or continental waters). Prey availability is probably one of the cues for animals to start emigrating, but other environmental cues may also play a role.

Once in Madeira archipelago, the animals are expected to have a distribution reflecting their habitat requirements, but also considering intra and interspecific interactions, such as competition. Ecological theory states that sympatric species with similar ecological requirements need some degree of habitat and resource differentiation to minimize competition, and thus coexist (Pianka, 1974). More similar co-occurring species are thought to compete for resources unless they occupy different physical locations or feed on different prey (Kiszka *et al.*, 2011). Moreover, a shared resource in limited supply (the habitats and prey in Madeira archipelago) will bring about intra-specific and/or inter-specific competition (Roughgarden, 1976).

As mentioned before, the species' sequential seasonal peaks of relative abundance in the study area seem to reflect, in general, the trophic levels at which the species feed. However, this temporal discrimination in the use of Madeira archipelago also contributes to minimize competition among some species expected to feed on similar type of prey like, for example, common dolphins, spotted dolphins and bottlenose dolphins. Nevertheless, co-occurrence between these species still happened and spatial discrimination would be expected in seasons with higher co-occurrence of two competing species.

The comparison of the overall distribution of the species in the study area (Section 4.3.4) gives insight into the habitat partitioning among cetacean species, expected to feed at similar trophic levels. For example, the average higher relative abundance of fin whales is reached further offshore (around 2 000 m depth; Figure 4.41) than Bryde's whales (< 1000 m depth over the escarpment; Figure 4.39). The average relative abundance of bottlenose dolphins is higher at shallower depths over the shelf (Figure 4.23), while for spotted dolphins it is over the slopes (Figure 4.25). The common dolphins had a much lower presence in the southwest of Madeira (Figure 4.27) where there is a high concentration of spotted dolphins, and the reverse occupancy pattern is seen around Desertas Islands. The striped dolphin higher predicted distribution is beyond the -3 000 m isobath (Figure 4.29) where the relative abundance of the other dolphin species reaches the minimum. The same general complementary use of the habitat is observed for deep diving species. The pilot whales occupy mostly a small area southeast of Madeira (Figure 4.32), sperm whales prefer the slope area north and northeast of the islands (Figure 4.34), while the beaked whales have in general a further offshore distribution in deeper waters (Figure 4.37).

The species' overall spatial patterns of distribution combine their more seasonal habitat preferences. The habitat partitioning patterns among species become clearer when they are compared by season taking into consideration the seasonal fluctuations in relative abundance. For example, in winter, when the presence of common dolphins increased in the area and the relative abundance of bottlenose dolphins and spotted dolphins reached minima, the former species had a wide inshore and offshore distribution northeast of Madeira (Figure 4.54), while the latter two species had a distribution closer to shore, around the islands (Figure 4.46 and Figure 4.51). In spring, when the relative abundance of common dolphins reached the maximum and the presence of spotted dolphins increased rapidly, the spotted dolphins occupied the southwest area of Madeira, mostly unoccupied by common dolphins during winter and spring. In this season the distribution of bottlenose dolphins was restricted to coastal waters north of Madeira. In summer, the distribution of spotted dolphins expanded to the slopes and offshore waters around the islands, while bottlenose dolphins maintained a coastal distribution but expanded to all waters around the islands. In the meantime, common dolphins left the area. The Bryde's whales occupied, in general, a complementary habitat (Figure 4.63) to spotted dolphins and, although there were spatial overlaps with bottlenose dolphins (around Desertas), the relative abundance of Bryde's whales was lower in the south and southwest of Madeira and around Porto Santo, where bottlenose dolphins had higher relative abundance. In autumn, when the relative abundance of bottlenose dolphins peaked and the relative abundance of spotted dolphins was slowly decreasing, the presence of bottlenose dolphins was higher over the shelf break and slopes of the islands but also expanding towards further offshore waters, while the distribution of spotted dolphins was concentrated in the deeper waters between Madeira and Porto Santo Islands.

In spite of the species' seasonal return to Madeira archipelago, there have been changes in their relative abundance over the years. Common dolphins had the highest ER of groups in the area between 2001 and 2004 (Freitas *et al.*, 2004b) but were later replaced by bottlenose dolphins and spotted dolphins. The relative abundance of these latter species, together with pilot whales, beaked whales and Bryde's whales, increased over the years. Among the possible reasons for such trends is the increase in primary productivity measured in the area around Madeira archipelago in the same period (Siemer *et al.*, 2021). No trend in relative abundance over the years was found for common dolphins, sperm whales or striped dolphins. However, the positive trend in relative abundance observed for spotted dolphins was in winter and for bottlenose dolphins in winter and spring. It may be that with an increase in productivity in the area, the animals stayed longer to take advantage of the increased prey availability rather than leaving in winter and spring. The prolonged presence of these animals in the area in winter and spring could prevent an increase in the number of common dolphins migrating into the area by using up the extra resources. The absence of trend over the years in relative abundance of striped dolphins and sperm whales in the study area is not surprising as these species presence in Madeira archipelago inshore waters does not seem to be related with fluctuations in local biological productivity.

Chapter 5

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NICHE PARTITIONING - HOW CETACEAN SPECIES USE SHARE AND COMPETE FOR MADEIRA INSHORE WATERS

NICHE PARTITIONING - HOW CETACEAN SPECIES USE SHARE AND COMPETE FOR MADEIRA INSHORE WATERS

5.1 INTRODUCTION

The open ocean islands have a multitude of local marine habitats, which provide a diversity of abiotic and biotic conditions to be explored by cetacean species, according to their characteristics and ecological requirements. However, these usually small insular marine habitats have limited productivity and thus limited prey availability, especially in oligotrophic seas. Consequently, competition for local resources is expected between co-occurring individuals of different species (inter-specific competition) (Roughgarden 1976). According to ecological theory, the coexistence of sympatric species with similar ecological needs is dependent on some degree of habitat and resource differentiation to minimize competition (Pianka, 1974), i.e. co-occurring species with similar ecological requirements are thought to compete for resources unless they occupy different niches; in simple terms, they feed on different prey and/or occupy different physical locations.

The concept of niche was independently formulated by Elton (1927) and by Grinnell (1917), although with differing views (Colwell and Rangel, 2009); the former author gave more emphasis to resources that species use ("Eltonian niche"), while the latter focused on the environmental conditions where species live ("Grinnellian niche")(Soberón, 2007). Hutchinson (1957) further developed and formalized the concept of niche as an abstract n-dimensional set of points in a space whose axes represent environmental variables that permit the species to exist and, in subsequent elaboration (Hutchinson, 1978), proposed the partitioning of the hypervolume into scenopoetic axes (representing environmental components) and bionomic axes (referring mostly to the trophic components) of niche space. The fundamental niche can be described as the entire hypervolume within which an organism can potentially exist, whereas the portion of the fundamental niche where the species actually lives as a result of, for example, competitive exclusion, is defined as its realized niche (Geange *et al.*, 2011).

Modelling techniques (e.g. species distribution models) to predict habitat use and the environmental conditions determining species distribution can inform on the scenopoetic axes of the Hutchinson definition of niche (equivalent to the "Grinnellian niche") (Rödder and Engler, 2011), while the bionomic axes (equivalent to the "Eltonian niche") can be addressed through stable isotope approaches (Giménez *et al.*, 2018b). Actually, the isotopic niche concept proposed by Newsome *et al.* (2007) considers both the bionomic (trophic) and scenopoetic (habitat) axes, informed through nitrogen (δ15N) and carbon (δ13C) stable isotope ratio signatures, respectively (Post, 2002; Bearhop *et al.*, 2004). Additionally, the variance of the stable isotope composition may be suited to investigate niche breadth (Bearhop et al., 2004). In simple terms, stable isotopes ratios can be seen as ecological indicators of trophic position (δ15N) and habitat (δ13C). Nitrogen stable isotope values reflect mainly the position of each species in the trophic web, while carbon stable isotope ratio values reflect the main source of primary production incorporated into food webs, providing an indication of benthic versus pelagic and inshore versus offshore consumption (Giménez *et al.*, 2018b).

Quantifying niche overlap can help understand cetacean species co-existence (Geange *et al.*, 2011). Several studies have investigated niche partitioning among cetacean species by quantifying isotopic niche overlaps (e.g. Young *et al.*, 2017; Borrell *et al.*, 2021); others have combined trophic data with spatial or temporal data to investigate the factors structuring cetacean communities (e.g. Kiszka *et al.*, 2011; Giménez *et al.*, 2017a, 2018b). However, there are very few such studies in open ocean islands (Section 2.4).

Chapter outline

In this chapter, Nitrogen and Carbon stable isotope ratios are used as proxies of trophic position and habitat use, respectively, to describe the trophic niches of several cetacean species in Madeira archipelago. The local ecological niches of these cetacean species are described and niche partitioning investigated through the degree of overlap among species in three dimensions: trophic niche (this chapter), temporal distribution and spatial distribution (Chapter 4). The results of chapters 3 to 5 are then combined, interpreted and discussed to give a more comprehensive, integrated and multispecies view of how cetaceans use and share (or compete for) insular marine environments, their relevance in a wider oceanic context and to shed light on some of the ecological processes that may be at play in these marine ecosystems, thus addressing the two overarching questions of this thesis.

5.2 MATERIAL AND METHODS

5.2.1 Trophic niches

5.2.1.1 Study area and sample collection

This study focused on Madeira archipelago waters, using skin biopsy samples collected from live animals at sea and dead animals stranded along the archipelago shores or found floating at sea (Figure 5.1). The biopsy samples of live animals were collected from adults or large subadults between 2016 and 2018, using arrows with darts specially designed for small or medium size cetaceans (F. Larsen, Ceta-Dart; Mathews *et al.*, 1988), deployed with a 125-lb Barnett crossbow. The biopsy samples from dead animals were collected from well preserved or moderately decomposed adult and subadult carcasses (preservation codes ≤ 3, Kuiken and García-Hartmann, 1991) by the MWM (Madeira Whale Museum) team in the context of RACAM (Madeira archipelago cetaceans stranding network), between 1995 and 2018. A total of 145 skin samples were considered in the study, 105 from live animals and 40 from stranded animals (Table 5.1).

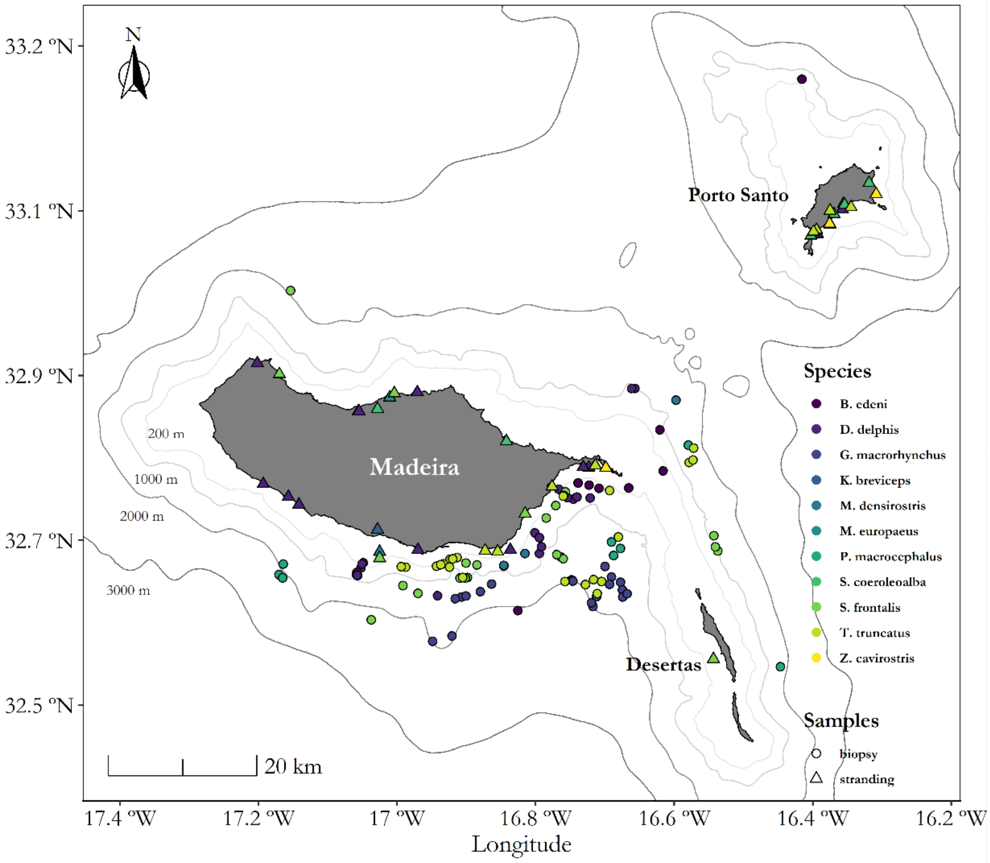


Figure 5.1. Cetacean trophic niche study area comprising the inshore waters of Madeira archipelago and the location of the the stranded carcasses (Δ) and the live animals (○) from which the skin biopsy samples were collected.

Table 5.1 – Number of skin biopsy samples collected from live animals between 2016 and 2018 and from stranded animals in Madeira archipelago between 1995 and 2018.

Species	Live	Stranded	total
Balaenoptera edeni	11	-	11
Delphinus delphis	20	14	34
Globicephala macrorhynchus	20	-	20
Kogia breviceps	-	1	1
Mesoplodon densirostris	4	2	6
Mesoplodon europaeus	-	1	1
Physeter macrocephalus	9	-	9
Stenella coeroleoalba	-	6	6
Stenella frontalis	20	4	25
Tursiops truncatus	21	7	30
Ziphius cavirostris	-	2	2
Total	105	37	142

The samples collected from live animals were kept on ice while at sea. All samples were then preserved at -20ºC until analysis.

The half-life turnover rates of carbon and nitrogen in the skin of the bottlenose dolphin (Giménez *et al.*, 2016) were estimated at 24.16 ± 8.19 days and 47.63 ± 19.55 days, respectively, thus being short enough to incorporate the local δ15N and δ13C signature in the animals' tissue while using Madeira inshore waters. However, that may not be the case for species with small residency times (e.g. striped dolphin or the sperm whale), for species that use a wider area around Madeira regularly (e.g. Bryde's whale) or for animals of other species that arrived in the sampling area from elsewhere shortly before being sampled. As such, the isotopic signatures of these samples probably represent Madeira inshore waters as well as a wider area around Madeira where animals migrating to the archipelago fed in the previous weeks. Due the scarcity of studies on other cetacean species, the half-life turnover rates of other cetacean species are assumed to be similar to those estimated for the bottlenose dolphin.

5.2.1.2 Stable isotope analyses

Skin samples were chosen over other tissues (e.g. muscle) because they can be easily collected from stranded carcasses as well as from live animals, with minimal impact on the individuals. The isotopic homogeneity between skin and muscle is not confirmed in cetaceans, with different studies showing contradictory results (Arregui *et al.*, 2017). As such, the use of both tissues in this study, to increase samples size, was not considered.

In preparation for laboratory analysis, the skin samples were dried at 50ºC for 48h, powdered with a mortar and pestle, and lipids extracted using a chloroform-methanol (2:1) solution, following standard protocols (Romero *et al.*, 2019). The stable isotope laboratory analysis was carried out at the "Centro de Recursos em Isótopos Estáveis - Stable Isotopes and Instrumental Analysis Facility", Science Faculty of Lisbon University (https://sites.google.com/site/siiafcba/), using continuous-flow isotope mass spectrometery (CF-IRMS) (Preston and Owens, 1983), on a Sercon Hydra 20-22 (Sercon, UK) coupled to a EuronEA (EuroVector, Italy) elemental analyser, which automates sample preparation. Stable isotope ratio values were calculated as:

$$\delta = \frac{(R_{sample} - R_{standard})}{R_{standard}} * 1000 \qquad \text{(Equation 6.1)}$$

where R is the ratio between the heavier isotope and the lighter one.

The results are expressed relative to the Vienna Pee Dee Belemnite standard for δ13C and to atmospheric nitrogen for δ15N. The precision of the analysis was ≤0.03‰ for δ15N and ≤0.09‰ for δ13C, calculated using values from six to nine replicates of laboratory standard material (casein).

To directly compare the carbon isotope composition of stranded animals sampled as early as 1995 and samples of stranded and live animals as recently as 2018, a correction factor was applied to δ13C values of all samples prior to analyses, equivalent to -0.022‰ yr^{-1} in the subtropical Atlantic (Quay *et al.*, 2003), to account for the decadal decrease in atmospheric δ13C (Suess effect), following Bode *et al.* (2022).

Isotopic ratios, especially δ15N, may change depending on the animals body condition (Valenzuela *et al.*, 2010). It is expected that animals with very poor body condition will have increased δ15N values as a result of using their own reserves, including proteins, rather than consuming prey at lower trophic levels (lower δ15N values). This may be the result of lack of available prey or due to the poor health of the animals. The body condition of animals stranded in Madeira was not systematically assessed over the years, preventing the identification and exclusion from the analysis of animals with very poor body condition, which may introduce an upwards bias in the nitrogen stable isotope ratio values. To overcome this limitation, the δ15N and δ13C values of samples from live animals were compared to samples from stranded animals with Welch's two sample t-test (Table VI.1.1-2, Appendix VI), for species with both type of samples, to assess if the mean values of each stable isotope ratio were significantly different between live and stranded animals. Previously, the normal distribution of the stable isotopes ratios of live and stranded animals subsets of each species were visually checked with QQ-plots (not presented) and tested using a Shapiro-Wilk test (Table VI.1.1-1, Appendix VI). The homoscedasticity of data was assessed using Levene's test (Table VI.1.1-3, Appendix VI).

Differences among species in the carbon and nitrogen isotopic ratios were compared using a one-way ANOVA and the Tukey multiple pairwise comparisons of means test. The homogeneity of variance and the normality assumptions were checked visually (Figure VI.1.2-1 and Figure VI.1.2-2, Appendix

VI) and with the Levene's test (Table VI.1.2-2, Appendix VI) and the Shapiro-Wilk test (Table VI.1.2-1, Appendix VI), respectively.

5.2.1.3 *Comparison of isotopic niches among species*

Variation in isotopic niche was quantified and compared among species using corrected standard ellipses areas (SEA_c, i.e. area encompassing approximately 40% of the data; Jackson *et al.*, 2011) and Layman metrics. As pointed out by Giménez *et al.* (2018), some Layman metrics are sensitive to extreme data points, namely, δ15N and δ13C range and Total Area (TA), measured via the convex hull). As such, only mean distance to centroid (CD), the mean nearest neighbour distance (NND) and the standard deviation of nearest neighbour distance (SDNND) were considered. These metrics were bootstrapped (n=2000) to obtain confidence limits (Jackson *et al.*, 2012). The same metrics were applied to two communities created by grouping dolphin species (*D. delphis, S. frontalis, S. coeruleoalba and T. truncatus*) and deep divers (*G. macrorhynchus, P. microcephalus and Ziphiidae*).

The trophic niche width and overlap between species was calculated with SEA_b (Bayesian SEA), considering 95% prediction ellipses computed using 10,000 posterior draws. The proportion of trophic niche overlapping area (PTRO) between two species was calculated as:

$$\mathrm{PTRO} = \frac{A_o}{A_{1+}A_2 - A_o} \qquad \text{(Equation 6.2)}$$

with A_o equal to the overlap area between the isotopic ellipses of the two species; A_n equal to area of species 1 and species 2, respectively.

As shown by Jackson *et al.* (2011), the estimation through Bayesian inference allows a robust comparison among data sets with different sample sizes. Furthermore, the Bayesian framework considers the uncertainty in the sampled data and incorporates the error resulting from the sampling process, propagating it through to the derived metric (Jackson *et al.*, 2011). The isotopic niche metrics were calculated with R package SIBER (version 2.1.4; Jackson *et al.*, 2011).

5.2.1.4 *Trophic positon*

The δ15N values were used to estimate trophic position (TP) for each species using the model (Post, 2002):

$$\mathrm{TP} = \frac{(\delta^{15}N_S - \delta^{15}N_P)}{\mathrm{TEF}} + \lambda \quad \text{(Equation 6.3)}$$

where $\delta 15N_s$ and $\delta 15N_p$ are the values for the secondary (cetacean species) and primary consumers, respectively, λ is the TP of the reference baseline and TEF is the trophic enrichment factor, i.e. the average increase in δ15N between adjacent trophic levels.

The mean ± SD values of TEF and $\delta 15N_p$ used to calculate the TP were 3.30 ± 0.26‰ (McCutchan *et al.*, 2003) and 3.40 ± 1.24‰ (Bode *et al.*, 2022), respectively, the same values used by the latter authors in a similar study encompassing Madeira archipelago waters. As explained by Bode *et al.* (2022), the δ15N values were obtained by averaging values of calanoid copepods and mesozooplankton samples collected in different surveys and seasons in the study region (Macaronesia)(Fernández *et al.*, 2014; Bode and Hernández-Léon, 2018). The λ used was 2, corresponding to the TP of primary consumers (calanoid copepods and mesozooplankton). The TP values were estimated in R, and the respective error was calculated by propagating the error of the terms of equation 6.3, using R package "propagate" (version 1.0.6; Spiess, 2018).

5.2.1.5 Isotopic signatures over time

The change of carbon and nitrogen isotopic ratios over time (within years and over years) was investigated to identify possible trends. Linear regression models were fitted to the isotopic data of each species for both δ13C and δ15N, by year and by month, using the "stats" R package (R Core Team, 2019), version 3.6.2). Diagnostic plots were used to assess whether or not the data violated the linear model assumptions (Figure VI.1.4-3 to Figure VI.1.4-7, Appendix VI).

5.2.2 Within-year temporal niche overlap

The relative abundance of animals of different cetacean species in Madeira archipelago throughout the year was modelled with Generalized Additive Models (GAMs) in Chapter 4, Section 4.3.3. The prediction of the relative abundance of encounter rates of individuals (ER) by month is used in this chapter to represent their seasonal patterns in the study area. The ER prediction uncertainty was not taken in consideration.

As explained in Chapter 4, the predictions of the GAMs are not directly comparable because the factor covariate (type of survey) is model specific. To overcome this limitation, the temporal ER predictions were standardized (bounded between zero and one, i.e. with the same scale) and thus comparable among species. Furthermore, the use of the original ER predictions to estimate overlap in the temporal use of the area by different species would be affected by the differences in their relative abundance (species with high ER of individuals vs species with low ER of individuals) and not only reflect their seasonal relative abundance patterns.

The area under the curve (standardized prediction curve over the year) for each species was calculated as well as the area under the curves when they overlapped (overlap area) for pairs of species. The proportion of temporal overlap (PTO) between pairs of species was calculated with equation 6.2 but using area under the curve rather than ellipse area.

5.2.3 Spatial niche overlap

Spatial relative distribution of abundance of several cetacean species was also modelled with GAM (Chapter 4, Section 4.3.4). As in the previous section, the ER predictions were standardized (bound between zero and one, i.e. with the same scale) to be comparable and reflect only the patterns of spatial distribution of each species and not be affected by the differences in their relative abundance. Unlike the trophic and temporal niches overlap, which were calculated as the proportion of overlap area between ellipses and area under the curves of two species, respectively, the standardized spatial niche overlap (SSO) was calculated as:

$$\mathrm{SO}_c = \mathrm{SERa}_c * \mathrm{SERb}_c \quad \text{(Equation 6.4)}$$

$$\mathrm{SSO}_c = \frac{\mathrm{SO}_c}{\max(\mathrm{SO}_c)} \quad \text{(Equation 6.5)}$$

$$\mathrm{SSO} = \frac{\sum_{c=1}^{n} \mathrm{SSO}_c}{n} \quad \text{(Equation 6.6)}$$

where SERa_c and SERb_c are the standardized ER values estimated for cell c for species a and species b, respectively; SO_c is the spatial niche overlap in prediction grid cell c, n is the total number of cells of the prediction grid used to estimate encounter rates (ER) of each species; and SSO_c is the standardized spatial niche overlap in cell c.

Although SSO is not strictly a measure of overlap, it reflects and integrates the relative distribution of two species and the differences in the standardized ER of those species in the study area.

5.2.4 Ecological niches

The ecological niche of different cetacean species was defined and described using three dimensions: trophic niche, temporal niche, and spatial niche. The ecological niche overlap (ENO) between two species was calculated as:

$$\mathrm{ENO} = \mathrm{PTRO} * \mathrm{PTO} * \mathrm{SSO} \quad \text{(Equation 6.7)}$$

Where PTRO is the proportion of trophic niche overlap, PTO is the proportion of temporal nich overlap and SSO is the standard spatial niche overlap.

However, the product of the overlap of two species in these three dimensions can give similar results from different combinations of overlap values in each dimension. Thus, to give meaning to ENO metrics, two approaches were followed to investigate the relationship between these metrics and the underlying overlap values in each of the dimensions. The first approach was to select a threshold overlap value for each of the dimensions and identify the pairs of species that have overlap values equal to or above that threshold in one, two or all the dimensions. Three thresholds (0.1, 0.2 and 0.3) were investigated and the threshold which discriminated (in the ENO scale) most pairs of species with one, two or three dimensions of overlap above the threshold was selected.

The second approach was to use clustering methods. K-means, divisive (DHC) and agglomerative (SHC) hierarchical methods were tested. The optimal number of clusters to group the pairs of species was selected using the average silhouette method and then used to group the pairs of species in the K-means method and to define the cut point in the DHC and AHC methods. The results were visualized as a principal component analysis (PCA) in the first two dimensions. The best method was selected for the analysis based on the within cluster sum of squares and the average silhouette width values. Further details on the methodological approach are given in Section 3.2.2.6, Chapter 3.

The mean ENO of one species with the remaining species in each ecological dimension ($\mathrm{mENO}_{\mathrm{d}}$, with d being tr – trophic; t – temporal; and s – spatial) was explored as an indicator of that species degree of specialization in that dimension. A species with high $\mathrm{mENO}_{\mathrm{d}}$ in one dimension is said to be a generalist in that dimension while a small $\mathrm{mENO}_{\mathrm{d}}$ indicates the species is a specialist in that dimension. The overall degree of ecological niche specialization of one species (ENS) was measured as a proportion of ENO of that species:

$$\mathrm{ENS}_a = \frac{m\mathrm{ENO}_a}{\sum_{s=1}^{n} \mathrm{ENO}_s} \qquad \text{(Equation 6.8)}$$

where $\mathrm{mENO}_{\mathrm{a}}$ is the mean ecological niche overlap of species *a* (in the three dimensions), calculated as the average of ENO values of species *a* with the remaining species, and *n* the total number of species.

A species with a higher ENS value is more generalist (higher average overlap in the three ecological dimensions) than a species with a lower ENS value, which is more specialized. To overcome the lack of trophic information (stable isotopes data) of fin whale for Madeira, for the purpose of ENO and ENS calculations it was assumed to be the same as the Bryde's whale.

The biomass of all taxa was estimated for Madeira inshore waters for the period 2007 – 2012, using average year-round abundance estimates (Freitas *et al* in prep.), and for the period 2017 – 2018, using abundance estimates for Summer/Autumn (Freitas, Cañadas, Esteban *et al* in prep.; Esteban, Cañadas, Freitas *et al* in prep.). The estimates for both periods were obtained from systematic line-transect surveys, covering the same area, using the same survey platform and similar protocols (SLS, chapter 4). In Section VI.5.1, Appendix VI, is explained how the biomass was calculated for each taxon. Furthermore, an approximated estimate of daily prey biomass consumption of those cetacean species was calculated as the product of the species total biomass and the average prey daily intake rates (adapted from Spitz *et al.* 2018), expressed as a percentage of body weight, for the periods for which there are abundance estimates. The biomass estimates for these taxa for Madeira archipelago, and the respective daily prey biomass consumptions, give context to the interpretation of their ecological niche results and helps in the comparison of those results among taxa, considering the limited productivity of the archipelago's inshore waters and thus its limited capacity to support many individuals of these taxa.

All analysis in this chapter was carried out in R (version 3.6.2; R Core Team, 2019), using RStudio (version 1.2.1335, RStudio Team 2019).

5.3 RESULTS

5.3.1 Trophic niches

The trophic niches of several cetacean species using Madeira waters are described using nitrogen and carbon stable isotopes of biopsies collected from live and stranded animals.

The results from the Welch two-sample t-test indicated no significant difference between biopsy samples of live and stranded animals for either δ13C or δ15N, except for δ15N in bottlenose dolphin (*T. truncatus*) (Appendix VI, Table VI.1.1-2). As such, the biopsy samples of bottlenose dolphins from stranded animals (n=7) were excluded from the analyses to avoid bias in the δ15N values of this species because of possible poor body condition of these animals. The Levene's test confirmed the homoscedasticity of the data for all species. In Figure VI.1.1-1, Figure VI.1.1-2 and Figure VI.1.1-3 (Appendix VI) are presented the boxplots of carbon and nitrogen stable isotope ratios by type of sample (live and stranded animals) and species, as well as the corresponding SEA_c (Standard Ellipse Area corrected), including the density plot. These plots show the nitrogen isotopic differences between live and stranded animals samples.

5.3.1.1 Stable Isotopes niches

A summary of the carbon and nitrogen isotope ratios is presented in Figure 5.2. The results of the one-way ANOVA showed significant differences in both δ13C and δ15N among species (Table 5.2). The pair-wise comparison (Tukey multiple pairwise comparisons of means test; Table 5.3) showed significant difference for δ13C between the short-finned pilot whale (*G. macrorynchus*, henceforward called pilot whale) and all other species, with the exception of the beaked whales (Ziphiidae), and between beaked whales and Bryde's whale (*B. edeni*) and common dolphin (*D. delphis*). Significant differences were also found for δ15N between Bryde's whale and all other species and between small dolphins (common dolphin, Atlantic spotted dolphin *S. frontalis,* henceforward called spotted dolphin, and bottlenose dolphin), with the exception of striped dolphin (*S. coeruleoalba*) and deep divers (pilot whale, sperm whale *P.macrocephalus* and beaked whales) (Table 5.3).

Table 5.2 – Results of the one-way ANOVA test to compare the means of δ13C and δ15N of seven cetacean species (*B. edeni, D. delphis, S. frontalis, S. coeruleoalba, T. truncatus, G. macrorhynchus* and *P. macrocephalus*) and one family (Ziphiidae).

SI	**Groups**	**df**	**Sum Sq**	**Mean Sq**	**F value**	**Pr[>F]**	**Residuals**		
							df	**Sum Sq**	**Mean Sq**
δ13C	8	7	44.611	6.373	12.416	0.000	126	64.676	0.513
δ15N	8	7	128.479	18.354	23.890	0.000	126	96.803	0.768

Table 5.3 – Results of the Tukey multiple pairwise-comparisons of the means test of δ13C and δ15N of seven cetacean species (*B. edeni, D. delphis, S. frontalis, S. coeruleoalba, T. truncatus, G. macrorhynchus* and *P. macrocephalus*) and one family (Ziphiidae). Pair-wise comparisons with significantly different means ($p<0.05$) in bold.

SI	Species	*D. delphis*	*S. frontalis*	*S. coeroleoalba*	*T. truncatus*	*G. macrorhynchus*	*P. macrocephalus*	*Ziphiidae*
δ13C	*B. edeni*	1.000	0.689	0.999	0.350	**0.000**	0.288	**0.009**
	D. delphis		0.706	1.000	0.276	**0.000**	0.287	**0.004**
	S. frontalis			0.996	0.997	**0.000**	0.957	0.165
	S. coeroleoalba				0.938	**0.000**	0.832	0.177
	T. truncatus					**0.000**	0.999	0.463
	G. macrorhynchus						**0.010**	0.392
	P. macrocephalus							0.914
δ15N	*B. edeni*	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
	D. delphis		0.112	0.369	1.000	**0.000**	**0.000**	**0.000**
	S. frontalis			1.000	0.124	**0.005**	**0.003**	**0.007**
	S. coeroleoalba				0.328	0.488	0.215	0.284
	T. truncatus					**0.000**	**0.000**	**0.000**
	G. macrorhynchus						0.982	0.995
	P. macrocephalus							1.000

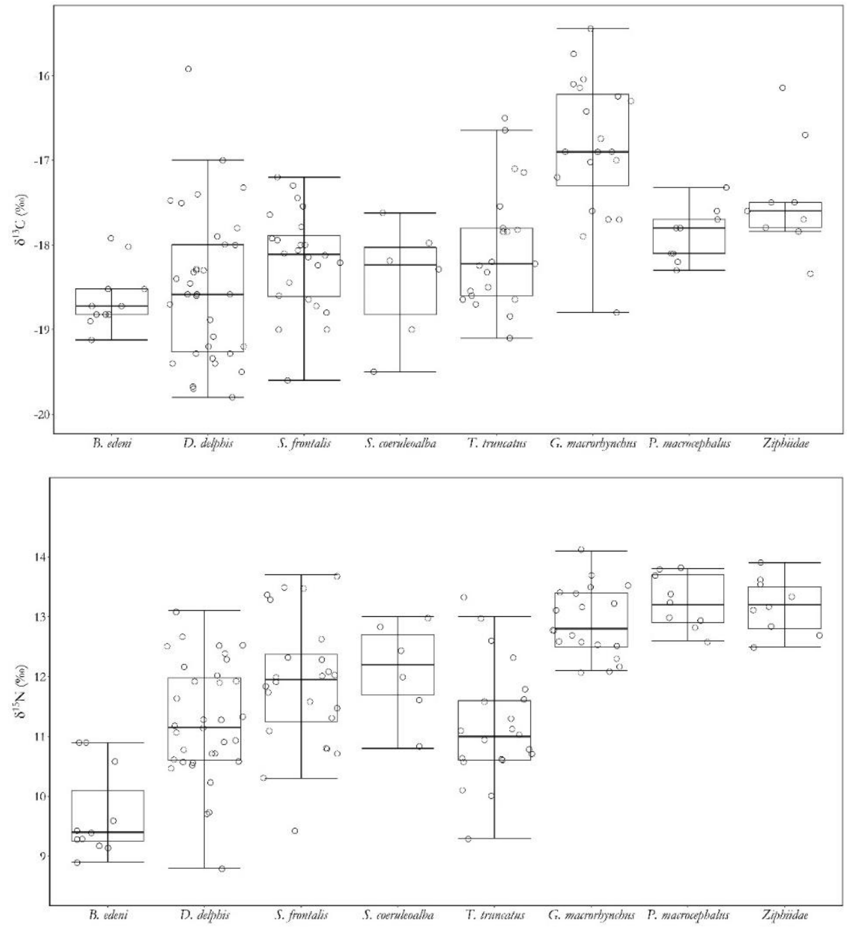


Figure 5.2. Boxplots of carbon (top) and nitrogen (bottom) stable isotopes ratio values of Bryde's whale (*B. edeni*), common dolphin (*D. delphis*), Atlantic spotted dolphin (*S. frontalis*), striped dolphin (*S. coeruleoalba*), bottlenose dolphin (*T. truncatus*), short-finned pilot whale (*G. macrorhynchus*), sperm whale (*P. macrocephalus*) and beaked whales (Ziphiidae). The raw data are plotted as dots. The whiskers, the box and the central line represent the minimum and maximum, the 25th and 75th percentile, and the median, respectively.

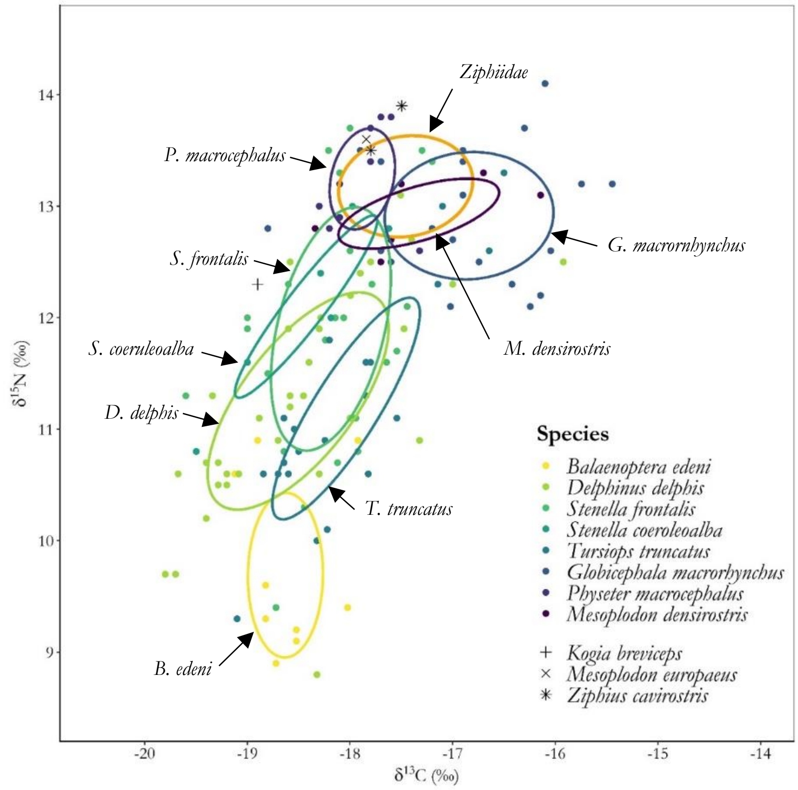


Figure 5.3. Standard Ellipse Area corrected (SEA$_c$) and respective samples' positions in the isotopic space, encompassing approximately 40% of the data. SEA$_c$ were calculated for species with five or more samples (colours) while for species with less samples (*K. breviceps, M. europaeus and Z. cavirostris*) only the positions of the samples in the isotopic space are shown. The orange ellipse is the SEAc for all species (*M. densirostris, M. europeus and Z. cavirostris*) of the family Ziphiidae combined.

The isotopic-biplot is in line with the results of the analysis of variance and clearly identifies three isotopic groups (Figure 5.3): a mono-species group comprising the Bryde's whale with lowest δ15N and low δ13C values; a group with intermediate δ15N values and low to intermediate δ13C values, including the small dolphins (common dolphin, spotted dolphin, striped dolphin and bottlenose dolphin); and a group with high δ15N values and intermediate to high δ13C values, including the deep divers (pilot whale, sperm whale and beaked whales). The discrimination between groups of species is clearer in the δ15N axis than in the δ13C axis.

The isotopic niche width, as expressed by isotopic standard ellipses area (SEA$_b$), is the smallest for sperm whale, followed by Bryde's whale, beaked whales, striped dolphin, bottlenose dolphin, pilot whale, and finally, spotted dolphin and common dolphin (Figure 5.4).

The isotopic niche of each species is also described by Layman metrics (Figure 5.4). The average degree of trophic diversity expressed by CD, is lowest for the sperm whale and striped dolphin, followed by beaked whales, Bryde's whale, pilot whale and finally the other dolphin species with the highest trophic diversity. The overall trophic redundancy, described by NND, is similar among species, except for the striped dolphin which shown a much higher overall trophic packing of the individuals. Finally, the evenness of packing of individuals in the bi-plot space, is the lowest for the striped dolphin (with very wide confidence intervals), followed by the sperm whale, other dolphin species, with similar values, the pilot whale and finally the Bryde's whale and beaked whales with the highest values of evenness of packing of individuals.

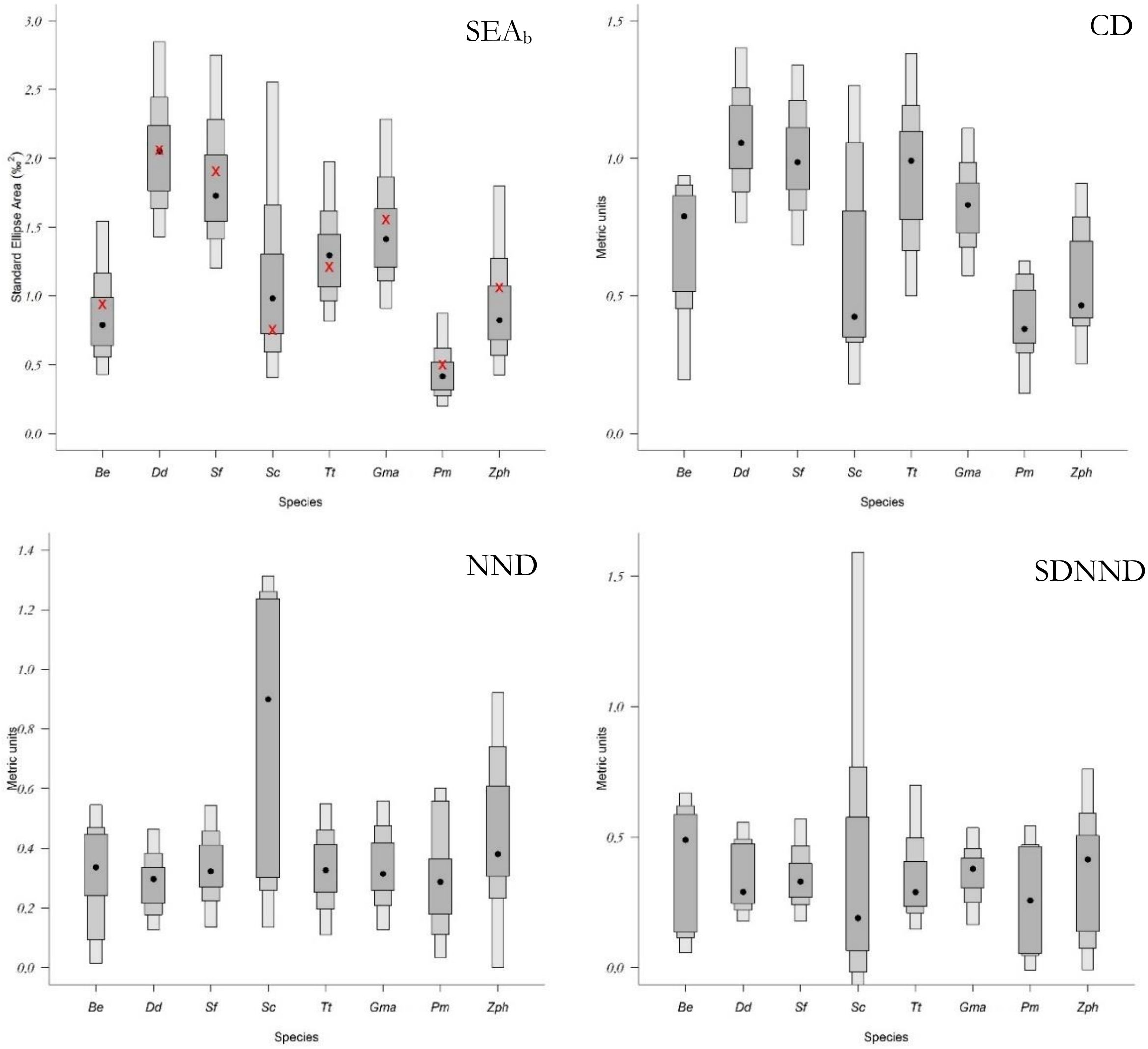


Figure 5.4. Density plot showing the SEA$_b$ (Bayesian standard ellipse Area) and the Layman metrics mean distance to centroid (CD), mean nearest neighbour distance (NND) and standard deviation of nearest neighbour distance (SDNND) of Brydes's whale (*Be*), common dolphin (*Dd*), Atlantic spotted dolphin (*Sf*), bottlenose dolphin (*Tt*), short-finned pilot whale (*Gma*), sperm whale (*Pm*) and beaked whales (Zph). The boxed areas reflect the 95, 75 and 50% credible intervals for the SEA$_b$, the confidence intervals for the rest of metrics, and the red x the maximum likelihood of SEA$_c$.

Comparison of the SEA$_b$ among the groups identified in Figure 5.5 (baleen whales, dolphins and deep divers) shows that the baleen whales have the smallest isotopic niche width, followed by the deep divers and the dolphins. The comparison of the isotopic niche metrics between the multispecies groups shows a similar degree of trophic diversity (CD), slightly higher trophic redundancy in dolphins than deep divers (MNND) and similar evenness of packing of individuals in the bi-plot space (SDNND) (Figure 5.5).

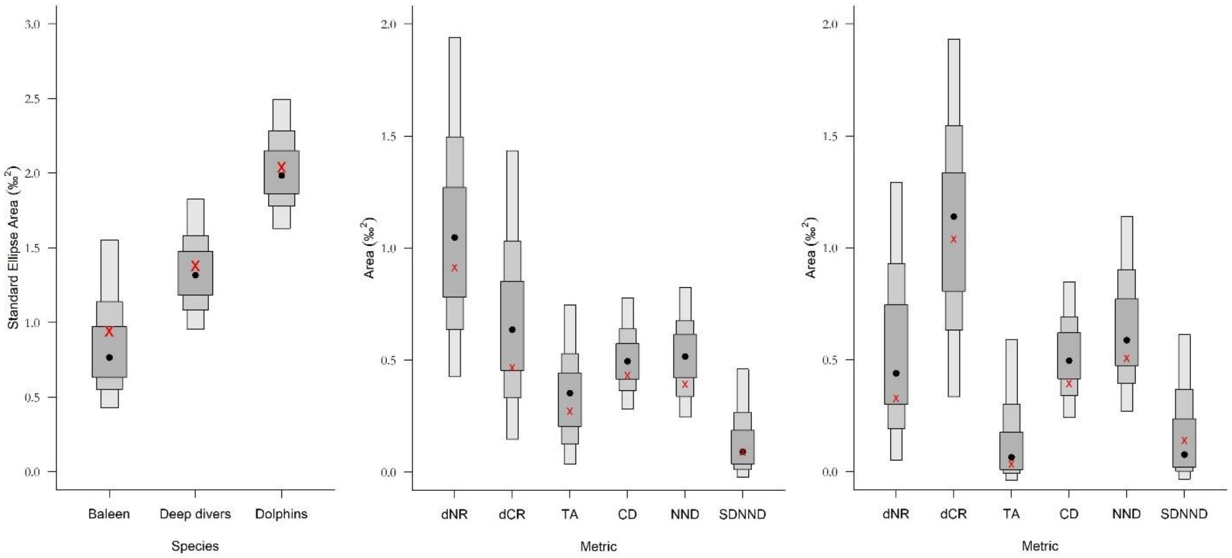


Figure 5.5. Density plots showing on the left the SEA$_b$ (Bayesian standard elipse Area) of baleen whales (Bryde's whale), deep divers (pilot, sperm and beaked whales) and dolphins (common, spotted, striped and bottlenose dolphins), and on the center and right, the isotopic niche metrics of deep divers and dolphins, respectively. dNR - nitrogen stable isotope range (δ15N range); dCR – carbon stable isotope range (δ13C range); TA - total area; CD – mean distance to centroid; MNND – mean nearest neighbour distance; and SDNND – standard deviation of the nearest neighbour distance. The boxed areas reflect the 95, 75 and 50% credible intervals and the red x the maximum likelihood of SEAc.

The proportion of SEA$_b$ overlap between pair of species is given in Table 5.4. The proportion of overlap ranges from almost zero, between Bryde's whales and the deep divers, to 0.52 between common dolphin and spotted dolphin. The proportion of SEA$_b$ overlap is relatively high among dolphins' species (≥0.39), except for the pair striped dolphin – bottlenose dolphin, and among deep divers (≥0.32), with the exception of the pair sperm whale – pilot whale. The proportion of overlap between the remaining pairs of species was ≤ 0.3.

Table 5.4 – Proportion of Bayesian standard ellipse Area overlap between pairs of species, and respective 95% confidence intervals in brackets. In bold is highlighted the proportion of overlap > 0.3.

	D. delphis	*S. frontalis*	*S. coeruleoalba*	*T. truncatus*	*G. macrorhynchus*	*P. macrocephalus*	*Ziphiidae*
B. edeni	0.22 (0.2 - 0.23)	0.19 (0.18 - 0.21)	0.09 (0.08 - 0.11)	0.27 (0.26 - 0.28)	0.01 (0 - 0.01)	0.01 (0 - 0.01)	0.003 (0 - 0.01)
D. delphis		**0.52** **(0.51 - 0.53)**	**0.39** **(0.36 - 0.41)**	**0.51** **(0.49 - 0.52)**	0.22 (0.2 - 0.23)	0.11 (0.1 - 0.12)	0.16 (0.15 - 0.18)
S. frontalis			**0.4** **(0.38 - 0.42)**	**0.44** **(0.42 - 0.45)**	0.26 (0.25 - 0.28)	0.21 (0.19 - 0.22)	0.26 (0.25 - 0.28)
S. coeruleoalba				0.24 (0.22 - 0.27)	0.23 (0.22 - 0.25)	0.21 (0.19 - 0.23)	0.24 (0.22 - 0.26)
T. truncatus					0.2 (0.19 - 0.22)	0.08 (0.06 - 0.09)	0.15 (0.14 - 0.16)
G. macrorhynchus						0.21 (0.2 - 0.23)	**0.42** **(0.39 - 0.45)**
P. macrocephalus							**0.32** **(0.3 - 0.35)**

5.3.1.2 *Trophic position*

The TP, and respective standard deviations, of several cetacean species in Madeira marine ecosystem, as calculated from the nitrogen isotope ratio, is presented in Figure 5.6. As expected, Bryde's whale has the lowest TP (3.91 ± 0.47), followed by the dolphin species with TP between 4.36 ± 0.52 (bottlenose dolphin) and 4.64 ± 0.50 (striped dolphin), and the deep divers with highest TP values, between 4.88 ± 0.47 (pilot whale) and 5.12 ± 0.46 (Cuvier's beaked whale), with the exception of pygmy sperm whale with a TP closer to the dolphins (4.69 ± 0.43).

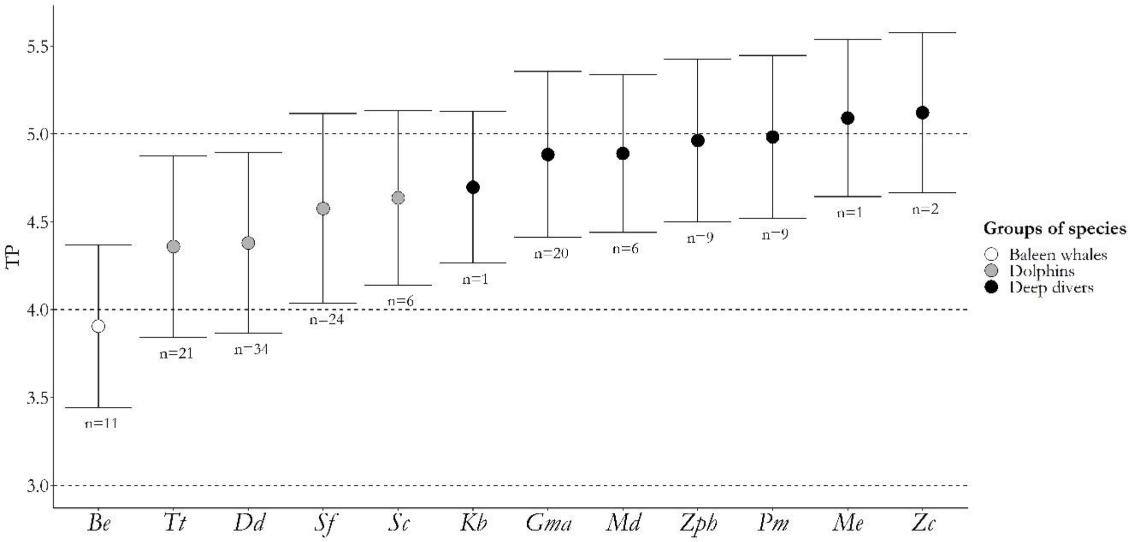


Figure 5.6. The trophic positions (TP), and respective standard deviations, of several cetacean species in Madeira marine ecosystem, as calculated from the nitrogen isotope ratio. The species are: *Be* – Bryde's whale; *Tt* – bottlenose dolphin; *Dd* – Common dolphin; *Sf* – spotted dolphin; *Sc* – striped dolphin; *Kb* – pigmy sperm whale; *Gma* – pilot whale; *Md* – Blainville beaked whale; *Zph* – Ziphiidae; *Pm* – sperm whale; *Me* – Gervais beaked whale; *Zc* – Cuvier's Beaked whale.

5.3.1.3 *Isotopic signatures over time*

Linear regression models were fitted to both the δ13C and δ15N values of cetacean species to identify possible within-year and annual trends. Annual trends were investigated for common dolphin, spotted dolphin, striped dolphin, bottlenose dolphin and beaked whales, for which there were historical samples covering multiple years (Figure VI.1.4-1 and Figure VI.1.4-2, Appendix VI). The linear regression results show a significant reduction of δ15N over years only for bottlenose dolphin (Table VI.1.4-1, Appendix VI). The diagnostic plots of these linear regression models are shown in Figure VI.1.4-3 to Figure VI.1.4-7, Appendix VI.

The results of the linear regression models to investigate within-year trends show a significant upward trend in δ13C for common dolphin and pilot whale and, for δ15N, a downward trend for spotted dolphin and an upward trend for pilot whale (Figure 5.7, Figure 5.8 and Table VI.1.4-2, Appendix VI). The remaining species show no significant trends for either isotope ratio.

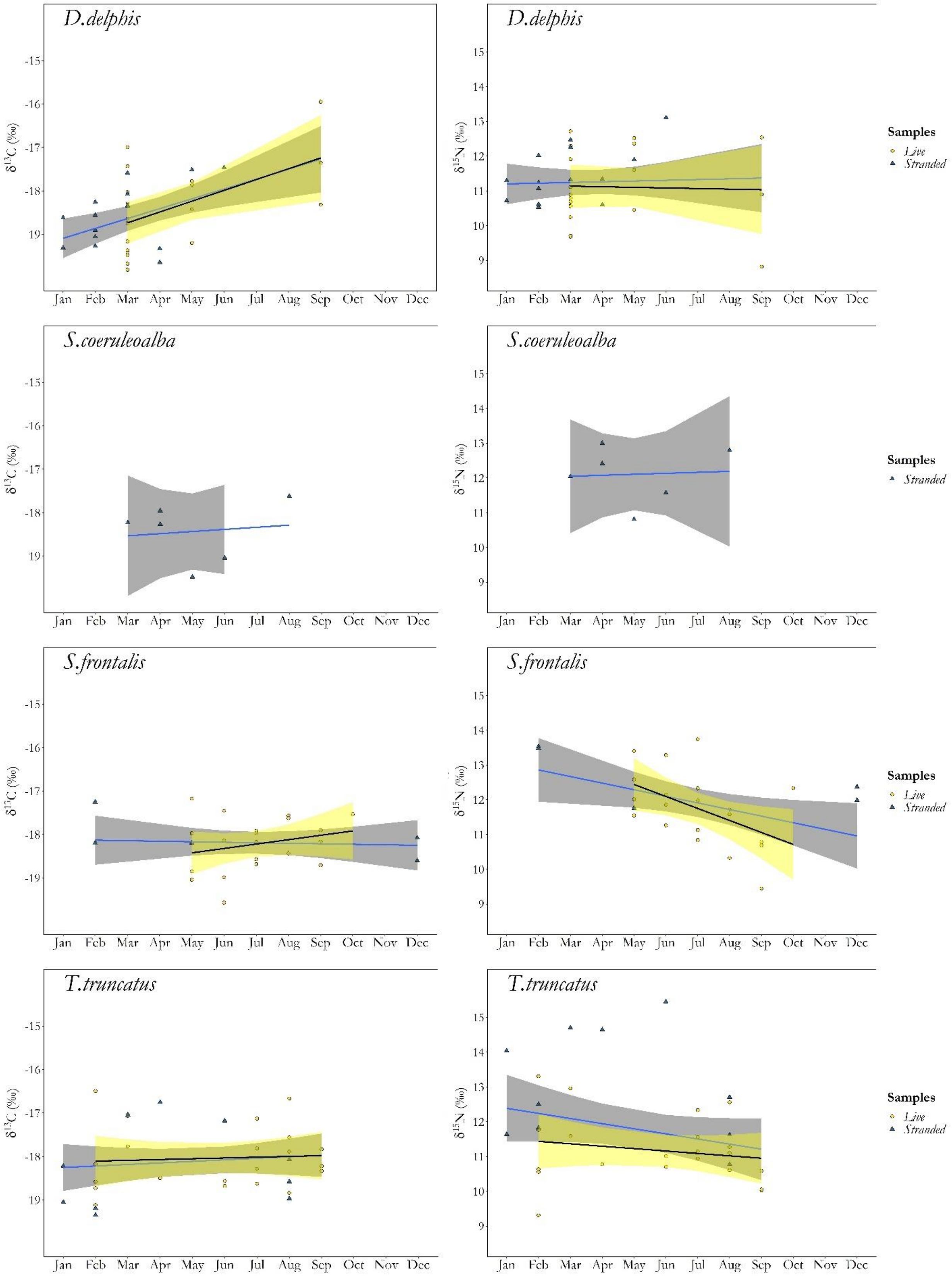


Figure 5.7. Carbon (left) and nitrogen (right) isotope ratio values by month of sampled dolphin species, and respective linear regression line, including 95% confidence intervals. For species with both live and stranded animal samples, a second regression line (black), and respective 95% confidence interval (yellow), are presented for the live animal samples only.

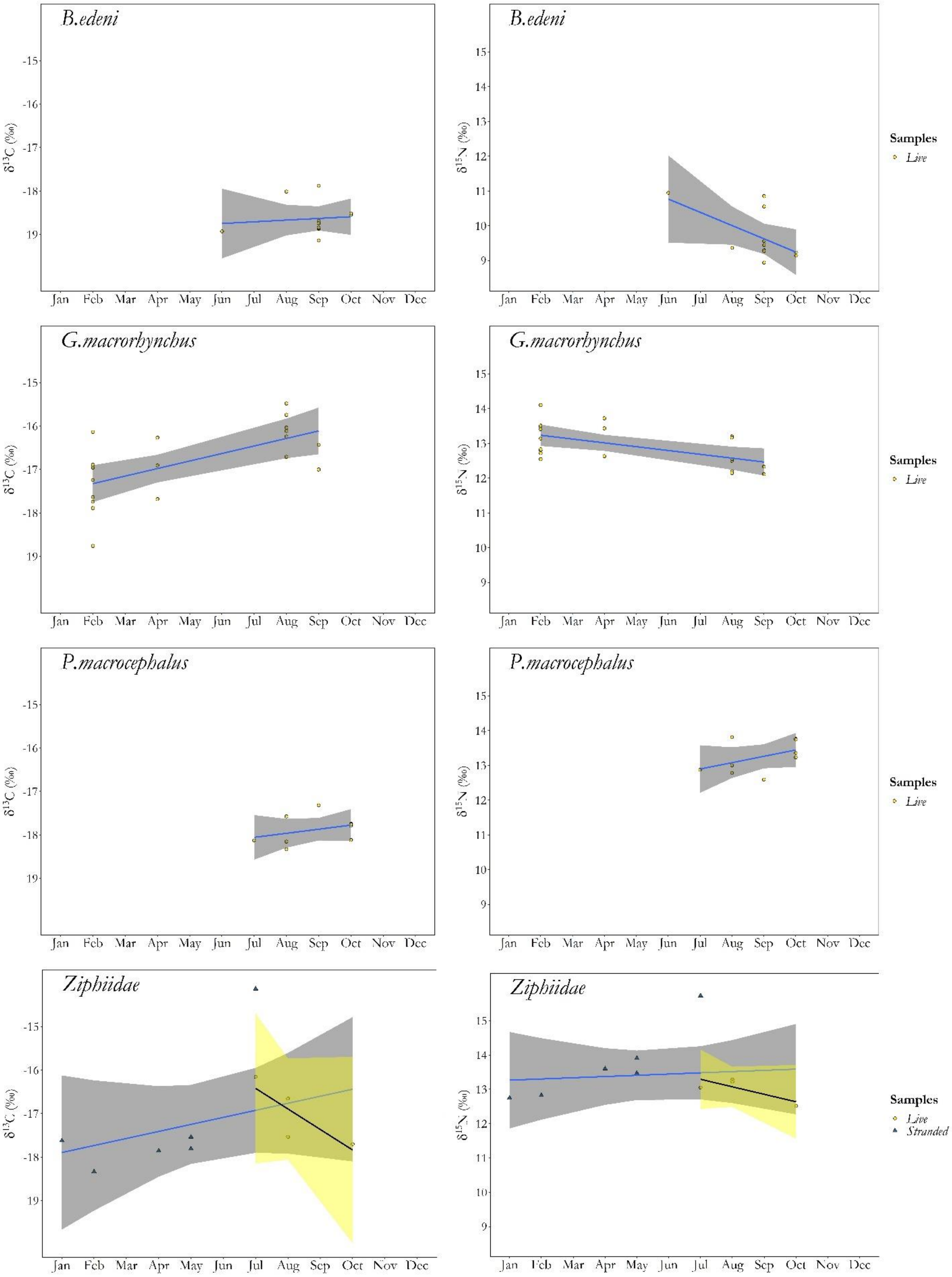


Figure 5.8. Carbon (left) and nitrogen (right) isotope ratio values by month of sampled baleen and deep diver species, and respective linear regression line, including 95% confidence intervals. For species with both live and stranded animal samples, a second regression line (black), and respective 95% confidence interval (yellow), are presented for the live samples only.

5.3.2 Within-year temporal niche overlap

The within-year temporal overlap between species with high proportion of isotopic niche overlap (>0.3) in Madeira archipelago is shown in Figure 5.9 and Figure 5.10, while the equivalent plots for the remaining pairs of species are given in Figure VI.2.1-1 to Figure VI.2.1-6, Appendix VI. The fin whale (*Balaenoptera physalus*), an extra species for which there are no stable isotope data, is considered in these comparisons.

Table 5.5 shows the proportion of within-year temporal overlap (PTO) between pair of species, from which no clear pattern emerged. The proportion of overlap ranged from 0.1, between Bryde's whales and the common dolphin, to 0.76, between the sperm whale and the striped dolphin and the bottlenose dolphin. The PTO was fairly low between the fin whale and three other species (spotted dolphin, pilot whale and beaked whales), as it was also between the common dolphin and those species (0.21 – 0.26). The remaining pairs of species have a PTO ≥ 0.3, with deep divers reaching values greater than 0.52 and as high as 0.76 between them, the dolphins' values from 0.21 to 0.75 and the baleen whales 0.13 between them. The comparison of PTO between groups (baleen whales, dolphins and deep divers) was variable with pair of species across the groups having both low and high PTO values. Finally, the pairs of species with high proportion of isotopic niche overlap (>0.3; underlined values in Table 5.5) had moderate to high PTO values (0.32 – 0.68) between them, except for the pair common dolphin – spotted dolphin.

Table 5.5 – Proportion of the within-year temporal overlap (PTO) between pairs of species. The proportions of overlap ≥ 0.2 are highlighted in bold; pairs of species with higher ecological niche overlap (ENO), either selected by the threshold criteria (≥ 0.2) or by the clustering approach (Section 5.3.4) are highlighted by grey boxes.

Species	*B. Physalus*	*D. delphis*	*S. frontalis*	*S. coeroleoalba*	*T. truncatus*	*G. macrorhynchus*	*P. macrocephalus*	*Ziphiidae*
B. edeni	0.13	0.10	**0.73**	**0.49**	**0.63**	**0.56**	**0.50**	**0.69**
B. Physalus		**0.71**	**0.22**	**0.30**	**0.30**	**0.27**	**0.34**	**0.26**
D. delphis			**0.21**	**0.36**	**0.32**	**0.27**	**0.37**	**0.23**
S. frontalis				**0.53**	**0.68**	**0.32**	**0.61**	**0.74**
S. coeruleoalba					**0.75**	**0.54**	**0.76**	**0.56**
T. truncatus						**0.68**	**0.76**	**0.70**
G. macrorhynchus							**0.67**	**0.56**
P. macrocephalus								**0.53**

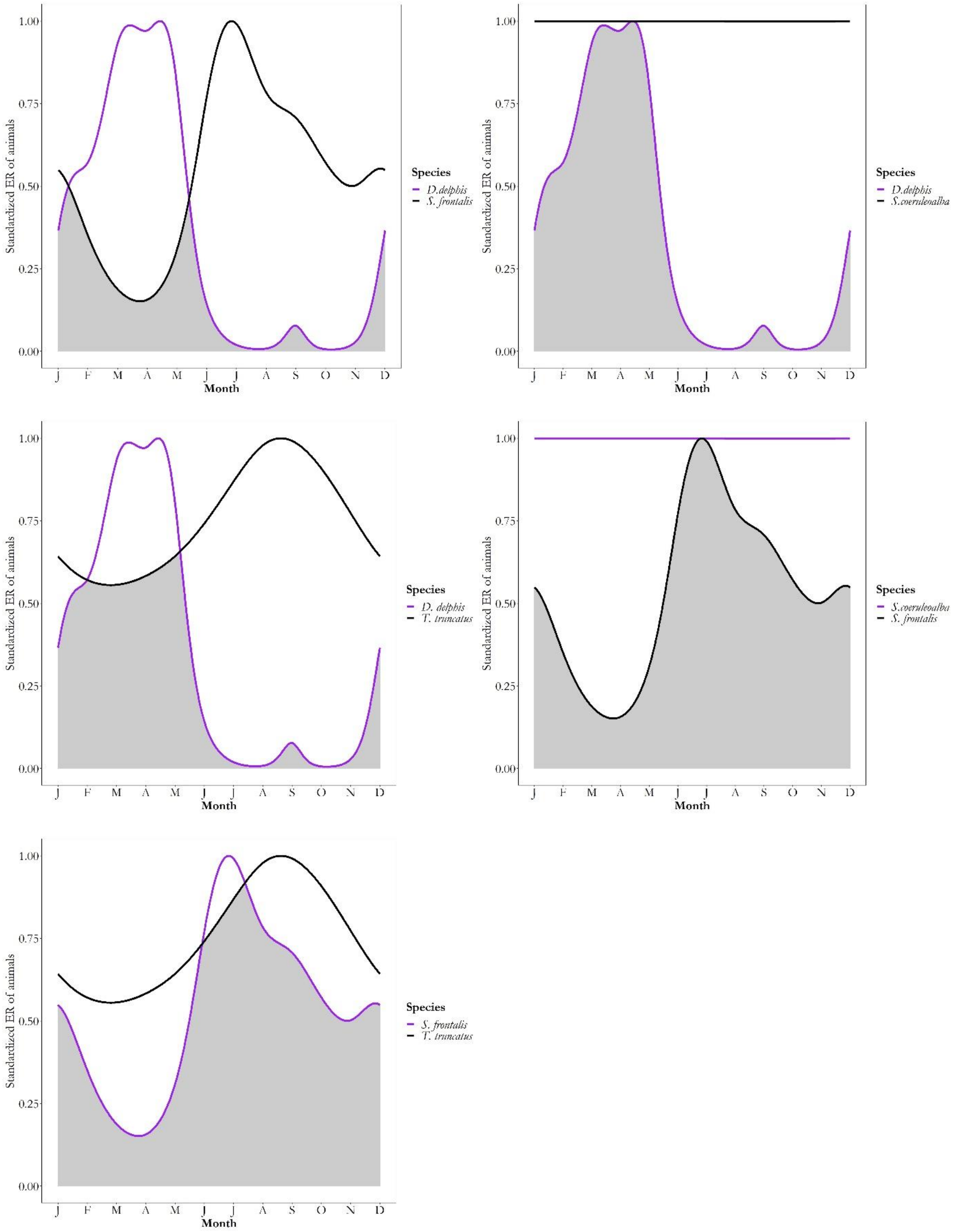


Figure 5.9. Standardized within-year temporal distribution, and respective proportion of temporal overlap, of the dolphin species with an isotopic niche overlap ≥ 0.3. The temporal overlap of the species is represented by the grey area under the curve.

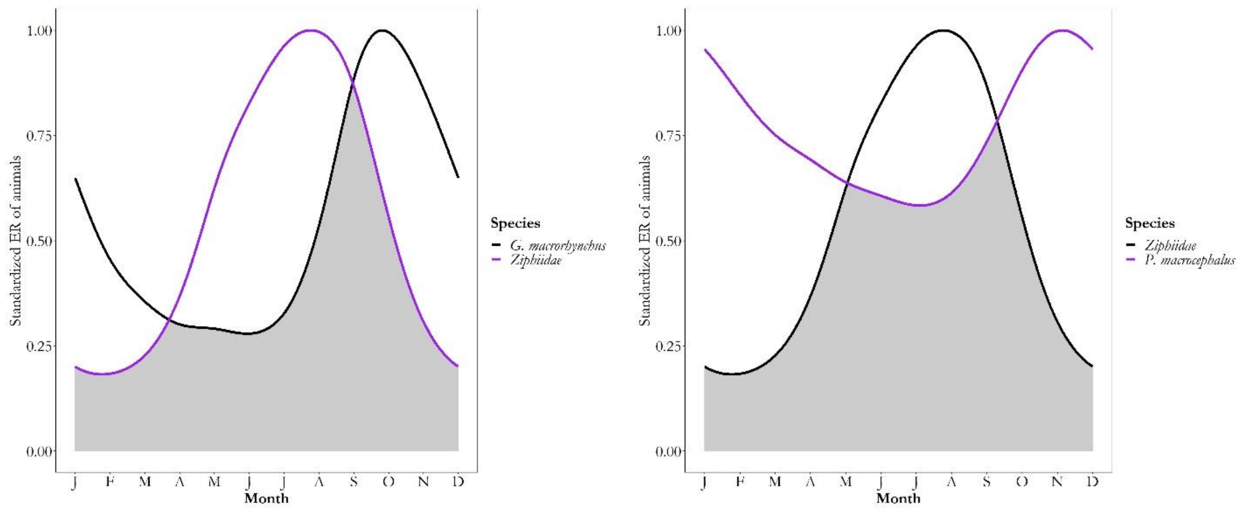


Figure 5.10. Standardized within-year temporal distribution, and respective proportion of temporal overlap, of the deep divers with an isotopic niche overlap ≥ 0.3. The temporal overlap of the species is represented by the grey area under the curve.

5.3.3 Spatial niche overlap

The standardized spatial niche overlap (SSO) between the different combinations of pairs of the cetacean taxa is given in Table 5.6. The overlap maps of each species with the remaining ones are presented in Figure 5.11 to Figure 5.19. The fin whale (*Balaenoptera physalus*), as in the previous section, is considered in these comparisons. The original prediction maps of the taxon and the corresponding overlap map are presented in Figure VI.3.1-1 to Figure VI.3.1-12, Appendix VI.

The SSO ranged from 0.05, between Bryde's whales and the pilot whale, to 0.40, between the bottlenose dolphin and the striped dolphin. The SSO was low to moderate between the baleen whales and the other species (0.05 – 0.22) and between pilot whale and the other species (0.05 – 0.19). The sperm whale had mostly moderate SSO with other species (0.19 – 0.21), with exception of baleen whales. The beaked whales varied between low and high (0.07 – 0.39) as did the dolphins (0.06 – 0.4), however, the latter had high spatial overlap among themselves (0.28 – 0.40).

Table 5.6 – Standardized spatial overlap (SSO) values between pairs of cetacean species, measured as the product of the standardized mean relative ER of each species, standardized to be bounded between 0 and 1. The proportions of overlap ≥ 0.2 are highlighted in bold; pairs of species with higher ecological niche overlap (ENO), either selected by the threshold criteria (≥ 0.2) or by the clustering approach (Section 5.3.4) are highlighted by grey boxes.

Species	*B. Physalus*	*D. delphis*	*S. frontalis*	*S. coeroleoalba*	*T. truncatus*	*G. macrorhynchus*	*P. macrocephalus*	*Ziphiidae*
B. edeni	0.10	0.18	**0.22**	**0.20**	0.15	0.05	0.13	0.16
B. Physalus		0.11	0.11	0.09	0.13	0.04	0.08	0.10
D. delphis			**0.30**	**0.39**	**0.34**	0.07	0.19	**0.33**
S. frontalis				**0.28**	**0.34**	0.06	**0.21**	**0.26**
S. coeruleoalba					**0.40**	0.15	**0.20**	0.17
T. truncatus						0.07	**0.21**	**0.39**
G. macrorhynchus							0.19	0.07
P. macrocephalus								0.19

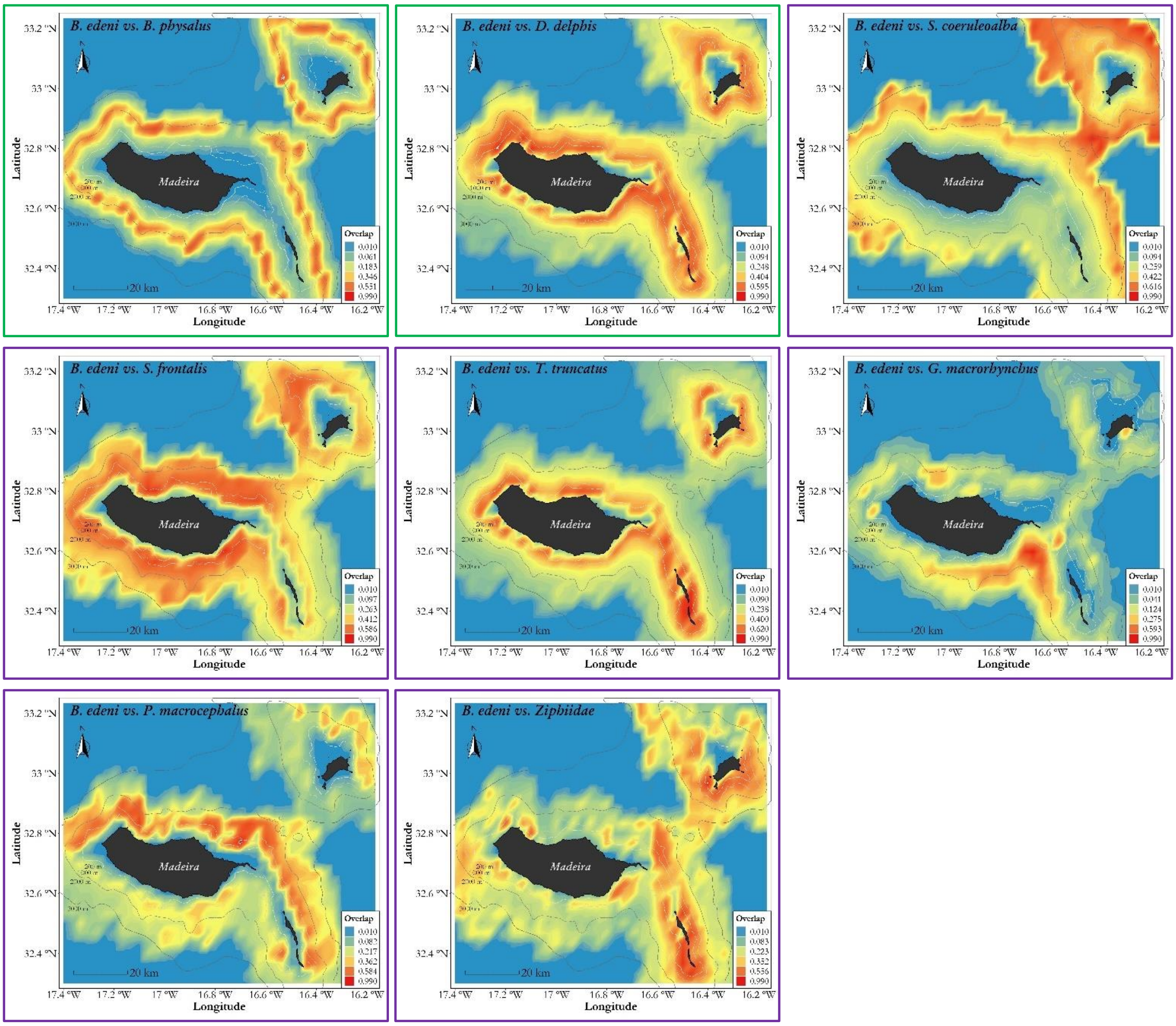


Figure 5.11. Standardized spatial overlap between Bryde's whale (*B. edeni*) and other cetacean species in Madeira archipelago waters. The maps of the species with temporal overlap, isotopic overlap or both ≥ 0.3 are identified with a coloured frame; violet, green and orange, respectively.

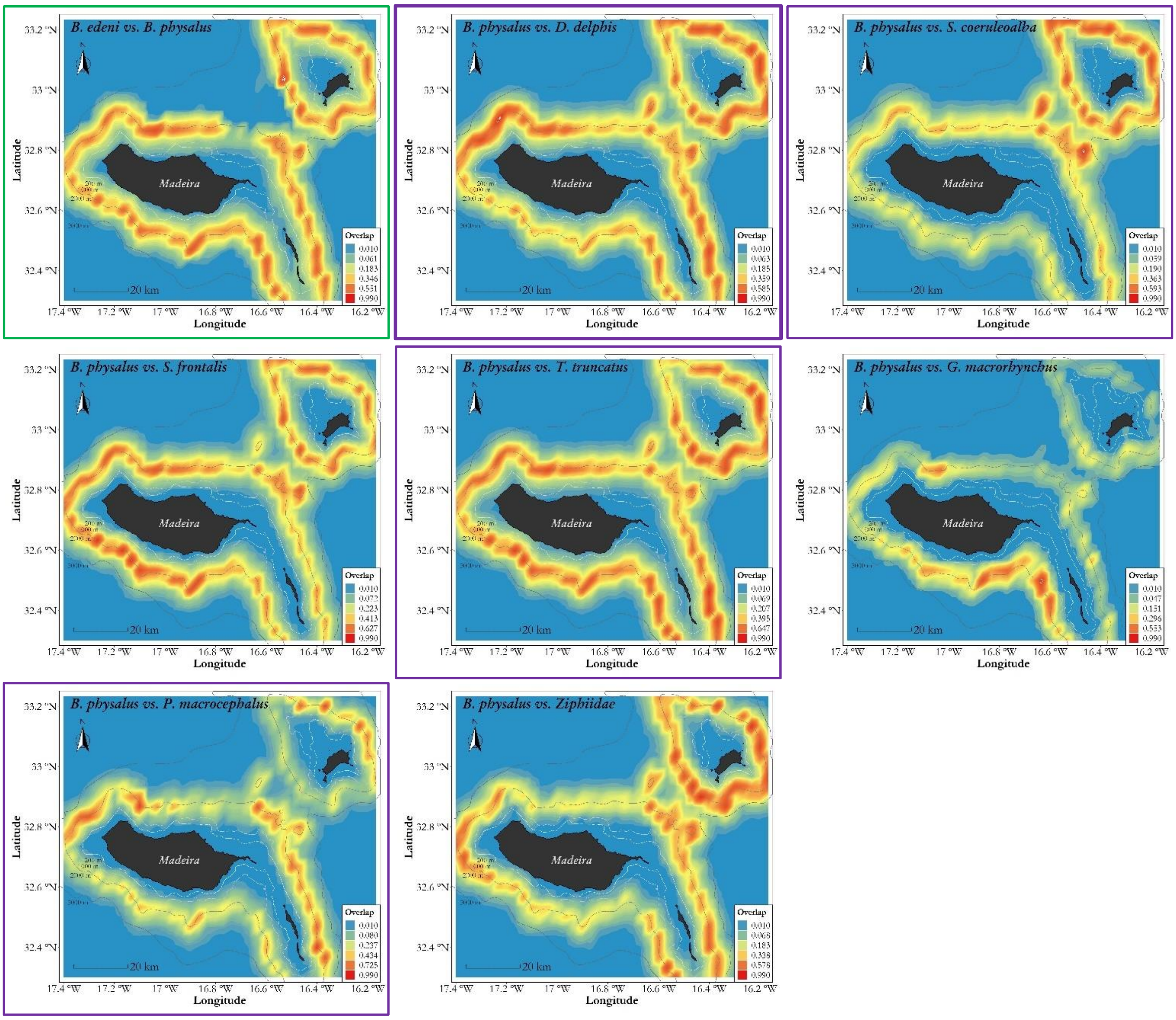


Figure 5.12. Standardized spatial overlap between fin whale (*B. physalus*) and other cetacean species in Madeira archipelago waters. The maps of the species with temporal overlap, isotopic overlap or both ≥ 0.3 are identified with a coloured frame; violet, green and orange, respectively.

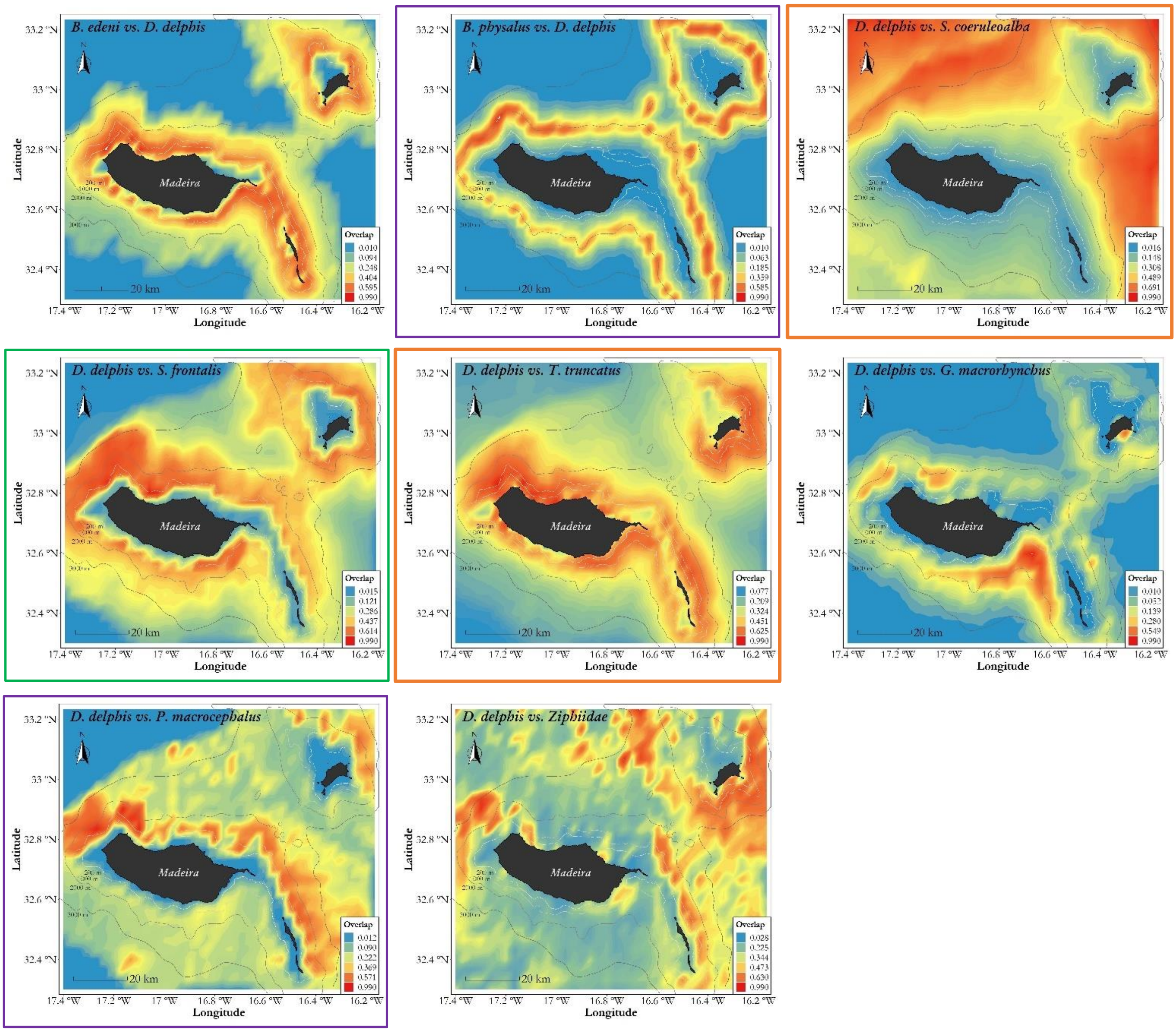


Figure 5.13. Standardized spatial overlap between common dolphin (*D. delphis*) and other cetacean species in Madeira archipelago waters. The maps of the species with temporal overlap, isotopic overlap or both ≥ 0.3 are identified with a coloured frame; violet, green and orange, respectively.

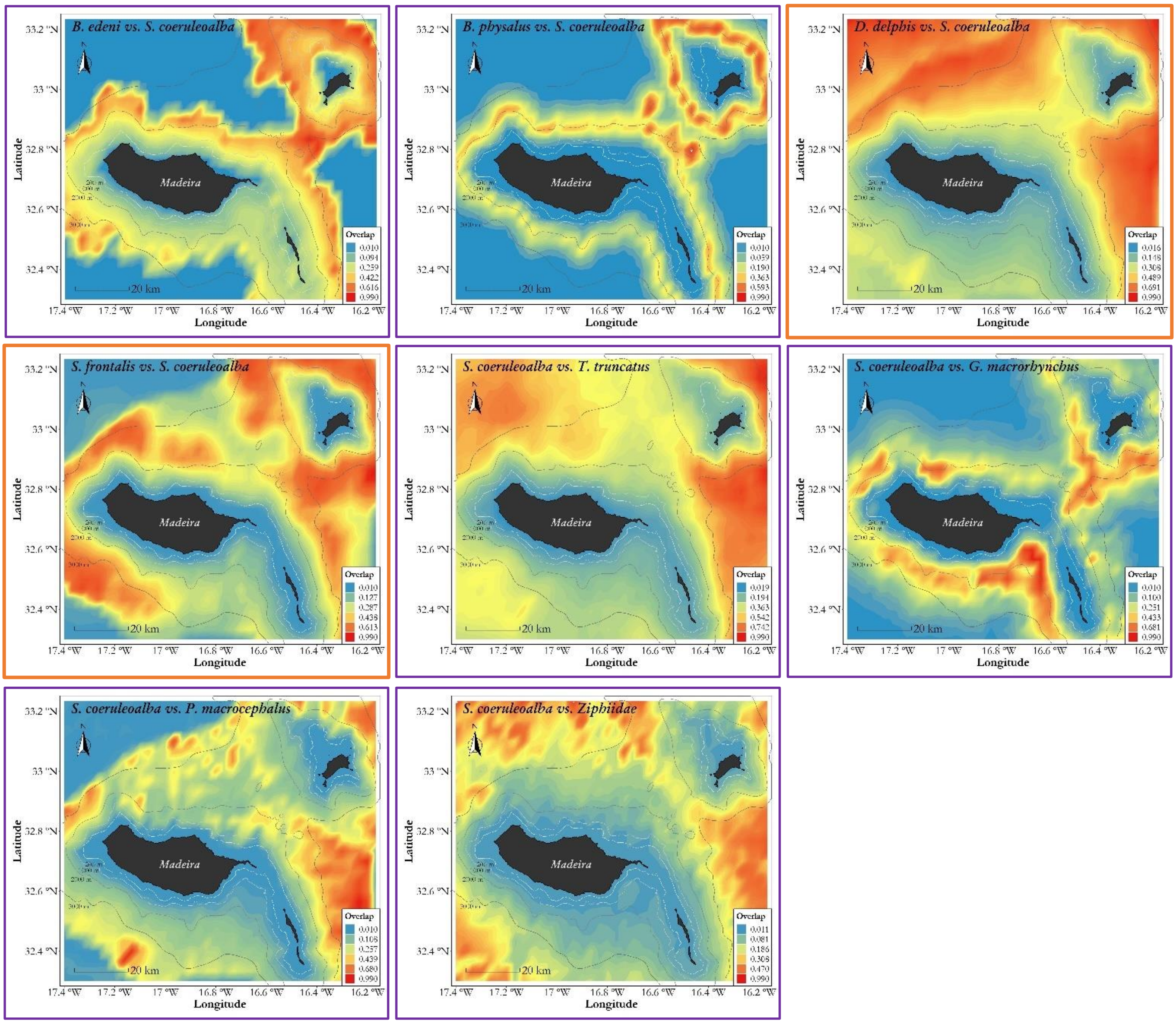


Figure 5.14. Standardized spatial overlap between striped dolphin (*S. coeruleoalba*) and other cetacean species in Madeira archipelago waters. The maps of the species with temporal overlap, isotopic overlap or both ≥ 0.3 are identified with a coloured frame; violet, green and orange, respectively.

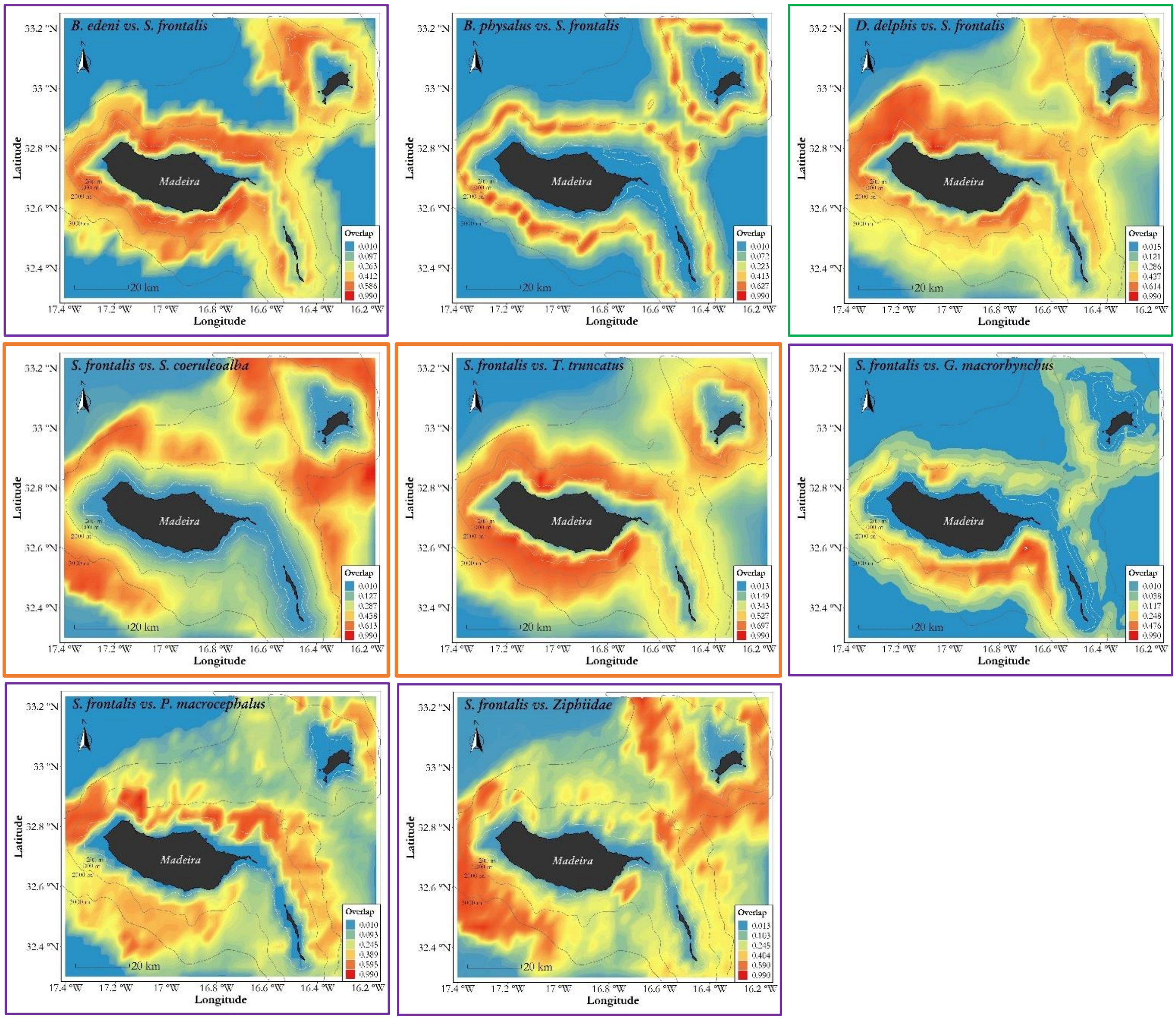


Figure 5.15. Standardized spatial overlap between spotted dolphin (*S. frontalis*) and other cetacean species in Madeira archipelago waters. The maps of the species with temporal overlap, isotopic overlap or both ≥ 0.3 are identified with a coloured frame; violet, green and orange, respectively.

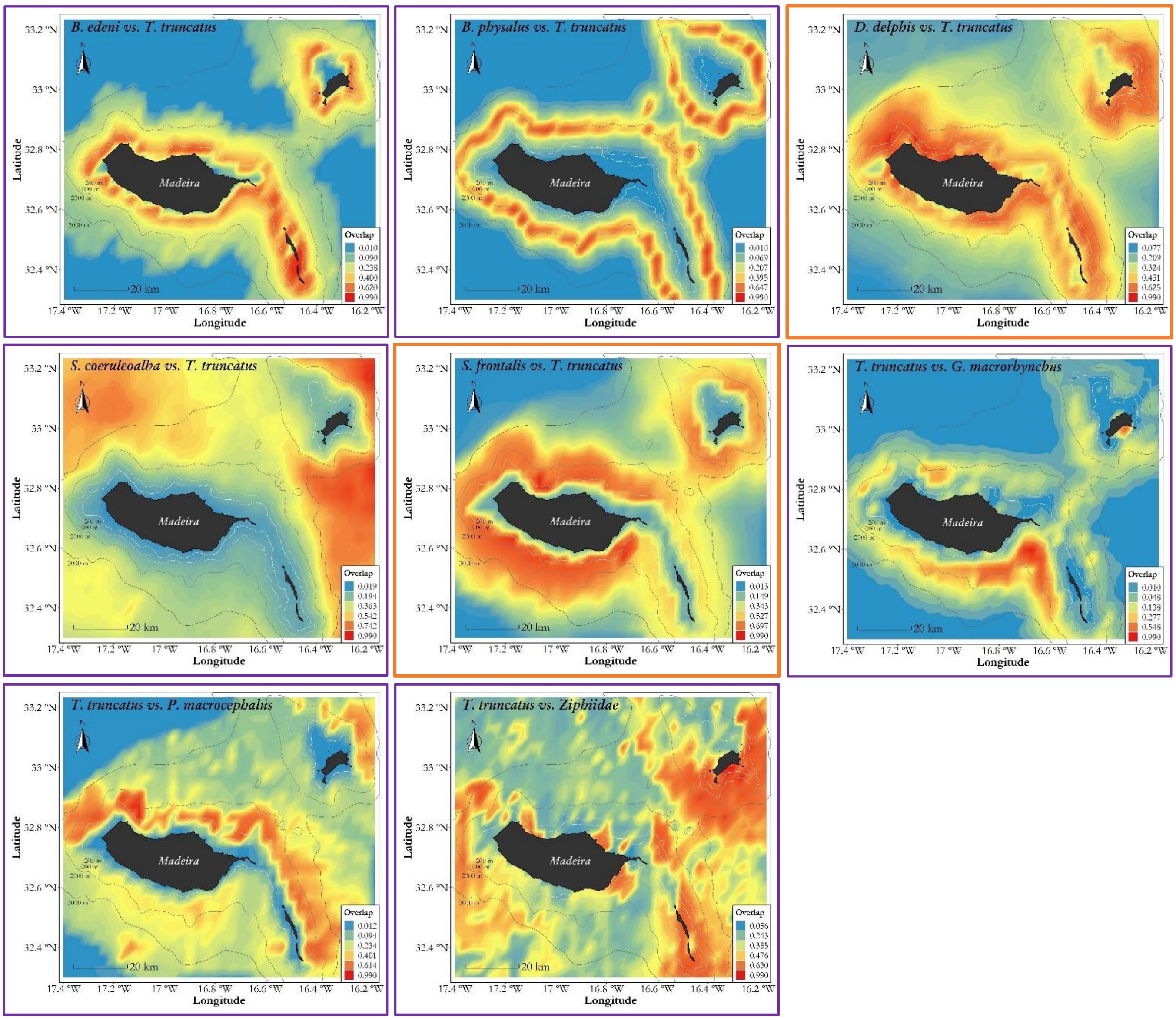


Figure 5.16. Standardized spatial overlap between bottlenose dolphin (*T. truncatus*) and other cetacean species in Madeira archipelago waters. The maps of the species with temporal overlap, isotopic overlap or both ≥ 0.3 are identified with a coloured frame; violet, green and orange, respectively.

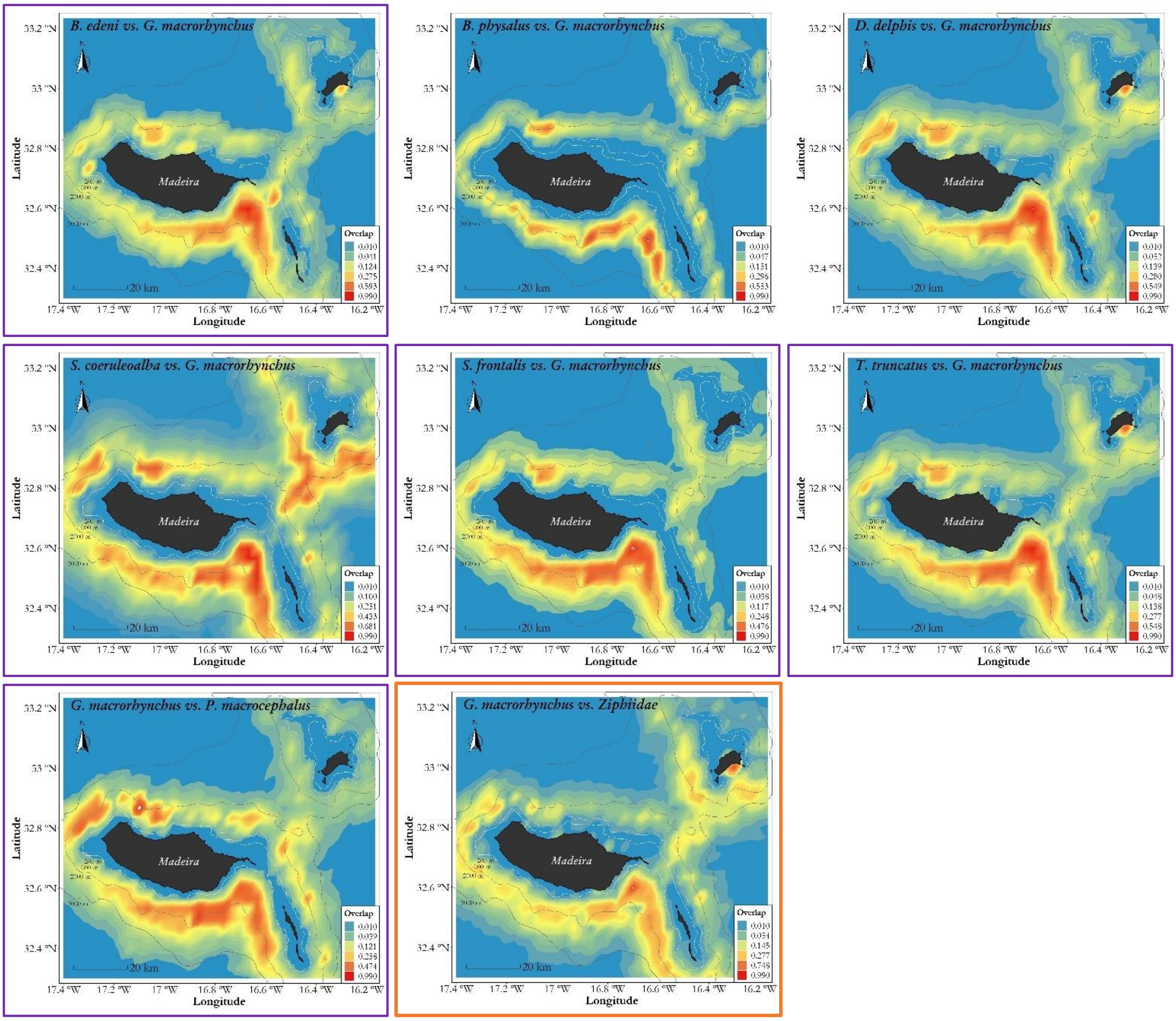


Figure 5.17. Standardized spatial overlap between short-finned pilot whale (*G. macrorhynchus*) and other cetacean species in Madeira archipelago waters. The maps of the species with temporal overlap, isotopic overlap or both ≥ 0.3 are identified with a coloured frame; violet, green and orange, respectively.

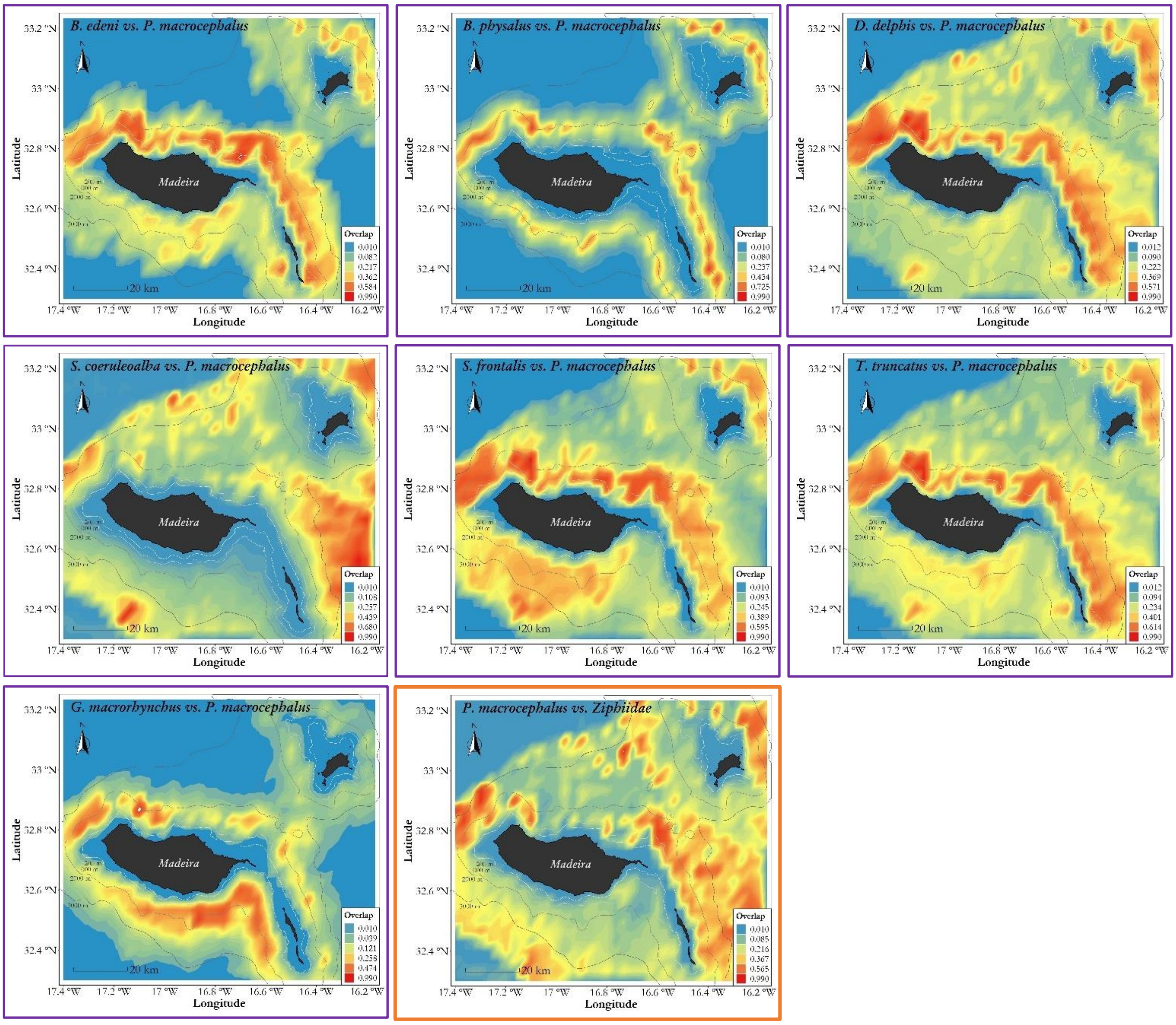


Figure 5.18. Standardized spatial overlap between sperm whale (*P. macrocephalus*) and other cetacean species in Madeira archipelago waters. The maps of the species with temporal overlap, isotopic overlap or both ≥ 0.3 are identified with a coloured frame; violet, green and orange, respectively.

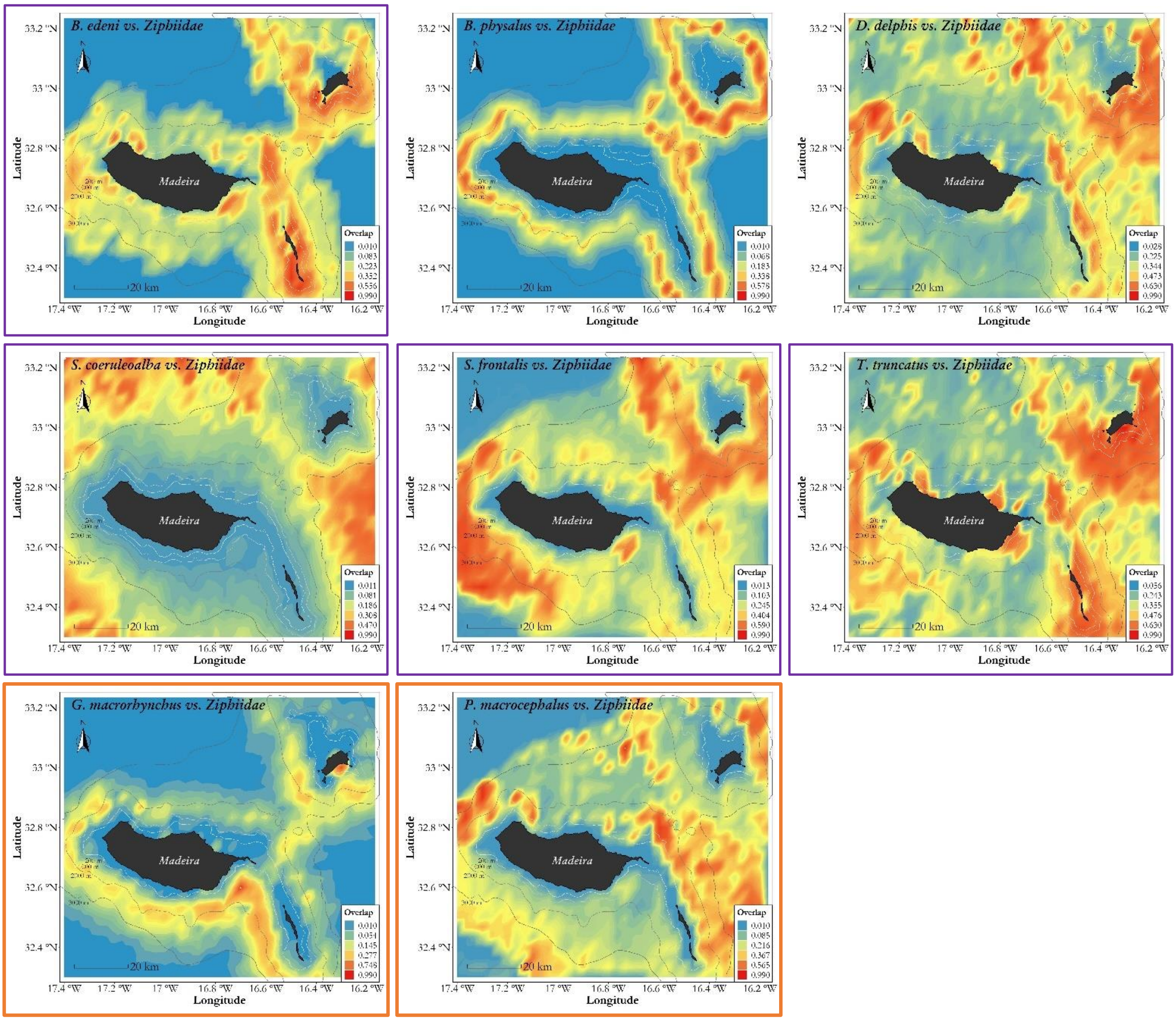


Figure 5.19. Standardized spatial overlap between beaked whales (Ziphiidae) and other cetacean species in Madeira archipelago waters. The maps of the species with temporal overlap, isotopic overlap or both ≥ 0.3 are identified with a coloured frame; violet, green and orange respectively.

5.3.4 Ecological niches

The ecological niches of each cetacean taxon studied were described and defined using the trophic, temporal and spatial dimensions (Table 5.7), and were interpreted and contextualized in the Madeira marine ecosystem considering each taxon's predicted biomass for the area.

Table 5.7 shows an interesting pattern in the temporal niche section related with ER fluctuations, namely the peak and trough of relative abundance of the species in the study area in relation to their TP. The species with lower TP values show a sequential temporal increase in their relative abundance as they increase in the TP, starting with the fin whale at the end of winter and beginning of spring, followed by the Bryde's whale at the beginning of summer and the bottlenose dolphin in mid-summer. The same pattern is repeated by the species with intermediate and higher TP, with a peak in the common dolphin presence at the end of winter and beginning of spring, followed by the spotted dolphin, the pilot whale and the sperm whale. The higher the average TP the later in the year is their peak in relative abundance. The only exceptions are the striped dolphin with no discernible peak and the beaked whales which, in spite being at a mean TP higher than the pilot whale have an ER peak in the summer before that species.

The relationship between the ENO metrics and the overlapped niche dimensions of pairs of species were investigated using thresholds and clustering methods. The threshold of 0.2 was selected over the others because it discriminated best the overlapped niche dimensions (one dimension: trophic, temporal and spatial; two dimensions: trophic-temporal, trophic-spatial and temporal-spatial; and three dimensions: trophic-temporal-spatial) of the pairs of species compared (Figure 5.20, top-left; Figure VI.4.1-1, Appendix VI).

The clustering method DHC was chosen over the other methods (Table VI.4.2-1, Appendix VI) and the optimal number of clusters was four (Figure VI.4.2-1, Appendix VI). In Figure 5.20 (bottom plot) are presented the boxplots of the overlap values between pairs of cetacean species clustered by DHC for each of the ecological niche dimensions. The same plots, but for K-means and AHC are presented in Figure VI.4.2-2 of Appendix VI, while in Figure VI.4.2-3 and Figure VI.4.2-4 are given the clusters configuration represented on the two first dimensions of PCA for Kmeans, DHC and AHC, and the dendrograms of DHC and AHC analysis, respectively.

Table 5.7 – Description and definition of cetacean species ecological niche according to their trophic, temporal and spatial niches. These niches dimensions are described making use of the GAMs selected for each species, both for the spatial and temporal dimensions (Chapter 4) and the stable isotope analysis results from Chapter 5. Also presented are the average depth and range for each species, calculated using the same dataset used for modelling, and the total biomass of each species, calculated as the product of the abundance estimates obtained in systematic line-transect surveys (Chapter 4) and average individual biomass estimate for each species.

	TROPIC NICHE					TEMPORAL NICHE															HABITAT / SPATIAL NICHE									BIOMASS			
									Peak and trough[7]																					Period 2007 - 2012 (Year-round average)		Period 2017- 2018 (Summer/autumn average)	
Species	δ15N	δ15N.SD	TP[1]	TP.SD	Relative position[2]	Yearly presence[3]	ER Differencial[4]	Seasonality (ER flutuations)[5]	J	F	M	A	M	J	J	A	S	O	N	D	δ13C	δ13C.SD	Trophic habitat	Average depth and ranges	Preference for specific areas	Preferencial habitats	Environmental variables	Type of variable	Smooth shape and slope	Abundance	Biomass (ton)	Abundance	Biomass (ton)
B. physalus	-	-	-	-	-	No	1	Strong			■	■									-	-	-	1 893 (556 - 3 183)	Waters with depths around the -2000 m depth contour	offshore	Dist. 2000 isobath	static	linear -	20	168	-	-
B. edeni	9.69	0.73	3.91	0.47	Low	No	1	Strong						■	■	■					-18.62	0.38	Pelagic	971 (70 - 3 262)	Waters around the islands over the escarpment, preferencially closer to the insular shelf	Slope	Dist. escarpment Escarpment area Maximum depth	static static static	linear - linear - linear +	20	125	94	725
T. truncatus	11.18	0.99	4.36	0.52	Medium	Yes	0.61	Low		░	░	░				■	■	■			-18.02	0.72	Pelagic	911 (49 - 3 664)	Preferencial use of coastal waters around the islands, diminishing towards the high seas	coastal	Dist. coast	static	linear -	561	103	765	141
D. delphis	11.26	0.98	4.38	0.52	Medium	No	0.99	Strong			■	■	■		░	░	░	░			-18.33	0.88	offshore/ pelagic	1 504 (65 - 3 906)	Coastal and offshore waters northwest of Madeira, northeast of Madeira and Desertas, Southeast of Madeira and south, east and north P. Santo	coastal/ offshore	Chlorophyl-a Sea surface anomaly Average slope slope area	dynamic dynamic static static	linear + linear + linear +	521	36	262	18
S. frontalis	11.92	1.07	4.58	0.55	Medium	Yes	0.92	Strong		░	░	░		■	■	■					-18.12	0.62	offshore/ pelagic	1 394 (67 - 3 406)	Waters over the escarpment, south, southeast and north of Madeira and west and north P. Santo	Slope	Dist. escarpment Slope area Part. organic carbon Sea surface height	static static dynamic dynamic	linear - linear + linear - linear +	1081	56	2 641	136
S. coeruleoalba	12.10	0.82	4.64	0.50	Medium	Yes	0.81	Medium	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	-18.27	0.71	offshore/ pelagic	2 010 (716 - 3 874)	Offshore deep waters over the abyssal plain	offshore	Chlorophyl-a Average depth Sea surface temp.	dynamic static dynamic	linear - linear - linear -	-	-	76	5
G. macrorhynchus	12.93	0.57	4.88	0.48	High	Yes	0.90	Strong				░	░	░			■	■	■		-16.82	0.83	Benthic	1 561 (344 - 3 852)	Waters over the escarmpent south and southeast of Madeira and west Desertas	Slope	Dist. 1500 isobath Part. organic carbon Contour index Maximum aspect Mixed layer depth	static dynamic static static dynamic	linear - linear + linear - non-linear linear -	103	54	271	141
Ziphiidae	13.43	0.91	4.96	0.47	High	Yes?	1	Strong	░	░	░				■	■	■			░	-16.98	1.15	Benthic	1 734 (329 - 3 673)	Deep offshore waters southwest of Madeira and south, west and east P. Santo	offshore	Mixed layer depth Aspect std dev.	dynamic static	linear + linear -	23	31	17	23
P. macrocephalus	13.24	0.46	4.98	0.47	High	Yes	0.92	Medium	▓					░	░	░		■	■	■	-17.88	0.33	offshore/ pelagic	1 667 (92 - 3 640)	Waters over the escarpment north and northeast of Desertas and east and northeast P. Santo	Slope	Slope area Average aspect Sea surface temp.	static static dynamic	linear + non-linear linear +	-	-	28	400

[1] Calculated from the δ15N values of each species

[2] Inferred from the δ15N range and trophic position of the species

[3] Inferred from the monthly encounter rates of each species presented in chapter 4

[4] Inferred from the monthly group encounter rates of each species presented in chapter 4 and calculated has the difference between maximum and minimum monthly ER scaled to 1. Species with some months not present in Madeira have a value of 1

[5] Inferred from the interpretation of monthly encounter rates of groups and monthly GAM smooth of individuals

[6] Aproximate periods of high, medium and low group encounter rates by trimestre, based on group ER data

[7] Inferred from the temporal distribution smooth curves presented in chapter 6

[8] Generalization the habitat preferences for specific areas of the species

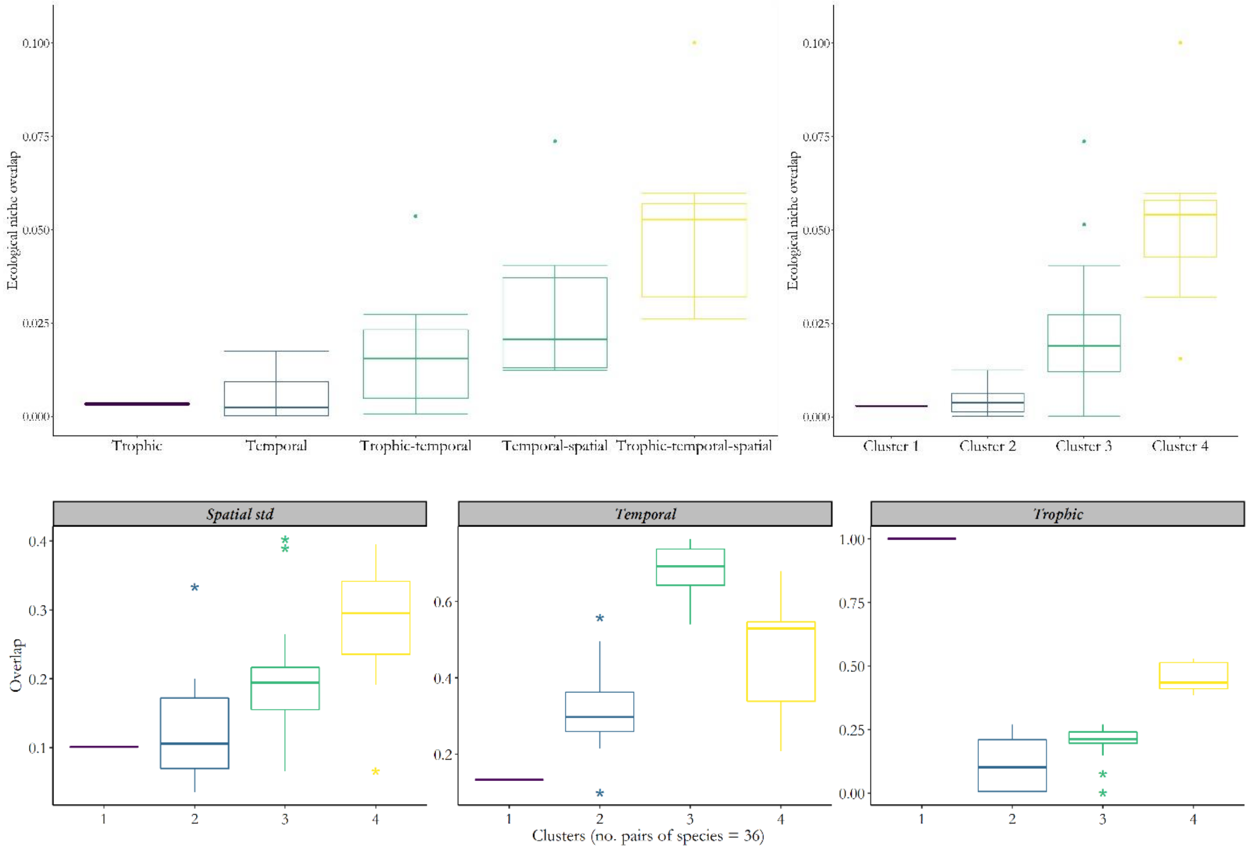
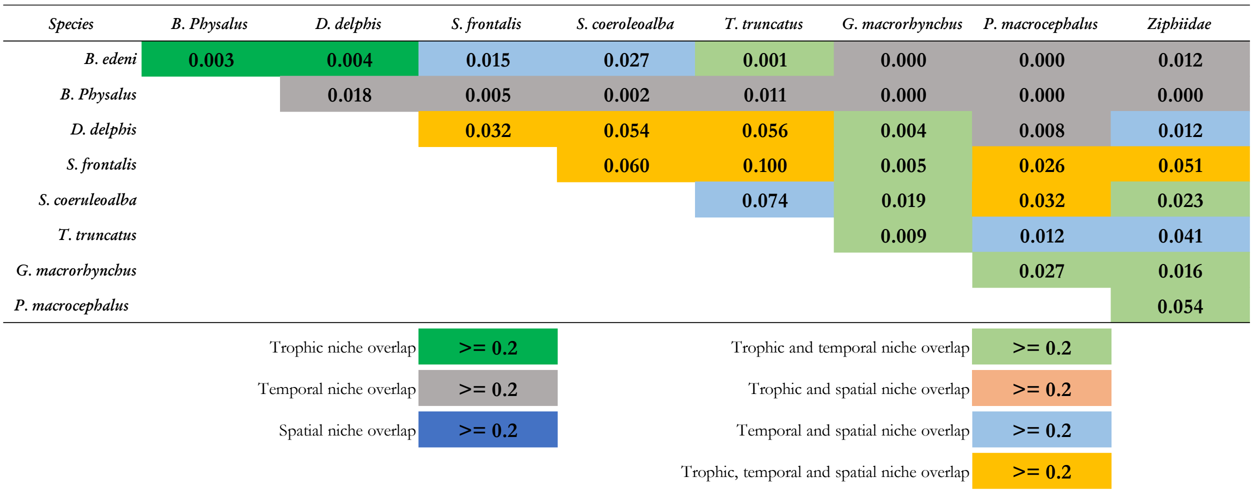


Figure 5.20. Top-left: boxplots of ecological niche overlap (ENO) values of pairs of cetacean species versus the combined overlap classes those pairs of species were allocated to when the overlap threshold was ≥0.2 in each of the dimensions (trophic, temporal and spatial). Top-right: boxplots of ENO values of pairs of cetacean species grouped by divisive hierarchical clustering (DHC). Bottom: Boxplots of the overlap values between pairs of cetacean species clustered by DHC, in the spatial, temporal and trophic dimensions. The whiskers, the box and the central line represent the minimum and maximum, the 25th and 75th percentile, and the median, respectively. The dots are outliers.

The threshold and the clustering approaches give similar and consistent results (Figure 5.20, top plots). Both approaches separate the Bryde's whale/fin whale pair because of the same trophic values (trophic/Cluster 1), group the remaining pairs with overlaps in one dimension (temporal/Cluster 2) and group all pairs with overlap in three dimensions (trophic-temporal-spatial/Cluster 4). The pairs with overlaps in two dimensions are grouped in Cluster 3 by DHC, while the threshold approach separates them in two groups with similar medians (trophic-temporal and temporal-spatial). In summary, both approaches show that the ENO metrics discriminate well pairs of species niches' overlap in one, two and three dimensions (different medians, percentiles and, in general, different ranges of values).

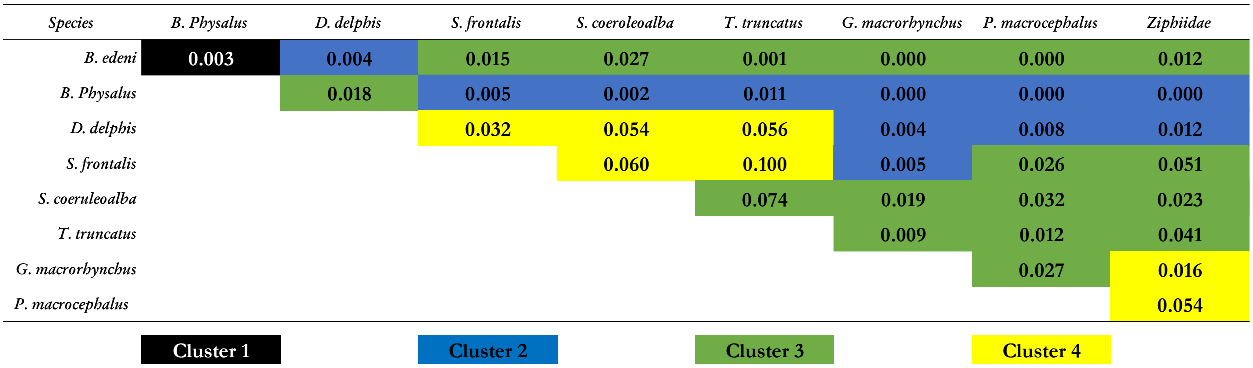
Table 5.8 – The ecological niche overlap (ENO) between pairs of cetacean taxa. The colour code identifies the pairs of species allocated to each group defined by the threshold approach with a value of 0.2.



Species	*B. Physalus*	*D. delphis*	*S. frontalis*	*S. coeroleoalba*	*T. truncatus*	*G. macrorhynchus*	*P. macrocephalus*	*Ziphiidae*
B. edeni	0.003	0.004	0.015	0.027	0.001	0.000	0.000	0.012
B. Physalus		0.018	0.005	0.002	0.011	0.000	0.000	0.000
D. delphis			0.032	0.054	0.056	0.004	0.008	0.012
S. frontalis				0.060	0.100	0.005	0.026	0.051
S. coeruleoalba					0.074	0.019	0.032	0.023
T. truncatus						0.009	0.012	0.041
G. macrorhynchus							0.027	0.016
P. macrocephalus								0.054

Trophic niche overlap	>= 0.2	Trophic and temporal niche overlap	>= 0.2
Temporal niche overlap	>= 0.2	Trophic and spatial niche overlap	>= 0.2
Spatial niche overlap	>= 0.2	Temporal and spatial niche overlap	>= 0.2
		Trophic, temporal and spatial niche overlap	>= 0.2

Table 5.9 – The ecological niche overlap (ENO) between pairs of cetacean taxa. The colour code identifies the pairs of species allocated to each cluster defined by the clustering approach.



Species	*B. Physalus*	*D. delphis*	*S. frontalis*	*S. coeroleoalba*	*T. truncatus*	*G. macrorhynchus*	*P. macrocephalus*	*Ziphiidae*
B. edeni	0.003	0.004	0.015	0.027	0.001	0.000	0.000	0.012
B. Physalus		0.018	0.005	0.002	0.011	0.000	0.000	0.000
D. delphis			0.032	0.054	0.056	0.004	0.008	0.012
S. frontalis				0.060	0.100	0.005	0.026	0.051
S. coeruleoalba					0.074	0.019	0.032	0.023
T. truncatus						0.009	0.012	0.041
G. macrorhynchus							0.027	0.016
P. macrocephalus								0.054

Cluster 1 **Cluster 2** **Cluster 3** **Cluster 4**

Table 5.8 and Table 5.9 show the ENO values for all the pairs of species and allocate them to the groups identified by the threshold and the clustering approach, respectively. In both tables the common dolphin and the spotted dolphin are identified by overlapping with the other dolphin species, namely each other, the striped dolphin and the bottlenose dolphin, in the three ecological niche dimensions. The overlap between these species in the three niche dimensions signals them as species potentially competing for the same food resources. The clustering approach also identified beaked whales potentially competing with pilot whales and sperm whales, while the threshold approach identified spotted dolphins potentially competing with sperm whales and beaked whales and striped dolphins with sperm whales. Table VI.4.2-1 and Table VI.4.2-2, Appendix V, show the allocation of pairs of taxa when the values of 0.1 and 0.3 were used in the threshold approach.

The mENO of each species with the remaining species for each ecological dimension is presented in Figure 5.21. The mENO gives an indication of each species degree of specialization in each of the ecological dimensions. All dolphin species and the beaked whales have a moderate trophic mENO

(mENO_{tr}), ranging between 0.25 and 0.35, followed by the pilot whales and sperm whale (~ 0.2) and, finally, the Bryde's whale with the lowest mENO_{tr} (~0.1) (Figure 5.21, top plots). Most taxa have a relatively high temporal mENO (mENO_{t}), ranging between ~0.5 and ~0.6, except the common dolphin and the fin whale with mENO_{t} around 0.3 (Figure 5.21, bottom plot). In the spatial dimension (mENO_{s}), the dolphin species and the beaked whales are group together, as in mENO_{tr}, with highest values (~0.2 – ~0.25), followed by the sperm whale (~0.18) and the Bryde's whale (~0.15), and finally the fin whale and pilot whale with values below 0.1 (Figure 5.21, top-right and bottom plots).

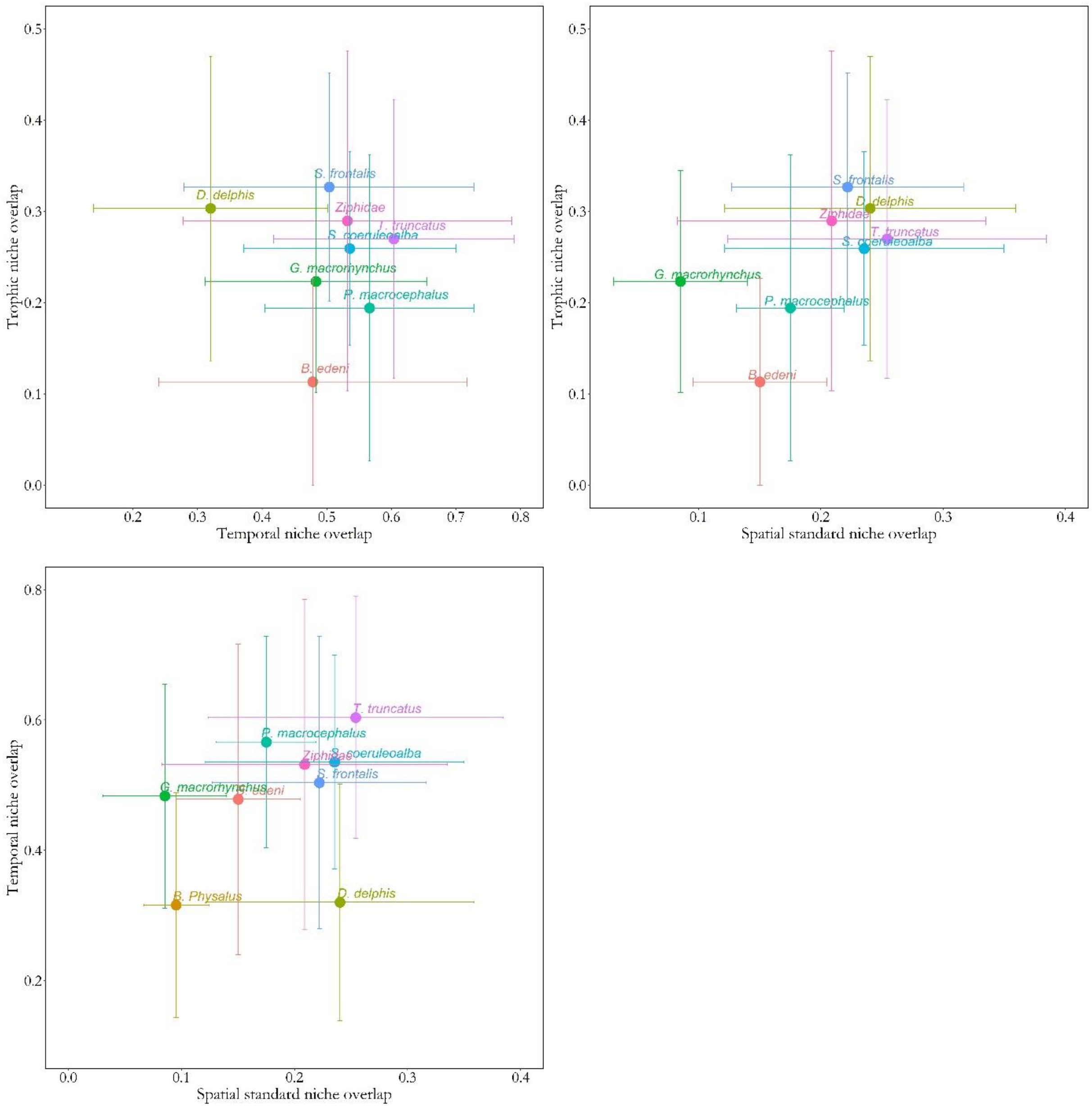


Figure 5.21. The visualization of the mean ecological niche overlap (mENO) of one species with the remaining species in each ecological dimension (trophic, temporal and spatial). Top-left: trophic vs temporal niche overlap; top-right: trophic vs spatial niche overlap; bottom: temporal vs spatial niche overlap.

The comparison of the mENO of taxa in the bi-dimentional space (Figure 5.21), show that in the mENO$_{tr}$ vs mENO$_{t}$ bi-dimensional space (top-left), most species group together with the exception of the common dolphin and the Bryde's whale, although the group is less obvious on the trophic dimension. In the mENO$_{tr}$ v mENO$_{s}$ bi-dimensional space (top-right), the dolphin species and beaked whales cluster tightly and the pilot whale, sperm whale and Bryde's whale are well separated from the cluster and from each other. The spotted dolphin, the common dolphin and the bottlenose dolphin are the more generalist species and the Bryde's whale is the most specialist species in this space. Finally, in the mENO$_{t}$ vs mENO$_{s}$ bi-dimensional space (down-left), most dolphin species cluster together with the sperm whale and the beaked whales, the pilot whale is close to the Bryde's whale in the degree of specialization in this space, and the common dolphin and the fin whale are well separated from each other and from the remaining clusters. The bottlenose dolphin is the most generalist species and the fin whale the most specialist species in this space.

The overall degree of ecological niche specialization of each species (ENS) is presented in Figure 5.22. The most generalist species (higher average overlap in the three ecological dimensions) is the bottlenose dolphin, followed by the spotted dolphin, and striped dolphin. The beaked whales and the common dolphin have an intermediate position and the pilot whale, the Bryde's whale and the fin whale are the most specialized. The closeness of taxa in the degree of specialization was also measured as the Euclidian distance between the taxa in the three-dimensional ecological niche space (Figure 5.23).

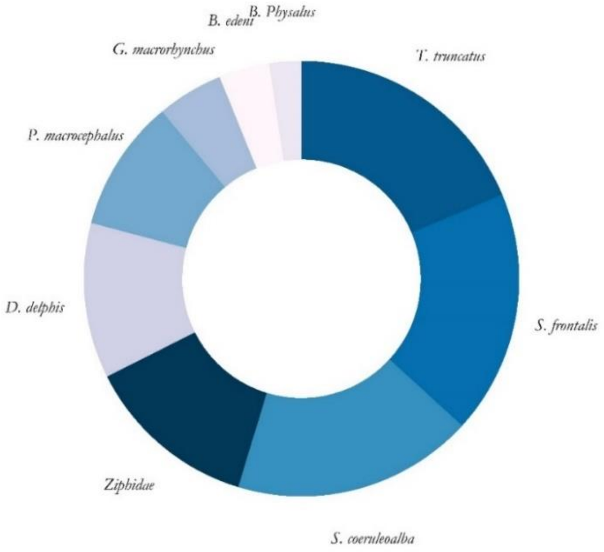


Figure 5.22. The overall degree of ecological niche specialization of the species (ENS), measured as a proportion of the mean ecological niche overlap (mENO).

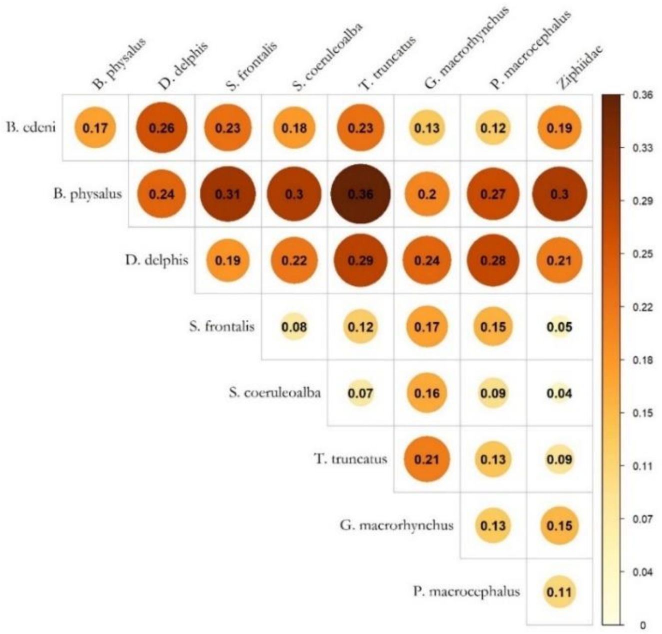


Figure 5.23. The Euclidian distance between pairs of species in the three-dimensional ecological niche space, measured in each dimension by the mean ecological niche overlap (mENO).

The fin whale has the highest year-average biomass in the study area (168 t), followed by the Bryde's whale (125 t), the bottlenose dolphin (103 t), the spotted dolphin (56 t), the pilot whale (54 t), common dolphin (36 t) and the beaked whales (31 t) (Table 5.11). In the summer/autumn, the species with most biomass continues to be a baleen whale, the Bryde's whale (725 t), followed by the bottlenose dolphin (141 t), the pilot whale (141 t), the spotted dolphin (136 t), the beaked whales (23 t) and the common dolphin (18 t). The striped dolphin and the sperm whale also have estimates of biomass for this period, with the first species having a residual value (5 t) and the sperm whale an important amount (400 t), which makes it the species with second highest biomass in summer/autumn in the study area. However, the lack of abundance estimates for the period 2007-2012 does not allow a year-average biomass estimates for this species.

The year-averaged biomass estimated for the cetacean taxa is approximately half of the biomass sustained by the Madeira inshore waters during summer/autumn, the peak of cetacean abundance in the study area (Table 5.10). In spite of the increase in the overall cetacean biomass in the summer/autumn period, the relative biomass of dolphins decreases and the relative biomass of baleen whales (Bryde's whale) increases when compared with the year-averaged biomass. The deep divers maintain their relative biomass during both time periods.

Table 5.11 shows the approximate estimated daily prey biomass consumption of the different cetacean species in Madeira archipelago, taking into consideration their energetic needs, i.e. the prey they need to consume on average daily to meet their energy demands.

Table 5.10 – Estimated biomass of cetaceans in Madeira archipelago by groups of species (baleen whales, dolphins and deep divers), expressed as an year-average, based on abundance estimates of SLS surveys carried out in 2007 – 2012, and as an average for summer/autumn, based on abundance estimates of SLS surveys carried out in 2017 – 2018. The striped dolphin and sperm whale were not considered in the comparison because there are no abundance estimates of these species for 2007 - 2012.

Period	Group	Metric tons	Proportion
2007 - 2012 (year average)	baleen whales	293	0.51
	dolphins*	195	0.34
	deep divers*	84	0.15
	total	573	1.00
2017- 2018 (Summer-Autumn)	baleen whales	725	0.61
	dolphins*	295	0.25
	deep divers*	164	0.14
	total	1183	1.00

* - Excluding *S. Coeruleoalba and P. macrocephalus* for which estimates are only available for 2017 - 2018

Table 5.11 – Approximate daily prey biomass consumption estimated adapting daily prey intake values of cetacean species from (Spitz *et al.*, 2018) for the Gulf of Biscay. The seasonal variations in daily prey intake rates and the differences among age classes were not taken in consideration. [1] the daily prey intake of Bryde's whale was assumed to be the mean value of minke whale and fin whale; [2] the mean prey intake values of common dolphin, Cuvier's beaked whale and long-finned pilot whale were adopted for the spotted dolphin, the beaked whales and the short-finned pilot whale, respectively; [3] the daily intake value for fin whale is probably overestimated as the species passes through Madeira archipelago in winter. In that season the species is fasting or is expected to feed more opportunistically. For this reason, fin whale daily prey consumption was not considered in the daily prey consumption of the baleen whales and in the proportions for the period 20017-2012.

Species / **groups**	**daily prey intake rate (% body weight)**	**Estimated cetacean species biomass (tonnes)**		**Period 2007 - 2012** *(Year-round average)*		**Period 2017- 2018** *(Summer/autumn average)*	
		Period 2007 - 2012 *(Year-round)*	**Period 2017- 2018** *(Summer/autumn)*	**Daily prey consumption (tonnes)**	**Proportion**	**Daily prey consumption (tonnes)**	**Proportion**
B. edeni	2.4[1]	125	725	2.95	0.13	17.03	0.30
B. physalus	1.9	168	-	3 19[3]	0.14	-	-
Baleen whales	-	293	725	2.95	0.27	17.03	0.30
D. delphis	8.6	36	18	3.09	0.14	1.55	0.03
T. truncatus	7.8	103	141	8.05	0.35	10.98	0.19
S. frontalis	8.6[2]	56	136	4.79	0.21	11.69	0.20
S. Coeruleoalba	7.8	-	5	-	-	0.40	0.01
Dolphins	-	195	300	15.93	0.70	24.63	0.43
G. macrorhynchus	4.3[2]	54	141	2.31	0.10	6.08	0.11
P. macrocephalus	2.1	-	400	-	-	8.39	0.15
zhipiidae	5.3[2]	31	23	1.62	0.07	1.20	0.02
Deep divers	-	84	563	3.93	0.17	15.66	0.27
Total	-	573	1 588	22.81	1.14	57.32	1.00

5.4 DISCUSSION

Ecological niche partitioning among the most ecologically relevant cetacean species in Madeira archipelago waters was investigated using a multidisciplinary approach. The trophic niche of each species was estimated using the isotopic niche (measured through nitrogen and carbon isotope ratios), while habitat use modelling was used to inform on spatial and temporal distribution (see Chapter 4). The comparison of the temporal distribution between species in the archipelago can be seen as a measure of their co-occurrence.

The overlap between species in the trophic, temporal and spatial dimensions was estimated to unveil the local cetacean community structure within this multivariate niche-space. The limited availability of habitat and resources, and the seasonal fluctuations of the latter, are expected to create the conditions for interspecific competition. However, the high cetacean diversity signifies that species have mechanisms that allow co-existence by minimizing competitive exclusion (Gause, 1934). This view is supported by the results of this study. Although intra-specific competition is not directly addressed in this study, the results are discussed in the context of the absolute abundance of each cetacean species using Madeira archipelago waters (expressed as biomass) and their energetic implications.

5.4.1 Trophic niches

Isotopic signatures and trophic positions

Stable isotopes ratios can be used as ecological indicators, with δ15N reflecting mostly the trophic position of each species in the trophic web (Deniro and Epstein, 1981; Post, 2002) and δ13C indicating the main source of primary production incorporated into food webs and providing an indication of benthic versus pelagic and inshore versus offshore consumption (DeNiro and Epstein, 1978; Rubenstein and Hobson, 2004).

The results of δ15N (Figure 5.2, bottom), and the derived trophic position, TP (Figure 5.6), positioned the Bryde's whale lower in the food web, followed by the dolphin species at intermediate positions and the deep divers at higher trophic positions. Statistical comparison of the mean δ15N values among species (Table 5.3) confirmed the significant trophic level differences among these groups, except for the striped dolphin (Table 5.3). These results are generally in agreement with previous studies comparing cetacean species trophic positions in Macaronesia (Quérouil *et al.*, 2013; Bode *et al.*, 2022) and with what is generally known about these species diets and some of their prey's δ15N values in Macaronesia and Madeira archipelago (e.g. Clarke, 1962; Dinis *et al.*, 2008; Fernández *et al.*, 2009; Freitas and Penry, 2021; Romero *et al.*, 2021).

TP were calculated to be compared with the values estimated by Bode *et al.* (2022) using also nitrogen isotope ratios, the same methodology and references values (δ15N_{p}, and TEF, Section 5.2.1.4) for the same species in Macaronesia, including some samples of stranded animals from Madeira. The TP estimated in this study were higher than the TP estimated by Bode *et al.* (2022) for all species, by varying amount (0.03 higher for sperm whale to 0.6 higher for spotted dolphin). The differences between the TP estimated in both studies may be due to several reasons, including: the small sample size of some species of one or both studies, which may not represent well the diet range that animals of a particular species have in the study areas; differences from the use of different tissues to measure the isotopic ratios (muscle and skin) (Arregui *et al.*, 2017); differences resulting from the analysis being done in different laboratories (Carter and Fry, 2013) and/or real differences among areas, considering that this study only includes Madeira and Bode *et al.* (2022) included some samples from the Madeira and Azores, but most samples were from the Canary Islands.

Nevertheless, the relative TP among species in both studies are similar, except for the bottlenose dolphin, the spotted dolphin and the Cuvier's beaked whale. The bottlenose dolphin in this study had the lowest median δ15N values among all the dolphin species. If the samples from stranded animals (not included in the estimation of TP, Figure 5.6) are considered, the TP of the species becomes 4.53 ± 1.47, higher than the common dolphin but still lower than the spotted dolphin and striped dolphin. Bode *et al.* (2022) reported a higher relative TP of the bottlenose dolphin for the whole Macaronesia, the highest among dolphin species. Besides the biases mentioned above, there are possible confounding factors that make the comparison of the results of both studies challenging, in particular, the unequal within year and among years coverage for species with changes in TP over time (Section 5.3.1.3; discussed below).

The open ocean characteristics of Madeira archipelago, with a very narrow insular shelf, means that the local habitats with the widest representation are in deeper offshore waters and have either pelagic or benthic characteristics. The narrow insular shelf provides a small fraction of the local inshore habitats with benthic or pelagic characteristics and is, thus, less likely to sustain an important part of the cetacean populations using Madeira archipelago, especially considering their general ecological preferences. Comparison of the median values of δ13C among species showed that Bryde's whale and dolphin species diets were associated with more pelagic/offshore habitats while the deep divers to more benthic/inshore habitats (Figure 5.2, top).

The association of the Bryde's whale and dolphin species with pelagic/offshore habitats is in accordance with what is known of their distribution in the study area (Section 4.3.4, Chapter 4). The Bryde's whale δ13C values indicate a clear preference of the species for prey associated with pelagic/offshore habitats in agreement with their preference for escarpment areas in the study area (Figure 4.39) and their movements to offshore waters, including seamounts (Section 3.3.2.2). The common dolphin's wide local distribution (Figure 4.27), ranging from coastal over the shelf waters to further offshore waters, is reflected in the wide range of δ13C values of the sampled animals; these results also suggest that some animals feed on more inshore and/or benthic prey, although most animals feed on prey from pelagic/offshore habitats. The spotted dolphin, the bottlenose dolphin and the striped dolphin had similar median δ13C values, slightly higher than the common dolphin, nevertheless not significantly different from that species, which indicates they also feed on prey mostly associated with pelagic habitats. However, narrower δ13C ranges and the slightly higher median δ13C values of these species when compared with the common dolphin, suggests a diet associated with less offshore/pelagic prey, which is in agreement with the spotted dolphin preference for the islands' slopes (Figure 4.25) and the bottlenose dolphin more coastal distribution (Figure 4.25 and Figure 4.23, respectively). Moreover, the skewed distribution of δ13C towards higher values, indicates that the diet of some bottlenose dolphins was more associated with prey from inshore and/or benthic habitats, in agreement with their local distribution and what is known of their diet (Fernández *et al.*, 2009; Wells and Scott, 2018). Lower values of δ13C would be expected for the striped dolphin, possibly closer to the median values of common dolphins and in line with its predicted further offshore distribution (Figure 4.29), rather than similar median values to spotted dolphins. This apparent mismatch may be a consequence of all samples analysed being from stranded animals, which probably represent mostly animals using the habitats closer to the islands (e.g. island slopes) rather than animals with a further offshore distribution, and thus less likely to strand.

All deep divers had higher median δ13C values than the other species (Figure 5.2, top), although the pilot whales were the highest with statistically significantly difference from remain species (Table 5.3). The more offshore distribution of pilot whales, over the slope and in deep waters (average depth of ~1 500 m; Figure 4.32), suggests that they feed on prey more associated with benthic habitats rather than on inshore waters, although their wide δ13C range also indicates they feed on pelagic prey. The narrow δ13C ranges of sperm whales and beaked whales possibly reflects their more specialised diets on prey that are in general more pelagic than the pilot whale, but not as pelagic as the other surface-dwelling species. The predicted distribution of sperm whales in deeper offshore waters over the islands' slopes give support to this interpretation, as well as the beaked whales distribution in further offshore waters. Nevertheless, the higher median δ13C values of beaked whales than sperm whales and the much higher δ13C values of a couple of Blainville's beaked whales (Figure 5.2, top; *M. densirostris*; Figure 5.3), suggest these animals may feed either closer to shore or feed on prey more associated with benthic habitats, in agreement with the general ecological differences among the species in this group (MacLeod, 2005). However, it should be acknowledged that the small sample size of these taxa may give an incomplete account of the general habitats they feed on.

Isotopic signatures over time

Linear trends were assumed for both within-year and annual changes in isotopic signatures. The visualization of the data did not suggest non-linear trends; however, it is difficult to rule them out for some species because of the small number of samples and the wide variation around the fitted lines.

No within-year significant linear trends of δ13C and δ15N were identified for most species (the striped dolphin, the bottlenose dolphin, the Bryde's whales, the sperm whales and the beaked whale species combined), based on the linear regression models. Species like the sperm whale, the striped dolphin and the Bryde's whale had a low number of samples covering half year or less, and in the latter two species with a wide variation around the fitted lines, thus being more difficult to identify existing significant within-year linear trends in any of the stable isotope ratios. When interpreting the within-year trends, it should be kept in mind that the stable isotope ratio values of a sample collected in one month reflect the integrated isotopic composition of the prey consumed by the sampled animal in the previous one to three months, considering, for example, the bottlenose dolphin's skin carbon and nitrogen half-life turnover rates of 24.16 ± 8.19 days and 47.63 ± 19.55 days, respectively (Giménez *et al.*, 2016). Furthermore, for most species, if not all, it is important to consider their seasonal fluctuations in relative abundance that probably reflect movement in and out of the study area. As such the stable isotope ratios, especially in first weeks of their arrival to Madeira archipelago may reflect the prey and habitats where they fed in the previous weeks.

However, significant within-year linear trends in one or both stable isotope ratios were identified for three species. The within-year δ13C positive linear trend of the common dolphin from January to September seems to be driven not only by the three samples with higher values in September, but also by the low values in January-February compared with May-June (Figure 5.7). The positive trend in the first six months of the year agrees with the change in the predicted distribution of the species between winter and spring (Figure 4.54). In winter, the species was spread out in offshore waters, while in spring the species had higher predicted relative abundance in some slope areas of the islands, probably feeding on prey further inshore and, possibly, in more benthic habitats over the islands' slopes. The higher δ13C values of the animals sampled in September probably reflect the primary production associated with the habitats of the prey consumed one to two months before, when the species is hardly present in Madeira archipelago waters. These higher δ13C values suggest these animals were feeding in summer elsewhere on prey associated with further inshore/benthic habitats, possibly continental waters. However, the species did not show significant changes in the trophic levels at which they fed throughout the year, whether in Madeira or outside, as suggested by the non-significant within-year linear trend of δ15N.

The spotted dolphin within-year δ15N negative linear trend, indicates a change in the trophic level at which the species feeds throughout the year. However, it is not clear if the negative trend is the result of animals feeding at lower trophic level prey as the period the species is most abundant in Madeira (spring-autumn) passes by, or the negative trend is driven by the animals sampled at the beginning of the season having consumed elsewhere higher trophic level prey. Nevertheless, animals sampled both in December and in January showed higher δ15N values, which suggests that animals in autumn and winter feed at higher trophic levels whether in Madeira or not. This pattern fits the seasonal cascade effect of the increase of primary productivity in Madeira archipelago, which starts in winter-spring, with expected increase in biomass at higher trophic levels throughout the rest of the year.

The pilot whale also showed a significant within-year negative trend (February to September; Figure 4.54) in δ15N as the spotted dolphin, giving some support to a possible relationship between the seasonal increase in primary productivity and its time-delayed cascade effect on the biomass at higher trophic levels. This shift in trophic level may be driven by the seasonal increase in abundance in summer of certain cephalopod species, like the European flying squid (*Todarodes sagittatus*) (Martínez-Escauriaza *et al.*, 2021), identified in stomach contents of pilot whales in the Canary Islands (Hernández-García and Martín, 1994; Fernández *et al.*, 2009), but it may also be driven by the increase in the trophic level at which some cephalopods species feed as they increase in size (Murphy *et al.*, 2020). In parallel, there is a within-year positive trend in δ13C values during the same time period, indicating either a change from more pelagic to benthic prey and/or a shift from more offshore to more inshore habitats. The seasonal distribution of relative abundance does not give clear support to an offshore-inshore shift in distribution from winter to summer (Figure 4.59).

No species showed a significant annual trend in both stable isotope ratios, except the bottlenose dolphin (Figure VI.1.4-1, Appendix VI). As for the within-year analysis, the small sample size for some taxa (striped dolphin and beaked whales) and the wide variation around the fitted line limited the possibility to detect trends. A clear δ15N negative trend was identified for the bottlenose dolphin between 1998 and 2018; however, the possibility cannot be ruled out that part of this trend may be driven by positive bias in the δ15N because of animals in very poor body condition. The linear regressions were made based on samples from stranded animals for most of the time series; biopsy samples of live animals covered only the period between 2016 and 2018. Nevertheless, except for one data point in 2012, the remaining samples from stranded animals confirm the negative trend, which would be unlikely to happen unless an underlaying trend was present. If the trend was only driven by bias associated with body condition, it would mean that stranded animals throughout the study period would be stranding progressively and consistently in better body conditions, which seems unlikely. A similar δ15N negative trend was identified in bottlenose dolphins in the Canary Islands between 2000 and 2020 (Bode *et al.*, 2022). Those authors suggested that a possible driver behind this trend were environmental changes, namely the increase in upwelling strength on the African coast, that if too strong will result in a decrease in primary productivity.

A possible reason for the δ15N negative trend in Madeira archipelago is competition for resources. The increase in relative abundance, mostly in winter and/or spring, of the bottlenose dolphin, spotted dolphin and pilot whale in Madeira archipelago over the years (Section 4.3.4 and 4.3.5) could contribute to intra- and inter-specific competition and thus drive the δ15N negative trend. However, although there is a within-year δ15N negative trend for those species, it is non-significant for the bottlenose dolphin. Furthermore, if intra- and inter-specific competition were forcing the bottlenose dolphin to feed at a lower trophic level, this would be expected to happen in winter and/or spring when their relative abundance increased over the years and not in summer, as shown by the δ15N values (Figure 5.8). A more likely reason is the increased competition with local fisheries. Between 2013 and 2018-2019 there was a three-fold increase in the amount of catch (in weight) landed in the archipelago by recreational and artisanal fisheries (Martínez-Escauriaza *et al.*, 2021). These fisheries operate close to shore, usually in waters shallower than 200 m depth, where the bottlenose dolphin has higher relative abundance, and targets mostly higher trophic level fish, such as *Dentex gibbosus*, *Phycis phycis* and *Pagrus pagrus* (Fishbase - https://www.fishbase.org; Bauchot and Hureau, 1986; Papaconstantinou and Caragitsou, 1989), and other species, some of them possibly preyed on by these dolphins (D. Pauly *et al.*, 1998; Santos *et al.*, 2007; Giménez *et al.*, 2017b). Fisheries overexploitation of resources has been also proposed as a possible cause for decrease in the mean trophic level (indicated by δ15N) at which striped dolphins feed in the northwestern Mediterranean (Borrell *et al.*, 2021)

Isotopic niche overlap

The isotopic biplot (Figure 5.3) shows an isotopic niche partitioning among Bryde's whale, dolphins and deep divers. When comparing the degree of overlap between the isotopic niche widths (expressed by the SEA_b, Table 5.4), the results confirm in general the higher degree of isotopic niche partitioning (lower proportion of SEA_b overlap between pairs of species) between species of different groups than within groups, with a few exceptions (the pair bottlenose dolphin – striped dolphin and the pair sperm whale – pilot whale). Curiously, the bottlenose dolphin and the pilot whale, both with a year-round presence in Madeira archipelago, have a lower trophic overlap with the striped dolphin and the sperm whale, respectively, both species with a year-round intermittent presence in Madeira archipelago, and thus less likely to compete for local prey resources. In the case of the bottlenose dolphin and striped dolphin, the isotopic niche partitioning seems to have increased recently because of the bottlenose dolphin δ15N negative annual trend. These results indicate a potentially higher trophic inter-specific competition for the archipelago's limited resources among dolphin species and among deep divers. Species with similar isotopic signatures do not necessarily feed on the same prey and thus compete for those resources; different prey may have similar isotopic composition (Newsome *et al.*, 2007; Giménez *et al.*, 2018b). However, the present knowledge of cetacean species diet in Madeira archipelago shows that the common dolphin, spotted dolphin and Bryde's whale share some prey, such as the blue jack mackerel (*Trachurus picturatus*) and the chub mackerel (*Scomber japonicus*) (Dinis *et al.*, 2008; Freitas and Penry, 2021).

The comparison of Layman metrics among groups of species suggests a decreasing degree of isotopic niche specialization from baleen whales (represented only by Bryde's whale) to the deep divers and dolphin species, as expressed by the SEA_b (Figure 5.5). However, the differences of SEA_b values among groups of species are probably partially driven by the number of species in each group, which increases with increasing SEA_b.

5.4.2 Ecological niche partitioning and specialization

The cetacean species in Madeira archipelago could be generally grouped according to ecological patterns observed in each of the ecological niche dimensions: trophic dimension - low, medium and high relative trophic positions; temporal dimension - low, medium and strong seasonality; spatial dimension - preference for coastal habitats, escarpment/slope habitats, offshore habitats or both coastal and offshore habitats (Table 5.7). From these patterns some level of ecological partitioning among species can be foreseen. However, the differences among species in one or more dimensions may not be well defined and with intra-species variability in each of those dimensions. Consequently, to have a better insight and understanding of how species use and share the habitat and resources in a limited marine environment like Madeira archipelago, it is important to quantify the degree of ecological niche partitioning among them by, for example, estimating niche overlap (ENO) in the above-mentioned dimensions. Although important, it was not possible to consider in this study the uncertainty associated with the estimates of each species niche dimensions because of limited time and space in the thesis. For the same reasons several available indices to measure niche overlap (e.g. Geange *et al.*, 2011; Rödder and Engler, 2011) were not thoroughly considered. Instead, the proportion of trophic, temporal and spatial overlap (PTRO, PTO and SSO) and the product of those proportions was used to measure the ecological niche overlap (Section 5.2.4).

The ENO values for pairs of species which include the striped dolphin are expected to be biased positively because of the way this species local temporal pattern of use was considered in the calculations of PTO. Although this species seems to have an intermittent use of the study area with no seasonal pattern (Section 4.3.4), it was represented as present year-round (Standardized ER of individuals equal to one across the months, e.g. Figure 5.9), for lack of a better way to represent its temporal intermittence. For example, the ENO values between the striped dolphin and the common and spotted dolphins were among the highest ENO values (0.054 and 0.06, respectively) in all species pairs. The sperm whale, despite showing a seasonal pattern in the use of the area, also has an intermittent presence throughout the year, with animals moving in and out of the area regularly (Section 4.3.4). As such, these species with local intermittent, and possibly more opportunistic presence, only compete with other cetacean species while they are in the area.

Most dolphin species pairs had the highest ENO values among all species pairs. Both the threshold method and the clustering method confirmed dolphin species pairs with considerable overlaps between them in the three dimensions assessed, indicating lower niche partitioning and thus higher potential competition for local resources. The common dolphin-spotted dolphin pair had the lowest ENO among dolphin species pairs (0.032) driven mostly by the complementary seasonal use of the study area (low overlap; Table 5.5). The bottlenose dolphin-spotted dolphin pair had the highest ENO value (0.1) of all cetacean pairs, almost double that of other pairs with overlap in all three dimensions, according to both approaches followed (Table 5.8 and Table 5.9).

The temporal resolution at which the ecological niche overlaps were estimated in each of the three dimensions is important, considering the local strong seasonal variation in overall relative abundance of species and their distributions. In this study, the trophic niche overlap and the spatial niche overlap between pairs of species were calculated using year-round averaged data, thus being effectively an annual averaged overlap trophic niche and spatial niche. However, the spatial modelling of distribution of relative abundance of dolphin species (common dolphin, spotted dolphin and bottlenose dolphin, Section 4.3.5) showed that at a finer temporal scale (seasons) these species had, for most seasons, a complementary spatial use of the area, thus suggesting a higher ecological niche partitioning than can be perceived from the SSO. Thus, the level of niche partitioning among these dolphin species is expected to be higher than shown by the ENO values. This finer niche partitioning (by season) does not seem to occur in the trophic dimension, as indicated by the absence of within-year trends in trophic level for most dolphin species (Figure 5.7).

The cluster approach identified two taxa pairs (pilot whale-beaked whales and sperm whale-beaked whales) with considerable overlap in the three niche dimensions (cluster 4). However, the ENO between pilot whale-beaked whales is very low and reflects the very low overlap in the spatial dimension (SSO), thus indicating higher niche partitioning of these two taxa. The comparison of niche overlap between beaked whales combined and other species is probably misleading. Beaked whales species have diverse ecological requirements both in terms of habitat preferences and trophic discrimination, including prey type and prey size (MacLeod *et al.*, 2003; MacLeod, 2005). As such, the ecological niche discrimination between individual beaked whale species and other cetacean species is probably higher than shown by the ENO values of beaked whales with other species, which means that the degree of specialisation of each beaked whale species would be higher than shown by the measure of ecological niche specialization (ENS) (Figure 5.22).

The threshold approach identified three taxa pairs (spotted dolphin-sperm whale, spotted dolphin-beaked whales and striped dolphin-sperm whale) with overlap values slightly above the threshold of 0.2 in two dimensions (trophic and spatial) and with moderate to high ENO values, mostly driven by high values of temporal overlap (PTO) (Table 5.8). The ENO values from 0.026 to 0.051 between these pairs of taxa, especially the latter value (spotted dolphin-beaked whales), could be interpreted as an indication of potential competition for resources between the taxa of these pairs. However, a high level of competition is less likely between surface dwelling species like the spotted dolphin and the striped dolphin and deep divers like the sperm whale and beaked whales, considering the different deep diving abilities and habitats usually explored by these species in the water column (Lambert *et al.*, 2014). Nevertheless, resources may, for example, be shared through the diel vertical migration of mesopelagic prey, which both spotted dolphins and striped dolphins also feed on (Ringelstein *et al.*, 2006; Silva *et al.*, 2021). Furthermore, the intermittent presence of striped dolphin and sperm whales in the study area reduces the potential competition with other species as explained above.

For most pairs of species, the ENO was low or very low and with higher overlap values in one or two of the three dimensions assessed (Table 5.8 and Table 5.9). This means that the ecological niche partitioning among these species is moderate to high and thus they do not compete or are less likely to compete for local resources.

Ecological specialization can be defined as the restricted ecological niche breadth (or width) of a species (Futuyma and Moreno, 1988). Ecological specialization can be seen in different perspectives (Grinnellian vs Eltonian and realized vs. fundamental, referring to the classical distinction between the fundamental and realized niche; Hutchinson, 1957) and thus addressed in different ways (Devictor *et al.*, 2010). In Futuyma and Moreno (1988) the concept of ecological specialization is reviewed and in Devictor *et al.* (2010) its complexity is recognised as highly context-dependent, with great variability of existing definitions and methods used to characterize it. For the purpose of this study, a simple and pragmatic approach was followed to assess the relative degree of specialisation of cetacean species using Madeira archipelago waters. The ecological niche breath (degree of specialization) of each species (ENS) was measured as the mean ENO of one species with the remaining species in each niche dimension (Section 5.2.4).

The dolphin species had the widest ecological niche breadth among all species, and thus were considered the most generalist species, except for the common dolphin (Figure 5.22). The common dolphin stood out from other dolphins because of its narrow niche width in the temporal dimension, i.e. the very well defined seasonal and narrow presence (peak from March to May, Figure 5.9) in Madeira archipelago (Figure 5.21). Conversely, the baleen whales and the pilot whale had the narrowest ecological niche breadth and thus were considered the most specialist species (Figure 5.22), in line with low ENO values (Table 5.8 and Table 5.9). This higher degree of specialisation is justified by narrow ecological niche breadths in more than one dimension (Figure 5.21). The fin whale had narrow niche widths in the spatial, temporal and trophic niches because of its predicted distribution mostly associated with the 2 000 m isobath (Figure 4.41 and Figure 5.12), its marked seasonal presence in March-April (Figure VI.2.1-5, Appendix VI) and its presumed narrow trophic niche width (assumed equal to Bryde's whale; Section 5.2.4), respectively. The Bryde's whale and the pilot whale had narrower niche widths in the trophic and spatial dimensions (Figure 5.21), driven in the former species by the trophic dimension and in the latter species by the spatial dimension. The Bryde's whale consumed prey at a lower trophic level (Figure 5.4) and with a distribution mostly over the escarpment (Figure 4.39 and Figure 5.11), while the pilot whale distribution was mostly concentrated southeast of Madeira (Figure 4.32 and Figure 5.17), and it consumed prey at a higher trophic level and had a specialised isotopic niche with higher δ13C values (Figure 5.4).

Cetacean species have varied energetic requirements that need to be met through prey consumption. Baleen whales have lower cost of living (i.e. energy requirements) than odontocetes, and within the odontocetes, dolphin species have as much as twice the cost of living as deep diving species (Spitz *et al.*, 2018). The differences in the cost of living are partially reflected in the average daily prey intake rates, for example as a percentage of body weight (Table 5.11), but also depend on the nutritional quality (energetic value) of the prey items consumed (Spitz *et al.*, 2018). It is important to recall that species have different strategies to maintain energy balance. Some species can maintain large energy reserves and thus sustain longer fasting periods (baleen whales; capital breeders) while other species need to feed at more regular intervals (odontoceti; income breeders). As such, average daily prey intake rate is not synonymous with daily feeding.

The biomass of cetacean species varied seasonally in Madeira archipelago waters reflecting in part the local biological productivity and consequently prey availability at different trophic levels. Although the baleen whales had the highest biomass in Madeira archipelago, they consumed 13% and 30% of the local average daily prey consumption (Table 5.11), based on the 2007-2012 year-round average and 2017-2018 summer/autumn abundance estimates, respectively. Fin whales were not considered in the calculations because of their opportunistic feeding while passing by the archipelago during winter, when they are expected to be mostly fasting (Lockyer, 1984). The estimated daily prey consumption of the Bryde's whales is the highest among all the cetacean species and confirms the importance of the archipelago for this species. However, the archipelago does not seem to provide all the energetic requirements of the animals using the area seasonally, as suggested by the movements data presented in Section 3.3.2.

The probable recent arrival of the Bryde's whales to Madeira archipelago (Section 3.4.5) raises the question of how the species has managed to harness local resources to sustain its seasonal presence in the area ever since. One possible explanation is that it has competed with other consumers (cetaceans or others) for local resources. There is no information to support the hypothesis that other cetacean species were feeding at the same trophic level at which the Bryde's whale feeds locally, so the competition could be with other consumers, such as fish or cephalopods, feeding on zooplankton and lower trophic level fish in the area. Alternatively, and not mutually exclusively, the increase in primary productivity in Madeira archipelago and surrounding area in the last two decades, as shown by Siemer *et al.* (2021), could have generated the local resources necessary to sustain the local presence of Bryde's whale. Furthermore, the extra increase in productivity seems to be mostly harnessed in summer/autumn by the Bryde's whale at lower trophic levels, as suggested by the increase in relative abundance of the bottlenose dolphin, the spotted dolphin and the pilot whale mostly in winter and/or spring, but not in summer or autumn (Section 4.3.5). The removal of prey at lower trophic levels by the Bryde's whale at the end of spring and summer is expected to have a negative cascade effect on the biomass available at higher trophic levels and effectively reduce the prey available to cetacean species feeding at higher trophic levels. This effect could force those species to feed at lower trophic levels where more biomass is available and justify the within-year downwards trend in δ15N values of bottlenose dolphin, spotted dolphin and pilot whale (Figure 5.8). All these species have an increase in abundance of animals in summer (Table 5.7 and Figure 4.21) and thus need more prey biomass available for consumption, as shown by Table 5.11. The common dolphin, with a higher presence in winter and spring, does not show such a trend because of its very low presence in summer and its already lower trophic level, closer to the Bryde's whale. Although no robust data exists on seasonal pattern of recreational and artisanal fishing activity in Madeira archipelago (Martínez-Escauriaza *et al.*, 2021), it cannot be ruled out that these activities may contribute also to the lower trophic level at which these species feed in summer, by removing upper trophic level prey.

The Bryde's whales removal of prey at lower trophic levels throughout the study period, together with the artisanal and recreational fisheries pressures (Section 5.4), may have also contributed to the downwards annual trend δ15N values of bottlenose dolphin (Figure VI.1.4-1, Appendix VI).

The overall average daily prey consumption of dolphin species and the pilot whale also increased in summer/autumn in relation to the year-round average (Table 5.11), in line with the predicted seasonal influx of animals to the study area (Figure 4.21). Most of the average daily prey intake needs in summer/autumn are from spotted dolphin (11.69 tonnes) and the bottlenose dolphin (10.98 tonnes), but with the former more than doubling in relation to its average year-round needs. The pilot whale almost triples its average daily prey intake needs in summer/autumn, but with more modest values (6.08 tonnes) when compared with the other two species. The sperm whale average daily prey intake needs (8.06 tonnes) in summer/autumn were higher than the pilot whale and driven by the large biomass of a few animals (28 animals, Table 5.7) using the area intermittently. Although the archipelago does not seem to be crucial for the survival of the species in the wider context of its distribution and considering the number of animals using the area, they have a reasonable local impact by potentially removing a considerable amount of prey biomass.

The absolute abundances (and biomasses) of the cetacean taxa in Madeira inshore waters considered here are likely underestimated and thus do not reflect the true abundances (and biomasses) of these taxa in the area, because the population size estimates are not corrected for either perception or availability bias (Table 5.7). These biases are very likely more acute in less conspicuous and longer-diving species like the beaked whales. Nevertheless, they provide a means to compare the year-average abundance and biomass to the corresponding estimates for summer/autumn, giving an insight into how the fluctuations in the productivity of Madeira inshore waters over the year can sustain these populations. Similarly, the daily prey biomass consumptions are also expected to be biased for several reasons, including negative bias in abundance and biomass estimates and adoption of daily prey intake rates from another area and different species. However, they take into consideration the different cetacean species energetic requirements and thus give an approximate idea of the resources (biomass) the cetacean species might depend on and consume in the archipelago.

As far as the author knows, there are no biomass estimates of cetaceans in open ocean islands with a similar geographical context and characteristics of Madeira archipelago. Alava (2009) gives biomass estimates for the Galápagos of three species that are also present in Madeira archipelago. The reported biomass estimates for the Galápagos of Bryde's whales, sperm whales and bottlenose dolphins were 8 071 tonnes, 3 278 tonnes and 2 250 tonnes (Alava, 2009), approximately 11 times, 8 times and 16 times more than in Madeira (Table VI.5.2-2., Appendix VI), respectively. However, the Galápagos archipelago is a much larger open ocean archipelago (with a land mass approximately 10 times larger than Madeira archipelago) and is located in the ETP more productive equatorial waters, when compared with the oligotrophic waters around Madeira archipelago. Furthermore, in the case of the Bryde's whale, the average individual body mass used by Alava (2009) was 16 143 kg, almost twice the value of the individual mass of adults used in this study. The comparison of absolute biomass estimates among different areas is very difficult to interpret because biomass estimates are prone to many biases and are related with the capacity of those areas to sustain animals at different trophic levels. In turn, the ability to sustain greater or fewer numbers of animals at different trophic levels is dependent on the size, characteristics and geographic context of the areas, on the local ecosystems' structure and on the underlying primary productivity. As such, the comparison of estimated biomasses and daily prey biomass consumptions among cetacean groups within an area (e.g. Madeira archipelago) and their seasonal fluctuations, is more reliable and informative (e.g. about structure and function of the local marine ecosystem) than the comparison with other areas.

Chapter 6

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FINAL DISCUSSION AND CONCLUSIONS

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Open ocean island marine environments are usually small but encompass a wide variety of local marine habitats (e.g. coastal, insular shelf and slope, local upwellings, nearby deep open ocean), which provide a diversity of abiotic and biotic conditions and prey availability to be explored by cetaceans according to their characteristics and ecological needs.

The role of open ocean islands in the life cycle of many open ocean cetacean species is expected to be determined by the trade-off between energetic benefits (prey intake) and energetic costs to access and use those habitats, at the spatial and temporal scale at which those species achieve energy balance. The geographic context of open ocean islands is important as cetacean species distribution in the world's oceans is shaped by latitude and distance to continental masses (e.g. Pompa *et al.*, 2011).

The usually small size of open ocean islands and their marine habitats, means that they are expected to have limited prey biomass available to sustain many cetaceans for extended periods, especially in oligotrophic seas. Seasonal changes in local productivity will further restrict the number of cetaceans using open ocean islands, including resident groups or populations. Consequently, a limited density of animals of each cetacean species can be supported by these habitats, with expected local interspecific competition among sympatric species, especially those with more similar ecological needs.

The small size of the Madeira archipelago and its location in relation to nearby continental waters, neighbouring archipelagos (Canary Islands and Azores) and seamounts, influenced by ocean dynamics, provide the conditions to investigate the role of open ocean islands in the lives of cetaceans and how they may share or compete for resources in such small insular marine environments. The local marine habitats are shaped by seasonal patterns of primary productivity due to the archipelago's subtropical latitude (Caldeira *et al.*, 2002; Martins *et al.*, 2007). Furthermore, the islands interfere with prevailing winds and currents generating water stirring, which in turn increases productivity ("island mass effect") (Caldeira *et al.*, 2002; Campuzano *et al.*, 2010). The impact of the islands' masses (Caldeira and Sangrà, 2012) seem to promote the export of biological productivity to offshore waters in the epipelagic layer through eddies (< 200 m) and prey aggregating effects around the islands at deeper layers (> 300 m), thus shaping the local distribution of biological productivity and of the cetacean community (surface dwellers and deep divers).

Although there are 28 cetacean species recorded for Madeira archipelago, most of them are occasional, nomadic or vagrant, usually passing by in low numbers, and thus with a low opportunistic dependence/impact on the local ecosystems, i.e., low local ecological relevance. In this study, 10 species (bottlenose dolphin, spotted dolphin, common dolphin, pilot whale, Bryde's whale, sperm whale, striped dolphin, fin whale, Blainville's beaked whale and Cuvier's beaked whale) were identified as having local ecological relevance, based on their use of the local habitats, although with different degrees of importance depending on their seasonality, relative abundance and roles in the local marine ecosystem (Chapter 4). These species account for ~98% of the sightings in the archipelago. Other species like the sei whale, Kogiidae species and other beaked whales may be under-represented in this study because of difficulty of identification or difficulty to detect them at sea.

Over the last 20 years there was an overall positive trend in relative abundance of bottlenose dolphin, spotted dolphin, pilot whale, Bryde's whale and beaked whales (Section 4.3.4), possibly driven by an increase in local productivity (Siemer *et al.*, 2021). These overall positive trends have different underlying patterns depending on the species. More tropical species (spotted dolphin and Bryde's whale) had cyclic fluctuations in relative abundance during the study period, while the remaining species showed an overall linear trend. These positive trends over the years were identified mostly in winter, but also in spring, indicating that the increase in local productivity was mostly available for cetaceans in the first two seasons of the year.

The presence and abundance of most cetacean species, and probably other predators, in Madeira archipelago is linked with the local seasonal primary productivity. Primary productivity is at its highest in winter and spring (Caldeira *et al.*, 2002; Martins *et al.*, 2007) and is expected to have a trophic and temporal cascade effect on the biomass at higher trophic levels in the local food chains. The indirect evidence of this phenomenon is the temporal sequence of peaks of relative abundance of cetacean species feeding higher and higher in the trophic chain through the year, starting with fin whale (lower trophic position), followed by dolphin species (intermediate trophic position) and ending in deep divers (upper trophic position), with three possible exceptions, the bottlenose dolphin, the Bryde's whale and the beaked whales (Table 5.7). The Bryde's whale, with the lowest TP among all cetacean species, and bottlenose dolphin, with the lowest TP among dolphin species, reached their peaks in relative abundance in the summer, later than other cetacean species with higher TP. The same occurred for the beaked whales which reached a peak in relative abundance in summer before pilot whales, although they have higher TPs. It is most likely that the timing of the increase in relative abundance in the area is also influenced by factors outside the study area.

The seasonal change in relative abundance of most cetacean species in Madeira archipelago (Section 4.3.3) show that these waters are for most, if not all, of these individuals only part of a much wider distributional range, encompassing other habitats also important to fulfil their biological and ecological needs. The temporary use, seasonal or not, of open ocean islands is also seen elsewhere (e.g. Dulau-

Drouot *et al.*, 2008; Carrillo *et al.*, 2010; Silva *et al.*, 2014). Nevertheless, the seasonal return of these species, and many times of the same animals (e.g. Bryde's whales, Chapter 3; pilot whales, Alves *et al.*, 2013), to the Madeira archipelago is a testimony of its importance.

The seasonal influx of animals of different species into the study area gives support to hypothesis 1 (Section 2.2) that animals seem to be attracted to the archipelago and stay for as long as there are prey available to give them an energetic advantage in relation to open ocean or other habitats, within the spatial and temporal scales over which they are able to maintain energetic balance (Section 2.2). However, the cues that trigger those displacements are unclear. They could be environmental cues such as changes in water temperature (e.g. increase in temperature for species with more tropical distribution), decrease in available prey in the habitats where these animals spent winter and/or an increasing energic deficit for animals spending winter in offshore oligotrophic habitats, impacting, for example, their capability to breed. This seasonal energetic advantage provided by Madeira archipelago, may be important if not crucial for species like the bottlenose dolphin, the pilot whale, the Bryde's whale, and most probably others species, to breed and give birth to their young (Alves *et al.*, 2013; Correia-Fagundes and Romano, 2013; Dinis *et al.*, 2016b; Freitas and Penry, 2021).

The overall habitat use models (Section 4.3.4) confirmed the general ecological preferences of many of the species studied: the preference of bottlenose dolphin for coastal waters (Wells and Scott, 2018); the preference of spotted dolphins for slopes areas (Silva *et al.*, 2021); and the association of pilot whales with depths between 1 000 m and 2 000 m (e.g. Baird *et al.*, 2013b; Servidio, 2014). The models also confirmed the general relationship between common dolphins and sea surface temperature (Amaral *et al.*, 2012) and the preference of striped dolphins, sperm whales and beaked whales for offshore waters (MacLeod, 2005; Ballance *et al.*, 2006; Whitehead, 2018).

The comparison of the models among species showed that, at the temporal (2001 – 2017) and spatial scale (predicted grid resolution of 3.704 km) of the study, there was for some species (bottlenose dolphin, spotted dolphin, pilot whale, sperm whale and Bryde's whale) a stronger effect of static/physiographic variables on encounter rate and for others species (common dolphin, striped dolphin and beaked whales) a stronger effect of dynamic variables. These results suggest that the former group of species have their habitat preferences more associated with the islands while the latter group may be more influenced by the surrounding open ocean dynamics. However, it should be taken into consideration that the spatial scale at which the variability of these dynamic variables is expressed in the open ocean, especially associated with more persistent dynamic features, is probably larger than the spatial scale of equivalent features closer to the islands. The small dimension of the islands and their influence (island mass effect) on the dynamic variables close to shore (e.g., primary productivity, mixed layer depth) is expected to generate variability at much smaller scales than in the open ocean. As such, a much finer spatial resolution would be needed to identify dynamic features that may influence these species habitat use closer to shore (Redfern *et al.*, 2006). At the spatial and temporal scale of this study the physiographic features seem to explain better the habitat use of species and their association to the islands. However, when looking at shorter temporal scales (e.g. by season) the dynamic variables become more important, even for species with an overwhelming influence of static variables in the overall models (e.g., bottlenose dolphin and Bryde's whale). This shows that, in spite of the importance of the association with the islands, these species habitat preferences change throughout the year influenced by the local dynamics, especially associated with primary productivity. Such an effect is particularly noticeable with Bryde's whale and time lagged variables.

Although unconfirmed, the presence of Bryde's whales appears to be recent in Macaronesia. Their arrival maybe an indication of distributional expansion driven by population growth, supported by very high apparent survival (Chapter 3). Other non-mutually exclusive possible reasons include an increase in primary productivity around Madeira archipelago (Siemer *et al.*, 2021) and a shift in their distribution or expansion of their population range, as a result of reduced food availability.

Madeira archipelago is part of this species summer grounds in the central East Atlantic (Freitas and Penry, 2021). Although the inshore waters are used by Bryde's whales with different levels of site fidelity, they also move between the Macaronesia archipelagos and regularly use offshore waters in the area, especially seamounts, presumably to feed (Section 3.3).

As in Madeira archipelago, Bryde's whales also show a seasonal pattern of occurrence in other areas like the Hauraki Gulf in New Zealand (Wiseman *et al.*, 2011) and Plettenberg Bay in South Africa (Penry *et al.*, 2011). Some animals had long-term site fidelity to Hauraki Gulf in a study carried out between 2004 and 2013 (Tezanos-Pinto *et al.*, 2017), while several animals were found to have some degree of site fidelity to Cabo Frio Region (Southeastern Brazil) in a two-year study (Figueiredo *et al.*, 2015). However, those results are not directly comparable to Madeira because of different site fidelity criteria and metrics.

Some of this chapter's results support hypothesis 1 (Section 2.2) that open ocean cetaceans, in this case Bryde's whales, are attracted to oceanic islands as long as the insular environment gives them an advantage to achieve an energy balance compared to open ocean habitat, both in terms of energy acquisition and minimization of energy costs, not only to survive but also to grow and reproduce. In summer, Bryde's whales use Macaronesia higher productivity habitats (inshore waters, seamounts and particular oceanographic features) (Section 3.3.2 and Section 4.3.3), moving away in winter, probably to more productive habitats along the west African coast. Seasonal latitudinal movements of Bryde's whales have also been reported for the Southwest African offshore population (Best, 2001). Furthermore, the South African inshore population of Bryde's whales also seems to have seasonal movements that are related with seasonal prey displacements (Best, 2001). Similar seasonal movements also believed to be driven by prey availability and distribution have been reported for other coastal populations (e.g. Tershy, 1992; Kato *et al.*, 1996; Zerbini *et al.*, 1997; Wiseman, 2008). Open ocean oligotrophic waters do not seem to be an important habitat to provide energy to Bryde's whales in Macaronesia.

The rarer presence of the species in Azores (farther away from continental waters), including fewer females with calves, when compared with Madeira and the Canary Islands (closer to continental waters), gives some support to hypothesis 3 (Section 2.2). Hypothesis 3 states that more isolated open ocean islands/archipelagos, especially in oligotrophic seas, will have lower density of cetaceans than equivalent islands/archipelagos much closer to other major predictable sources of food (e.g. major archipelagos or seamount chains, more predictable (stable over time) fronts, and continental masses).

Mysticeti whales have traditionally been considered capital breeders, however, Bryde's whales have characteristics closer to income breeders. The lactation period estimated in this study is longer than generally thought for the species and gives support to a breeding strategy, with longer nursing periods, closer to income breeders than to capital breeders (Trillmich and Cantor, 2018). The calving intervals calculated in this study are closer to killer whales and pilot whales (income breeders) than to humpback whales (capital breeders), and also give support to this view. Furthermore, the evidence of regular feeding from satellite telemetry, even when closer to winter, and the possible synchrony between latitudinal movements of animals and alternating periods of higher upwelling strength between the northwest Africa upwelling zone in summer (26-35ºN) and the seasonal Mauritania-Senegalese upwelling zone in winter (12-19ºN), suggest they may feed regularly throughout the year, like income breeders.

Niche partitioning has been observed in several cetacean species in continental waters (e.g. MacLeod *et al.*, 2004; Giménez *et al.*, 2018a; Borrell *et al.*, 2021) and to a lesser extent in open ocean marine environments (e.g. Gross *et al.*, 2009; Kiszka *et al.*, 2011; Young *et al.*, 2017). The ecological mechanisms identified by these and other studies to minimize competition among species using the same region include temporal (e.g. daily activity) and habitat partitioning (e.g. spatial distribution, depth ranges), consuming prey at different trophic levels, consuming different prey at similar trophic levels or even selecting prey by size class.

The overall habitat use models and their predictions (Section 4.3.4) showed a considerable degree of temporal and/or spatial differentiation in the habitat use among species with known similar trophic levels and thus more likely to compete for prey resources. Baleen whales, dolphins and deep divers all show both temporal and spatial discrimination in their relative abundances among species of those groups, albeit at different degrees between pair of species. The overall complementary use of Madeira archipelago waters in time and space among those groups was also observed throughout the seasons.

The limited availability of habitat and resources, and the seasonal fluctuations of the latter clearly defined the patterns of use of Madeira archipelago waters and even patterns of succession of species and their abundances throughout the year. This study described and defined the ecological niche using three dimensions: trophic, temporal and spatial (Chapter 5). The author recognizes that the description of the ecological niche of each species based only on these dimensions is likely an oversimplification of the hypervolume described by Hutchinson (1957); however, it does reflect three important axes that represent the true ecological niche of these species, as a result of their biological, evolutionary, energetic, etc. requirements and ecological interactions.

The results of this study (Section 5.3.4) showed different degrees of niche partitioning among the main cetacean species using Madeira archipelago waters, with the dolphin species having higher ecological niche overlaps (ENO) in the three dimensions. Most pairs of species showed low or no overlap in one or two dimensions and overall low ENO values, indicating clear niche partitioning, which allow the presence of a considerable number of species in the study area and minimizes competitive exclusion. For bottlenose dolphins and spotted dolphins, the niche partitioning is probably happening at levels and resolutions not considered in the calculation of ENO. For example, although these species feed at fairly similar trophic levels they may target different types of prey. Additionally, they showed much higher habitat partitioning when their spatial distribution was compared seasonally (Section 4.3.5 and Section 4.4.6) than when compared at the yearly temporal resolution used to estimate ENO.

As expected, in Madeira archipelago cetacean species utilised local resources at different trophic levels with baleen whales feeding at lower, dolphin species intermediate and the deep divers higher trophic levels (Section 5.3), in line with another study in Macaronesia (Bode *et al.*, 2022). Within these groups there was considerable trophic overlap, and thus potential competition for resources. According to ecologic theory it is expected that these species with overlapping trophic (isotopic) niche consume, for example, different prey at a similar trophic level or similar prey in different areas or times of the year.

Besides clear spatial partitioning among most sympatric species in Madeira archipelago at different temporal scales (yearly and seasonally), different patterns of temporal partitioning between species were identified, including complementary presence/abundance (common dolphin and spotted dolphin), lagged presence/abundance (fin whale and Bryde's whale; spotted dolphin and bottlenose dolphin; beaked whales, pilot whale and sperm whale) or intermittent presence (sperm whale and striped dolphin) (Section 4.3.3, Section 5.3.2 and Section 5.3.4). These different temporal patterns of occurrence are an indication that Madeira archipelago marine habitats are unable to sustain many co-occurring species due to their limited biological productivity. Spatial and trophic discrimination may not be sufficient to minimize competitive exclusion as in more productive continental habitats (e.g. Giménez *et al.*, 2018b), and temporal partitioning may be important, if not crucial, for the archipelago to sustain such high cetacean species diversity.

In the seasonal adjustments and replacement of cetacean species using Madeira archipelago waters, the distribution of one species in one season may influence the distribution of another species in that season or the season after, and not only be driven by habitat preferences. For example, with the increase in abundance of spotted dolphins during spring, the species tends to occupy the areas over the slope in the south-southwest of Madeira less occupied by other potentially competing dolphin species during that season (common dolphin or bottlenose dolphin) or the previous season (common dolphin) (Section 4.3.5). These results suggest that the species local distribution is not only driven by their habitat preferences but also by the need to minimize competition among species, in accordance with ecological theory. As such, their distribution is not only influenced by the local environmental conditions (abiotic factors) but also by the other species' distributions (biotic factors).

In this study, the clustering approach proved more appropriate than the threshold approach to identify pairs of species with potentially ecologically meaningful overlaps. All the pairs of species with reasonable overlap values in the three niche dimensions and with moderate to high ENO values were identified. However, unlike the threshold approach, the clustering approach only selected pairs of species with potential competition based on their ecological similarities (e.g. dolphin species or deep divers).

The dolphin species are more generalist, while the deep divers and the baleen whales are more specialist, as expressed by the average degree of overlap of the species in these groups with the remaining species. It seems that the limited biomass available at lower trophic levels in the archipelago only allows one baleen whale species (the Bryde's whale) to be supported, in a defined period of the year and in very localised habitats (escarpment), thus forcing the species to have a restricted ecological niche breadth, i.e. be a specialist. The biomass available at highest trophic levels is even more restricted for obvious reasons and species like the pilot whale explored them in a very specialised way (narrow ecological niche breath in the spatial and trophic dimensions, consistent throughout the year). In contrast, the dolphin species show a wider ecological niche breath that allows them to have the trophic flexibility to take advantage of the prey available at intermediate trophic levels and thus sustain the highest daily prey consumptions among the three groups. However, the niche breath may change with the seasons as suggested by the change in spatial distribution and trophic level. Furthermore, although they may appear generalists as species, ecological generalists are often heterogeneous collections of specialized individuals (Bolnick *et al.*, 2003).

The apparently recent arrival of Bryde's whales to Madeira archipelago, and their seasonal presence ever since, may have induced adjustments in the local marine pelagic trophic web. The local resources consumed by this species were not gained from another cetacean species feeding previously at the same trophic level by competitive exclusion, but may have been achieved through competition with other consumers at that trophic level (fish or cephalopods feeding on zooplankton and lower trophic level fish) or alternatively, and not mutually exclusively, sustained by an increase in primary productivity in the Madeira archipelago and surrounding area in the last two decades (Siemer *et al.*, 2021). Nevertheless, it seems that the Madeira archipelago may have reached its capacity to sustain animals that use the area to feed regularly, as suggested by the increase of rare visitors and transients in relation to regular and occasional visitors in 2014 – 2021, when compared to 2005 – 2012.

The removal by the Bryde's whale of prey at lower trophic levels at the end of spring and in summer is expected to have a negative cascade effect on the biomass available at higher trophic levels and effectively reduce the prey available to cetacean species feeding at those trophic levels. Consequently, that impact could force those species to feed at lower trophic levels where more biomass is available, an effect that does have some support from the data. It cannot be ruled out that the recreational and artisanal fishing activity in Madeira archipelago may have a similar impact, but in this case by removing upper trophic level prey. These fisheries may be impacting the Mediterranean monk seal as well, which also suffers from scarcity of local prey resources (Karamanlidis *et al.*, 2016; Pires *et al.*, 2023). The removal of prey at lower trophic levels by the Bryde's whale throughout the study period, together with fisheries pressures, may have also contributed to the apparent downwards shift over the years in the trophic level at which the bottlenose dolphin feeds in Madeira archipelago.

To deepen the understanding of the importance of open ocean islands to cetaceans and how they use them, future work should consider, among other aspects: modelling habitat use with dynamic variables at finer temporal and spatial scales, including prey related variables relevant for dolphins, baleen whales and deep divers (e.g. SEAPODYM) (Lambert *et al.*, 2014; Pérez-Jorge *et al.*, 2020); improve the habitat use models for striped dolphins and beaked whales (by species) by adding more data and restricting the study area to understand their habitat preferences closer to shore; carry out cetacean stomach content analysis for Madeira archipelago to give dietary context to the stable isotope ratio and ecological niche results; incorporate uncertainty into the estimation of ENO; and minimize biomass estimate biases (e.g. correct abundance estimates for availability bias) to allow better comparison among species, namely with beaked whales.

The results of this thesis can be relevant for managers to fine-tune the management plans of the "SIC Cetáceos", a Special Area of Conservation created in the context of the Habitats Directive, encompassing all coastal waters of Madeira archipelago up to 12 nm from the coast. For example, conservation measures can consider the seasonal patterns of occurrence and habitat use (Section 4.3.5 and Section 4.3.6) to minimize the impacts of human activities at sea on particular cetacean species, without compromising those activities. Furthermore, the information on the trophic positions of cetacean species over time (Section 5.3.1), namely the possible trophic downwards shift of the bottlenose dolphin, should be further investigated to understand to what extent such change is due to the impact of coastal fisheries. The confirmation of such impact should trigger management measures to ensure enough resources for top predators in the area. The information presented in this thesis is also valuable as reference knowledge to contextualize and understand changes in the local marine ecosystems, identified through monitoring programmes, implemented for example in the context of the European Union Marine Strategy Framework Directive.

This study showed that open ocean marine habitats are important to cetacean species survival and play a role in many individuals' life cycles. However, their relevance is dependent on the energetic requirements of the species (from capital breeders to income breeders) and on the geographic context of the open ocean islands, including their productivity in comparison with offshore waters and nearby habitats, shaped by latitude and distance to continental waters. Madeira archipelago's subtropical location offers a seasonal increase in biological productivity in relation to open ocean waters that attracts cetacean species, generally in a temporal succession according to the trophic level at which they feed, and with differences between surface dwellers and deep divers. However, the study also found that the limited local resources are shared among species through ecological niche partitioning and differences in their degree of ecological specialisation, to minimize competitive exclusion. Nevertheless, some degree of competition among a few species may be present, and together with other factors, may shape their use of the local habitat, the trophic level at which they feed and their seasonal succession in the archipelago.

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APPENDIX I

APPENDIX I.

Table I.1.1 – Summary table describing some of the open ocean islands/archipelagos and atolls compared in the review, considering several variable such as, mean geographic location, longitudinal and latitudinal span of these insular environments, maximum distance between islands within an archipelago, and distance to other islands, seamounts and continental masses. Also presented is the known number of cetacean species in each of these islands/archipelagos as well as known species with resident animals/populations.

					characterization of the islands											
Ocean	**Oceanic regions**	**Region**	**Archipelago**	**Islands**	**nº of Islands/ Atolls**	**Mean Longitude**	**Mean Latitude**	**Longitude span**	**Latitude span**	**Maximum distance between islands**	**Closest distance to other islands or seamounts**	**Closest distance to continental masses**	**Oceanic context**	**Nº Cetacean species**	**Known resident species**	**References**
Atlantic Ocean	Equatorial	Golf of Guinea	São Tomé e Príncipe	São Tomé; Príncipe	2	~7ºE	~1ºN	~1.3º	~1.6º	~207 km	~110 km	~234 km	Equatorial waters in the East Atlantic basin; Close to continental waters	≥ 6	unknown	Picanço *et al* 2009
	Sub-tropical	Macaronesia	Canary Islands	La Palma; El Hierro; La Gomera; Tenerife; Gran Canaria; Lanzarote; Fuerteventura	7	-15.6ºW	29.5ºN	~4.9º	~1.9º	~490 km	~100 km	~90 km	Sub-tropical oligotrophic waters; close to upwelling area	30	4	Martín *et al* 2003; Ruiz *et al* 2011; Mayr and Ritter 2005 Servidio *et al* 2019 Aguilar de Soto, 2006
	Sub-tropical	Macaronesia	Madeira	Madeira; P. Santo; Ilhas Desertas	5	-16.4ºW	32.8ºN	~1º	~1.3º	100 km	~191 km	~630 km	Sub-tropical/warm-temperate oligotrophic waters; surounded by abyssal plain	28	2	Freitas *et al* 2012; Alves *et al* 2013; Dinis *et al* 2016
	Warm-temperate	Macaronesia	Azores	Corvo; Flores; Faial; Pico; S. Jorge; Graciosa; Terceira; S. Miguel; S. Maria	9	-28.16ºW	38.6ºN	~6.2º	~2º	~620 km	~300 km	~1 360 km	Warm-temperate oligotrophic waters; Mid-Atlantic Ridge	28	3	Prieto and Silva 2010; Silva *et al* 2008 Hartmann 2018;
Pacific Ocean	Equatorial	Eastern Tropical Pacific	Galápagos Islands	Isabela, Fernandina, São Tiago, Santa Cruz and others	>18	-90.5ºW	-0.48ºS	~1º	~1.2º	287 km	~375 km	~900 km	Equatorial waters in the Eastern Tropical Pacific; close to the equatorial divergence	13	unknown	Palacios et al 2004
	Equatorial	Costa Rica Dome	Cocos Island	Cocos Island	1	~-87.1ºW	~5.5ºN	-	-	-	~100 km	~500 km	Equatorial productive waters in the Eastern Tropical Pacific; surrounded by abyssal plain	-	unknown	
	Equatorial	Central Pacífic	Palmyra Atoll (part of Northern Sentinel Islands)	Palmyra Atoll	1	~162ºE	~5.9ºN	-	-	-	~60 km	> 5 000 km	Equatorial waters in Central Pacific, in a range of seamounts and other islands, close to the equatorial divergence	-	unknown	
	Equatorial	French Polynesia	Marquese Islands	Eiao, Hatutu, Motu Iti, Nuku Hiva, Ua Huka, Fatu Hiva, Terihi and others	15	~-139ºW	~-9.4ºS	~2.1º	~2.8º	~370 km	~500 km	~4 500 km	Equatorial waters in Central Pacific, close to the equatorial divergence	≥20	unknown	Gannier 2002
	Tropical	French Polynesia	Society Islands	Mehetia, Tahiti. Teti'aroa Moorea, Raiatea, Bora Bora Tupai, Maupiti and others	14	~-152ºW	~-16.9ºS	~5 .6º	~1.7º	~620 km	~300 km	~3 700 km	Tropical oligotrophic waters; surounded by seamounts and atolls and the abyssal plain	≥13	2	Gannier 2000 Oremus *et al* 2007 Oremus *et al* 2012
	Tropical	Hawaii	Hawaiian Islands	Hawai'i, 4-Islands, O'ahu, Kauai'i, Ni'ihau, Pearl & Hermes Reef, Midway Atoll, Kure Atoll and others	> 11	~-166ºW	~24ºN	~23º	~9.3º	~2 500 km	~1 100 km	~3 700 km	Tropical/subtropcial oligotrophic waters; surounded by abyssal plain	25	10	Baird et al 2015; Bradford 2017
	Tropical	Western Tropical Pacific	Mariana	Guam, Saipan, Tinian, Rota, Aguigan and the northern islands	16	~146ºE	~16.6ºN	~2.4º	~8.4º	890 km	~480 km	~1 800 km	Tropical oligotrophic waters; located in an underwater mountain range linking to Japan	29	1	Hill *et al* 2019 Fulling *et al* 2011
Indian ocean	Equatorial	Central Indian Ocean	Maldives	North Male, South Male, Ari Atoll, Mulak Atoll, Kolhmadulu, and other islands and atolls	26	~73.2ºE	~3ºN	~0.7º	~7.7º	880 km	300 km	~440 km	Equatorial waters in Central Indian Ocean; close to continent	20	unknown	Anderson 2005
	Equatorial	West Indian Ocean	Seychelles Islands	Mahé, Praslin, Silhouette, La Digue, Curieuse, Félicité, Frégate and others	155	~54.6ºE	-5.2ºS	~2.7º	2.2º	~330 km	~400 km	~1 600 km	Equatorial waters in West indian ocean; most islands located in a Plateau	?	unknown	
	Tropical	Southwest Indian Ocean	Mascarenes	La Réunion; Mauricius and Rodrigues	3	~59ºE	-20.3ºS	8.4º	1.4º	~880 km	~200 km	~715 km	Tropical oligotrophic waters; located south of an underwater mountain range linking to Seychelles	≥15	≥2	Dulau-Drouot et al 2008; Estrade and Dulau 2020

Table I.1.2 – Summary table describing qualitatively some of the open ocean islands/archipelagos characteristics in comparison with cetacean species local ecological characteristics (e.g. density, group size, seasonality and residency patterns). Spatial coverage information is added to give context geographical context to the density values presented, e.g. inshore, offshore, both inshore and offshore (in/off) and specific areas in archipelagos. The size of archipelagos was represented by the "Max dist. between islands" and classified as: S - < 200 km; M – 200-800 km; L – > 800 km; The proximity of closest nearby habitats (e.g. other archipelagos, seamounts) was represented by "Dist. to other habitats" and classified as: S - < 200 km; M – 200-800 km; L – > 800 km; and distance to the nearest continent (Dist. continent) , classified as: S – < 500 km; M – 500-2 000 km; and L – > 2 000 km. * - Summer.

Species	**Ocean**	**Oceanic regions**	**Archipelago**	**nº of Islands /Atolls**	**Max dist. between islands**	**Dist. to other habitats**	**Dist. Continent**	**Density (animals/ 1 000 km^2)**	**Spatial coverate**	**Group size**	**Seasonality**	**Residency patterns (% residents)**	**Sources (densities; residency patterns)**
T. truncatus	Atlantic	Sub-tropical	Canary Is.	7	M	S	S	77*	inshore	21-40	year-round	-	Freitas et al in prep;
		Sub-tropical	Madeira	5	S	S	M	110 (126*)	inshore	14	year-round	4.3% residents; 9.3% migrants; 86.4% transients	Freitas *et al* 2014; Freitas et al in prep; Dinis *et al* 2016;
		Warm-temperate	Azores	9	M	S	M	29*	in/off	21	year-round	6.8% residents; 93.2% migrants and transients	Freitas et al in prep; Silva *et al* 2008
	Pacific	Equatorial	Galápagos	>18	M	M	M	-	inshore	24	-	-	-
		Equatorial	Cocos Is.	> 11	S	S	M	-	inshore	10	-	most animals transients	-
		Estearn Tropical pacific		-	-	-	-	12.71	offshore	23	-	-	Wade & Gerrodette 1993
		Tropical	Hawaii	> 11	L	L	L	2.18	Main Is.	-	year-round	resident and offshore populations	Barlow 2006 (Bradford *et al* 2017); Baird *et al* 2009, Martien *et al* 2012
								1.23	offshore	-	-		
								1.31(8.99)	in/off	5 (33)	-		
	Indian	Tropical	Mascarenes (La Réunion)	3	L	S	M	-	inshore	48	year-round	33% residents; 33% long-term visitors and 34% short-term visitors (inc. Transients)	; Estrade and Dulau-Drouot, 2020
G. macrorhynchus	Atlantic	Sub-tropical	Canary Is.	7	M	S	S	88 (104*)	inshore	26	year-round	4% core residents; 21% residents; 13% occasional visitors and 63% transients	Servidio *et al* 2014 (Esteban et al in prep.); Servidio *et al* 2019
		Sub-tropical	Madeira	5	S	S	M	30 (42*)	inshore	16	year-round	11% residents; 21% visitors and 68% transients	Freitas *et al* 2014 (Esteban et al in prep.); Alves *et al* 2013
		Warm-temperate	Azores	9	M	S	M	10*	in/off	9	-	-	Esteban et al in prep.
	Pacific	Estearn Tropical pacific		-	-	-	-	8.46	offshore	18	-	-	Wade & Gerrodette 1993
		Tropical	Hawaii	> 11	L	L	L	14.98	Main Is.	20	year-round	35% residents; 33% visitors and 32% transients	Barlow 2006 (Bradford *et al* 2017); Mahaffy *et al* 2015
								2.54	offshore				
								3.62 (7.97)	in/off	41			
		Tropical	Mariana	16	L	M	M	1.59	in/off	26/18	year-round	75% see two or more times; 25% seen only once	Fulling *et al* 2011; Hill *et al* 2019
	Indian	Equatorial	Maldives	26	L	M	S		inshore	16	-	-	-
		Tropical	Mascarenes	3	L	S	M	-	inshore	50	-	-	-

Species	**Ocean**	**Oceanic regions**	**Archipelago**	**nº of Islands /Atolls**	**Max dist. between islands**	**Dist. to other habitats**	**Dist. Continent**	**Density** (animals/ 1 000 km^2)	**Spatial coverate**	**Group size**	**Seasonality**	**Residency pattern (% residents)**	**Sources (densities; residency patterns)**
D. delphis	Atlantic	Sub-tropical	Madeira	5	S	S	M	168 (55*)	inshore	12	Winter-spring	-	Freitas *et al* 2014;
		Warm-temperate	Azores	9	M	S	M	11*	in/off	7	Winter-spring	-	Freitas et al in prep;
	Pacific	Equatorial	Galápagos	>18	M	M	M	-	-	125	-	-	-
		Equatorial	Cocos Is.	> 11	S	S	M	-	inshore	10	-	-	-
		Estearn Tropical pacific		-	-	-	-	165	offshore	254-473	-	-	Wade & Gerrodette 1993
	Indian	Western Tropical Indian		-	-	-	-	-	-	221	-	-	-
		Tropical	Mascarenes	3	L	S	M	-	inshore	48	-	-	-
S. attenuata	Pacific	Estearn Tropical pacific		-	-	-	-	108	offshore	134	-	-	Wade & Gerrodette 1993
		Equatorial	Marquese	15	M	M	L	-	-	150	-	-	-
		Tropical	Society	14	M	M	L	-	-	126	-	-	-
		Tropical	Hawaii	> 11	L	L	L	-	Norhern Is.	211	-	-	-
								20	Main Is.	60 (43)	-	-	Barlow 2006 (Bradford *et al* 2017);
								2.1	offshore		-	-	
								4 (23)	in/off		-	-	
	Indian	Equatorial	Maldives	26	L	M	S	-	-	161	-	-	-
		Western Tropical Indian		-	-	-	-	-	-	147	-	-	-
S. longirostris	Pacific	Estearn Tropical pacific		-	-	-	-	86	offshore	112	-	-	Wade & Gerrodette 1993
		Equatorial	Marquese	15	M	M	L	-	-	19	-	-	-
		Tropical	Society	14	M	M	L	-	-	29	-	-	-
		Tropical	Hawai	> 11	L	L	L	-	Norhern Is.	211	-	-	-
								6.99	Main Is.	32	-	-	Barlow 2006 (Bradford et al 2017);
								0.83	offshore		-	-	
								1.37	in/off		-	-	
	Indian	Equatorial	Maldives	26	L	M	S	-	-	58	-	-	-
		Western Tropical Indian Ocean						-	-	121	-	-	-
S. frontalis	Atlantic	Sub-tropical	Canary Is.	7	M	S	S	186	Eastern Islands	32-83	-	-	Servidio *et al* 2015;
								860	inshore		-	-	Freitas et al in prep;
		Sub-tropical	Madeira	5	S	S	M	240 (449*)	inshore	18-42	Spring-Autumn	-	Freitas *et al* 2014 (Freitas et al in prep.);
		Warm-temperate	Azores	9	M	S	M	117*	in/off	15-42	Spring-Autumn	-	Freitas et al in prep;

Species	Ocean	Oceanic regions	Archipelago	nº of Islands /Atolls	Max dist. between islands	Dist. to other habitats	Dist. Continent	Density (animals/ 1 000 km^2)	Spatial coverate	Group size	Seasonality	Residency pattern (% residents)	Sources (densities; residency patterns)
S. coeruleoalba	Atlantic	Sub-tropical	Canary Is.	7	M	S	S	604	Channel Islands-Africa	69	-	-	Servidio *et al* 2015
								71*	inshore				Freitas et al in prep.
		Sub-tropical	Madeira	5	S	S	M	16*	inshore	14-28	-	-	-
		Warm-temperate	Azores	9	M	S	M	26*	in/off	43	-	-	Freitas et al in prep.
	Pacific	Estearn Tropical pacific		-	-	-	-	100	offshore	61	-	-	Wade & Gerrodette 1993
		Tropical	Hawaii	> 11	L	L	L	3.1	Main Is.	37 (53)	-	-	Barlow 2006 (Bradford et al 2017);
								5.57	offshore		-	-	
								5.36 (25)	in/off		-	-	
	Indian	Equatorial	Maldives	26	L	M	S	-	-	48	-	-	-
		Western Tropical Indian Ocean						-	-	43	-	-	-
Z. cavirostris	Atlantic	Sub-tropical	Canary Is.	7	M	S	S	70	Lanzarote-Fuerteventura	-	-	-	
Z. cavirostris		Sub-tropical	Canary Is.	7	M	S	S	2*	inshore	2	-	-	Esteban et al in prep.
Z. cavirostris		Sub-tropical	Madeira	5	S	S	M	1*	inshore	-			Esteban et al in prep.
Z. cavirostris		Warm-temperate	Azores	9	M	S	M	3*	in/off	-			Esteban et al in prep.
all Ziphiidae		Sub-tropical	Canary Is.	7	M	S	S	11.79 (6*)	Channel Islands-Africa	-	-	-	Servidio *et al* 2015; (Esteban et al in prep.)
all Ziphiidae		Sub-tropical	Madeira	5	S	S	M	6 (3*)	inshore	2	-	-	Freitas *et al* 2014; (Esteban et al in prep.)
all Ziphiidae		Warm-temperate	Azores	9	M	S	M	43*	in/off	3	-	-	Esteban et al in prep.

Species	**Ocean**	**Oceanic regions**	**Archipelago**	**nº of Islands /Atolls**	**Max dist. between islands**	**Dist. to other habitats**	**Dist. Continent**	**Density (animals/ 1 000 km^2)**	**Spatial coverate**	**Group size**	**Seasonality**	**Residency pattern (% residents)**	**Sources (densities; residency patterns)**
Z. cavirostris	Pacific	Estearn Tropical pacific		-	-	-	-	1.04	offshore	2.2	-	-	Wade & Gerrodette 1993
Mesoplodon sp.								1.32	offshore	3	-	-	
Z. cavirostris		Tropical	Hawaii	> 11	L	L	L	0	Main Is.	-	-	-	Barlow 2006 (Bradford et al 2017);
								6.8	offshore	02 (01)	-	-	
								6.21 (0.3)	in/off		-	-	
M. densirostris								0	Main Is.	-	-	-	
								1.28	offshore	2.3 (7)	-	-	
								1.17 (0.86)	in/off		-	-	
all Ziphiidae								1.74	Main Is.	-	-	-	
								8.53	offshore	-	-	-	
								7.95	in/off	-	-	-	
Physeter macrocephalus	Atlantic	Sub-tropical	Canary Is.	7	M	S	S	4.23	in/off	-	-	-	Fais *et al* 2016
		Sub-tropical	Madeira	5	S	S	M	4*	inshore	2	-	-	Esteban et al in prep.
		Warm-temperate	Azores	9	M	S	M	6*	in/off	2	-	-	Esteban et al in prep.
	Pacific	Estearn Tropical pacific		-	-	-	-	1.19	offshore	8	-	-	Wade & Gerrodette 1993
		Tropical	Hawaii	> 11	L	L	L	0.59	Main Is.	7.3 (7.4)	-	-	Barlow 2006 (Bradford et al 2017);
								3.03	offshore		-	-	
								2.82 (1.86)	In/off		-	-	

APPENDIX II

APPENDIX II.

II.1 Photo quality grading criteria

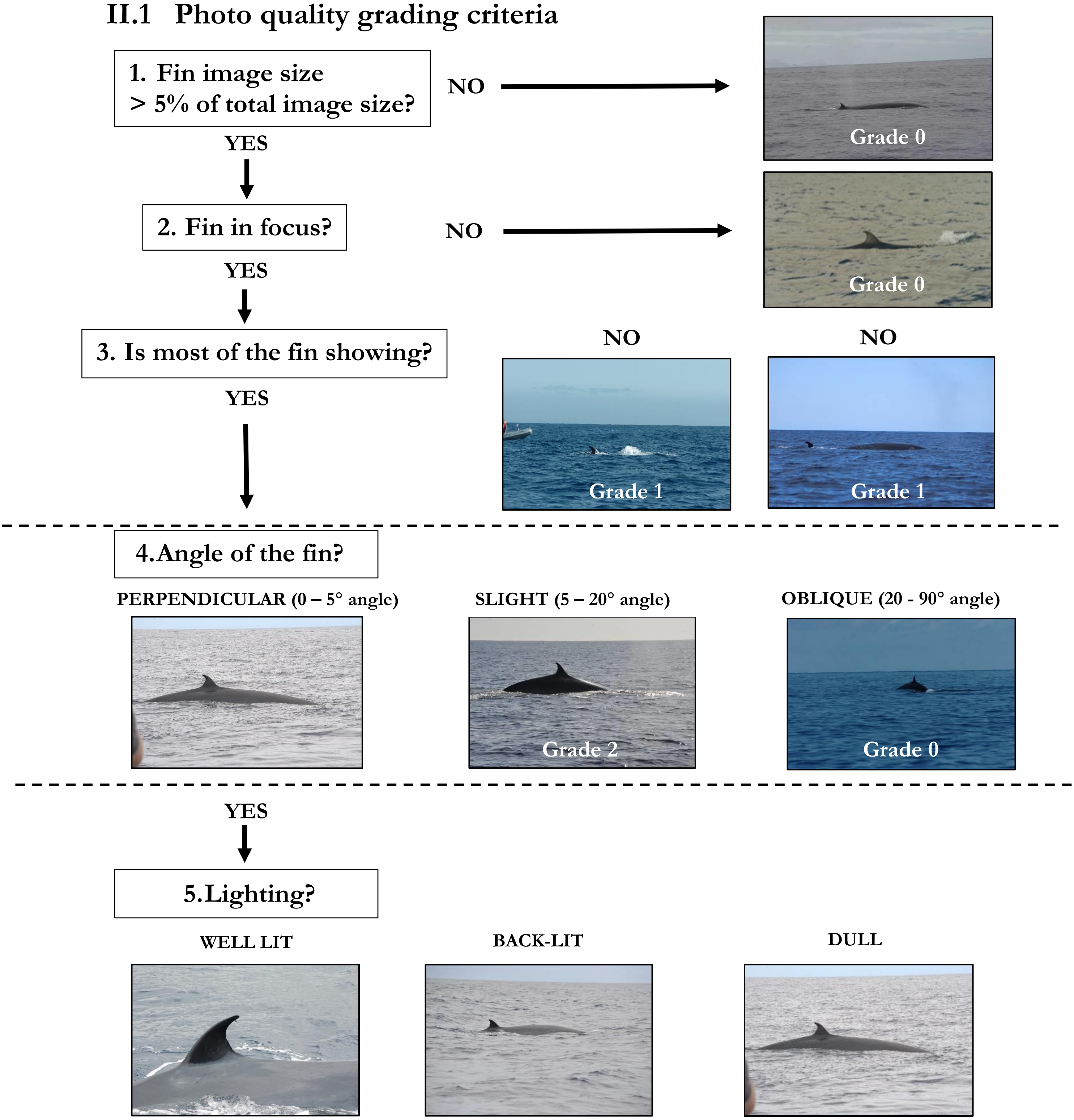

Figure II.1-1 – Scheme explaining the criteria used to rate the quality of the images used in the photo-identification of Bryde's whales. The rationale on photo-quality criteria selection is presented in the next page.

Rationale on photo-quality criteria selection

1. **Fin < 5% of the picture (10 mm at 50% zoom in a 15" screen)** –> A photo with a fin too small does not have enough resolution for nicks and other marks in the dorsal fin trailing edge to be recognized. It is also harder to recognized clearly the dorsal fin contour and shape as you enlarge de picture (pixelized image), and fins in such pictures tend to be out of focus- increases heterogeneity in capture probability - > **graded 0**;
2. **Pictures out of focus** -> An animal photo-identified with a picture out of focus will be harder to be recognized later for the same reasons pointed out before – harder to identify nicks and shape of the fin. Thus, it will also contribute to increase heterogeneity in capture probabilities (animals with very distinct features will be more easily identified than animals with moderate or poor features of distinctiveness), resulting in an increase of both false negatives and false positives -> **graded 0**;
3. **Partial fins** –> although partial fins with nicks and other marks can be recognized if those marks are in the visible part of the fin, it is much harder to be certain if we also consider the shape of the fin. In the case of Bryde's whales the shape of the fin is also an important feature (although it should be considered secondary) to identify an animal, because many animals do not have nicks and cuts in dorsal fin, but have a sufficiently distinct fin shape to allow their individual identification -> **graded 1**;
4. **Angle of the fin:**

   -> Fins photographed **perpendicular (0-5º)** to the camera have the fin contour well visible as well as nicks, cuts, and other indentations -> **graded 3**;

   -> With fins photographed at **slight angles (5-20º)**, the smaller nicks, cuts and indentations may start to be obscured, or its perception distorted by the angle of the fin. The perception of the shape of the fin may also be affected making it more difficult to recognize an individual from the fin shape -> **graded 2**;

   -> It will be much harder to identify correctly nicks cuts and other indentations at the trailing edge of fins photographed at **considerable angles (>20º)**, increasing considerably the uncertainty of a correct identification of the animal. The perception of the shape of fin will be considerably distorted making an identification of an animals based on this criterion very unreliable -> **graded 0**;

5. **Lighting**:

   -> **Well-lit pictures** – when the fin and the background (sea) are both well lid. This happens when the sun is behind the photographer lighting well both the background (sea) and the side of the fin facing the camera -> **graded 3.3**;

   -> **Back-lid pictures** – when the fin is evenly dark or totally black, being very difficult or impossible to identify scars and colouring patterns on the fin's surface. This is the result of the sunlight coming from behind the dorsal fin (animal between the sun and the camera), lighting well the background (sea) but not the side of fin being photographed. Usually the dark contour of the fin is well defined against the lid background –> **graded 3.2**;

   -> **Dull pictures** - when the photo-id pictures are greyish and evenly lighted, i.e. the fin and the background are equally under lighted. Happens when pictures are taken in a cloudy day -> **graded 3.1;**

Adapted from:

Ashe, Erin. 2015. 'Ecology of Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*) in the Coastal Waters of British Columbia, Canada'. Thesis, University of St Andrews. https://research-repository.st-andrews.ac.uk/handle/10023/9483.

Penry, Gwenith S. 2010. 'The Biology of South African Bryde's Whales'. Thesis, University of St Andrews. https://research-repository.st-andrews.ac.uk/handle/10023/921.

II.2. Tables with number of processed images by year and type of survey

Table II.2-1 – Table with the number of processed images of Bryde's whales dorsal fins that were compared with the catalogue (whether an animal ID was given to the image or not), by area, year and type of survey. NSS – Non-systematic shipboard surveys (research dedicated surveys, usually for photo-identification and biopsy sampling); SLS – Systematic line-transect shipboard surveys; OS – Other surveys (e.g. seismic surveys); OE – Opportunistic encounters (citizen science); WW – whale-watching trips.

Area Type of survey	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**	**2021**	**Total**	**%**
Azores			4						2			11	3	3		81	25	2		3	134	100%
NSS									1												1	0.7%
SLS																	3				3	2.2%
OE																4				1	5	3.7%
WW			4						1			11	3	3		77	22	2		2	125	93.3%
Canary Islands	4		1	3	1	6	5		4		24	7	43	37	131	118	13				397	100%
NSS				1	1				2		9		11	10	33	18					85	21.4%
SLS													5			17					22	5.5%
OE						2							9	7	10	5					33	8.3%
WW	4		1	2		4	5		2		15	7	18	20	88	78	13				257	64.7%
Madeira	8	20	29	37	28	32	90	19	54	24	35	7	500	217	50	486	126	178	78	257	2275	100%
NSS			7	14	18	17	29		14	4	4			1		1	16	36	12		173	7.6%
SLS	8		2			3	6		2	1	1					85	6				114	5.0%
OE				1		3										1	1	3		2	10	0.4%
WW		20	20	22	10	9	55	19	38	19	30	7	500	216	50	399	103	139	66	255	1977	86.9%
Algarve																			2	9	11	100%
NSS																			2		2	18.2%
WW																				9	9	81.8%
Mauritania																		2			2	100%
OS																		2			2	100%
Senegal																	1				1	100%
OS																	1				1	100%
Guinea-Bissau									3												3	100%
OE									3												3	100%
Total	12	20	34	40	29	38	95	19	63	24	59	25	546	257	181	685	165	182	80	269	2823	

Table II.2-2 – Table with the number of images of Bryde's whales dorsal fins that were compared with the catalogue and an animal ID was assigned to the image, by area, year and type of survey. NSS – Non-systematic shipboard surveys (research dedicated surveys, usually for photo-identification and biopsy sampling); SLS – Systematic line-transect shipboard surveys; OS – Other surveys (e.g. seismic surveys); OE – Opportunistic encounters (citizen science); WW – whale-watching trips.

Area Type of survey	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**	**2021**	**Total**	**%**
Azores			2						2			11	3	3		71	20	1		3	116	100%
NSS									1												1	0.9%
SLS																	1				1	0.9%
OE																4				1	5	4.3%
WW			2						1			11	3	3		67	19	1		2	109	94.0%
Canary Islands	1		1	1		6	5		4		18	2	29	30	113	81	7				298	100%
NSS									2		9		9	7	31	14					72	24.2%
SLS													4			17					21	7.0%
OE						2							8	7	9	5					31	10.4%
WW	1		1	1		4	5		2		9	2	8	16	73	45	7				174	58.4%
Madeira	3	16	21	32	22	23	67	17	45	21	29	4	418	189	41	406	104	129	60	228	1875	100%
NSS			6	12	13	10	21		11	4	3			1		1	12	34	11		139	7.4%
SLS	3		2			2	5		2	1						69	4				88	4.7%
OE						3										1	1			2	7	0.4%
WW		16	13	20	9	8	41	17	32	16	26	4	418	188	41	335	87	95	49	226	1641	87.5%
Algarve																			2	9	11	100%
NSS																			2		2	18.2%
WW																				9	9	81.8%
Mauritania																		2			2	100%
OS																		2			2	100%
Senegal																	1				1	100%
OS																	1				1	100%
Guinea-Bissau									3												3	100%
OE									3												3	100%
Total	4	16	24	33	22	29	72	17	54	21	47	17	450	222	154	558	132	132	62	240	2306	

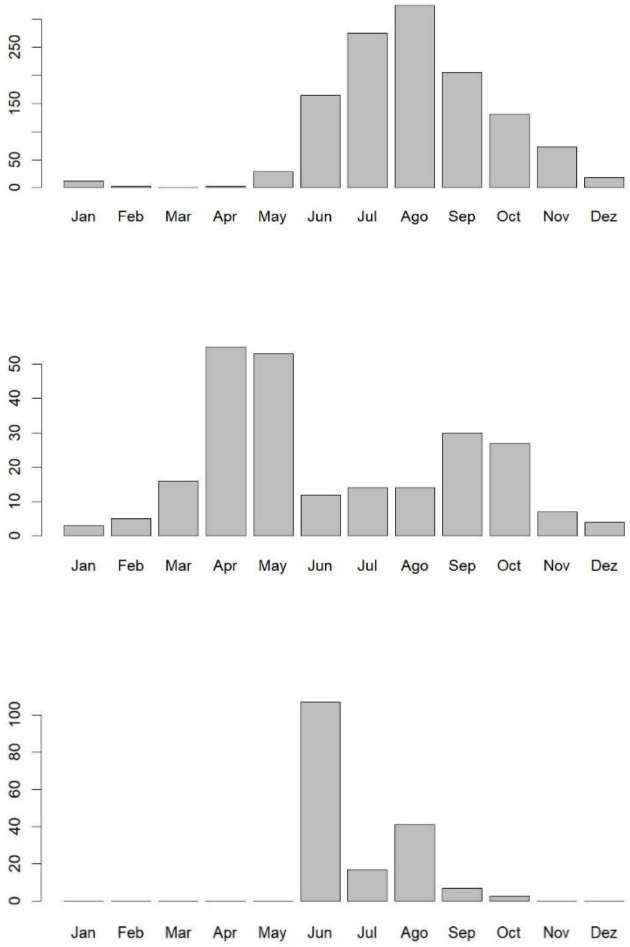

Figure II.2-1 – Sightings of Bryde's whales per month for Madeira (top), Canary Islands (centre) and Azores (bottom), and for which there was photo-identification images collected.

II.2. Table with the “captures” of animals seen multiple occasions in the same location of the study area

Table II.3-1 – Table showing the “captures” over time of photo-identified animals seen only in one location of the study area in multiple occasions. The animals’ identification (Ind), distinctiveness (CL) and site fidelity to Madeira (SF; 1–regular visitors, 2–occasional visitors, 3–rare visitors, 0–transients) are presented on the left side of the table, as well as, the number of times animals were photo-identified in an area, identified by letters and colours (M – Madeira, green; C – Canary Is., blue; A – Azores, yellow; GU – Guinea, grey; MA – Mauritania, violet). On the right side of the table their “captures” between 2002 and 2021 are presented and also identified with letters and colours. The sampling unit was 2 months (J – January-February; M – March-April; M – May-June, J – July-August, S – September-October, N – November-December).

											2002						2003						2004						2005						2006						2007						2008						2009						2010						2011						2012						2013						2014						2015						2016						2017						2018						2019						2020						2021					
Ind	CL	SF	M	C	A	AL	MA	GU	GA	total	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N
Be0001	1	-	3							3										M						M																																										M																																																														
Be0003	1	1	12							12											M					M						M					M	M						M	M					M	M						M				M	M																																																																				
Be0006	1	1	5							5																																			M																	M																								M	M																													M														
Be0010	0	-	2							2																M	M																																																																																																							
Be0017	1	-	2							2																						M		M																																																																																																
Be0020	1	1	5							5																							M																																																					M	M					M																														M								
Be0021	1	2	4							4																								M																																																				M												M													M																			
Be0024	1	1	3							3																												M																																																	M																																			M								
Be0025	1	2	2							2																												M																																			M																																																									
Be0030	1	2	3							3																																							M												M						M																																																															
Be0035	1	1	3							3																																		M																																										M																			M																									
Be0036	1	2	2							2																																		M		M																																																																																				
Be0038	1	1	4							4																																																				M																														M	M																																		M			
Be0043	1	1	4							4																																							M		M																														M											M																																						
Be0044	1	1	5							5																																																						M																	M						M					M																								M														
Be0047	1	1	2							2																																								M																																																							M																									
Be0048	1	-		3						3																																		C																													C																								C																																	
Be0049	0	-		3						3																																									C																																																C					C																										
Be0050	1	1	7							7																																									M						M																M												M	M																																									M	M		
Be0052	1	1	5							5																																									M																																			M	M																		M																						M			
Be0054	1	1	7							7																																		M																																																M												M	M										M	M												M		
Be0056	1	-		4						4																																										C																																			C												C						C																									
Be0057	1	1	4							4																																														M						M																								M																																											M	
Be0059	1	1	3							3																																																				M																																											M				M																					
Be0066	1	-	3							3																																																												M															M						M																																							
Be0068	0	-		2						2																																																															C											C																																														
Be0073	1	2	2							2																																																																																		M																		M																				
Be0076	1	2	2							2																																																															M																																				M																					
Be0079	1	2	3							3																																																																							M					M						M																																						
Be0080	1	2	3							3																																																											M												M					M																																												
Be0081	0	-			2					2																																																																						A	A																																																	
Be0088	1	2	2							2																																																																											M	M																																												
Be0090	1	2	2							2																																																																												M	M																																											
Be0092	0	-	2							2																																																																												M					M																																							
Be0093	0	2	2							2																																																																												M																																										M		
Be0095	1	2	2							2																																																																												M	M																																											
Be0098	1	2	2							2																																																																												M						M																																						
Be0100	1	2	3							3																																																																												M						M																	M																					
Be0105	1	2	5							5																																								M																																				M	M	M	M																																									
Be0106	0	2	2							2																																																																												M						M																																						
Be0107	1	2	2							2																																																																												M																									M																			

Table II.3-2 – Table showing the "captures" over time of photo-identified animals seen only in one location of the study area in multiple occasions. The animals' identification (Ind), distinctiveness (CL) and site fidelity to Madeira (SF; 1–regular visitors, 2–occasional visitors, 3–rare visitors, 0–transients) are presented on the left side of the table, as well as, the number of times animals were photo-identified in an area, identified by letters and colours (M – Madeira, green; C – Canary Is., blue; A – Azores, yellow; GU – Guinea, grey; MA – Mauritania, violet). On the right side of the table their "captures" between 2002 and 2021 are presented and also identified with letters and colours. The sampling unit was 2 months (J – January-February; M – March-April; M – May-June, J – July-August, S – September-October, N – November-December) (continuation).

											2002						2003						2004						2005						2006						2007						2008						2009						2010						2011						2012						2013						2014						2015						2016						2017						2018						2019						2020						2021					
Ind	CL	SF	M	C	A	AL	MA	GU	SE	total	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N
Be0110	1	2	4							4																																																																											M	M					M		M																																						
Be0111	1	2	2							2																																																																											M	M																																												
Be0112	1	2	2							2																																																																												M																																	M															
Be0113	0	1	2							2																					M																																																									M																																											
Be0114	1	3	2							2																																																																												M	M																																											
Be0121	1	2	2							2																																																																																			M																			M																			
Be0122	1	2	4							4																																																																																			M													M	M									M														
Be0134	1	-		2						2																																																																																									C		C																														
Be0138	1	-		2						2																																																																																										C				C																											
Be0146	1	2	2							2																																																																																																								M						M													
Be0173	1	2	2							2																																																																																M																									M														
Be0174	1	-			2					2																																																																																														A	A																								
Be0183	1	2	2							2																																																																																														M	M																								
Be0187	1	2	3							3																																																																												M																	M	M																							
Be0192	1	2	2							2																																																																																															M	M																							
Be0194	1	1	5							5																																						M																																																																																			M	M					M																			M
Be0195	1	2	4							4																																																																																															M	M									M									M								
Be0201	0	2	2							2																																																																											M	M																																												
Be0212	1	2	2							2																																																																										M	M																																													
Be0213	1	2	2							2																																																																											M	M																																												
Be0216	1	1	2							2																																													M																																																																																											M			
Be0227	1	2	2							2																																																																																															M	M																							
Be0228	1	2	2							2																																																																																															M									M														
Be0239	1	2	2							2																																																																																															M									M														
Be0242	1	2	2							2																																																																																															M	M																							
Be0252	0	2	2							2																																																																																																M																	M								
Be0254	1	2	2							2																																																																																																M										M															
Be0265	1	2	2							2																																																																																																					M																			M			
Be0286	1	2	2							2																																																																																																											M		M														
Be0288	1	2	2							2																																																																											M																												M															
Be0300	0	2	2							2																																																																											M																											M																
Be0316	1	2	2							2																																																																																																																						M	M						
Be0317	1	2	2							2																																																																																																																							M					M			
Be0321	0	2	2							2																																																																																																																							M					M			
Be0323	0	2	2							2																																																																																															M	M																							
Be0324	1	-				2				2																																																																																																																																											AL	AL
Be0346	1	2	3							3																																																																											M	M																							M																				
Be0351	1	2	2							2																																																																																				M														M																					
Be0363	1	-		2						2																																																																																														C	C																														
Be0379	0	2	3							3																																																																										M																										M			M																					

II.3 Table with the “captures” of animals seen only once in any location of the study area

Table II.4-1 – Table showing the “capture” over time of photo-identified animals seen only once in any of the locations of the study area. The animals’ identification (Ind), distinctiveness (CL) and site fidelity to Madeira (SF; 1–regular visitors, 2–occasional visitors, 3–rare visitors, 0–transients) are presented on the left side of the table, as well as, when it was photo-identified in an area, identified by letters and colours (M – Madeira, green; C – Canary Is., blue; A – Azores, yellow; GU – Guinea, grey; MA – Mauritania, violet; light green - Senegal). On the right side of the table their “captures” between 2002 and 2021 are presented and also identified with letters and colours. The sampling unit was 2 months (J – January-February; M – March-April; M – May-June, J – July-August, S – September-October, N – November-December).

											2002						2003						2004						2005						2006						2007						2008						2009						2010						2011						2012						2013						2014						2015						2016						2017						2018						2019						2020						2021					
Ind	**CL**	**SF**	**M**	**C**	**A**	**AL**	**MA**	**GU**	**SE**	**total**	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N
Be0009	1	0	1							1																																																																																																			M																									
Be0011	1	0	1							1																																									M																																																																																								
Be0012	1	-		1						1																																																																C																																																																
Be0013	1	0	1							1																					M																																																																																																												
Be0014	0	-	1							1																	M																																																																																																																						
Be0028	1	0	1							1																															M																																																																																																						
Be0032	1	-		1						1																																	C																																																																																																		
Be0033	0	-		1						1																																			C																																																																																													
Be0034	1	0	1							1																																				M																																																																																												
Be0037	1	0	1							1																																																															M																																																																		
Be0039	0	0	1							1																																				M																																																																																														
Be0040	1	0	1							1																																				M																																																																																															
Be0041	0	0	1							1																																																																																					M																																																								
Be0053	1	0	1							1																																									M																																																																																										
Be0060	0	-						1		1																																																								GU																																																																										
Be0063	0	0	1							1																																																													M																																																																														
Be0067	0	-		1						1																																																																		C																																																															
Be0071	1	-		1						1																																																																		C																																																															
Be0074	0	0	1							1																																																																			M																																																														
Be0077	1	0	1							1																																																																				M																																																													
Be0078	1	0	1							1																																																																																																				M																										
Be0082	0	-			1					1																																																																																	A																																																								
Be0083	0	-		1						1																																																																														C																																																													
Be0085	1	-		1						1																																																																															C																																																													
Be0091	1	0	1							1																																																																													M																																																												
Be0094	1	2	1							1																																																																													M																																																												
Be0096	0	-		1						1																																																																														C																																																										
Be0109	1	0	1							1																																																																													M																																																												
Be0116	0	-	1							1																																																																																M																																																									
Be0119	0	-		1						1																																																																																			C																																																								
Be0120	1	2	1							1																																																																																			M																																																								
Be0127	1	-		1						1																																																																																				C																																																							
Be0130	0	-		1						1																																																																																					C																																																								
Be0133	1	-		1						1																																																																																						C																																																							
Be0136	1	-		1						1																																																																																						C																																																							
Be0137	1	0	1							1																																																																																						M																																																								
Be0139	1	-		1						1																																																																																								C																																																						
Be0140	1	-		1						1																																																																																									C																																																						
Be0141	1	-		1						1																																																																																								C																																																						
Be0144	1	-		1						1																																																																																									C																																																						
Be0145	1	-		1						1																																																																																									C																																																							
Be0149	1	-		1						1																																																																																								C																																																						
Be0150	1	-			1					1																																																																																																									A																										
Be0151	1	-		1						1																																																																																									C																																																						
Be0155	1	2	1							1																																																																																																								M																									
Be0157	0	0	1							1																																																																																																								M																									
Be0158	1	0	1							1																																																																M																																																																	
Be0159	1	-		1						1																																																																																																					C																													

Table II.4-2 – Table showing the "capture" over time of photo-identified animals seen only once in any of the locations of the study area. The animals' identification (Ind), distinctiveness (CL) and site fidelity to Madeira (SF; 1–regular visitors, 2–occasional visitors, 3–rare visitors, 0–transients) are presented on the left side of the table, as well as, when it was photo-identified in an area, identified by letters and colours (M – Madeira, green; C – Canary Is., blue; A – Azores, yellow; GU – Guinea, grey; MA – Mauritania, violet light green - Senegal). On the right side of the table, their "captures" between 2002 and 2021 are presented and also identified with letters and colours. The sampling unit was 2 months (J – January-February; M – March-April; M – May-June, J – July-August, S – September-October, N – November-December) (continuation).

											2002						2003						2004						2005						2006						2007						2008						2009						2010						2011						2012						2013						2014						2015						2016						2017						2018						2019						2020						2021					
Ind	CL	SF	M	C	A	AL	MA	GU	SE	total	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N
Be0162	1	-		1						1																																																																																												C																												
Be0163	0	-		1						1																																																																																												C																												
Be0164	1	-		1						1																																																																																												C																												
Be0165	1	0	1							1																																																																																																																							M	
Be0166	0	-		1						1																																																																																												C																												
Be0170	0	-			1					1																																																																																														A																										
Be0172	0	-			1					1																																																																																														A																										
Be0176	0	-		1						1																																																																																						C																																		
Be0177	1	-			1					1																																																																																														A																										
Be0179	0	-			1					1																																																																																														A																										
Be0180	0	-			1					1																																																																																														A																										
Be0181	0	0	1							1																																																																																														M																										
Be0184	0	-			1					1																																																																																														A																										
Be0185	1	0	1							1																																																																																																									M															
Be0186	1	0	1							1																																																																																															M																									
Be0188	1	2	1							1																																																																																															M																									
Be0190	1	0	1							1																																																																																															M																									
Be0193	1	2	1							1																																																																																															M																									
Be0197	0	-		1						1																																																																																															C																									
Be0198	0	-		1						1																																																																																									C																															
Be0200	0	0	1							1																																																																																																										M														
Be0202	0	-		1						1																																																		C																																																																						
Be0206	0	0	1							1																																																																												M																																												
Be0210	1	0	1							1																																																																																															M																									
Be0211	1	3	1							1																																																																																		M																																						
Be0215	1	0	1							1																																																																																																									M															
Be0217	0	-		1						1																																																																																															C																									
Be0219	0	-	1							1																																					M																																																																																			
Be0222	0	-		1						1																																																																																															C																									
Be0223	1	0	1							1																																																																																															M																									
Be0226	0	0	1							1																																																																																															M																									
Be0231	0	-		1						1																																																																																															C																									
Be0234	1	-		1						1																																																																																															C																									
Be0237	1	-		1						1																																																																																							C																																	
Be0238	0	0	1							1																																																					M																																																																			
Be0240	1	3	1							1																																																																																			M																																					
Be0244	1	0	1							1																																																																																															M																									
Be0245	0	0	1							1																																																																												M																																												
Be0246	1	0	1							1																																																																																																M																								
Be0253	0	-							1	1																																																																																																			GA																					
Be0255	0	0	1							1																																																																																																M																								
Be0256	0	0	1							1																																																																																																											M													
Be0257	1	2	1							1																																																																																		M																																						
Be0264	1	-		1						1																																																																																																		C																						
Be0266	1	3	1							1																																																																																																			M																					
Be0268	1	0	1							1																																																																																																			M																					
Be0269	0	-		1						1																																																																																																C																								
Be0270	1	0	1							1																																																																																																M																								
Be0271	1	0	1							1																																																																																																			M																					

Table II.4-3 – Table showing the “capture” over time of photo-identified animals seen only once in any of the locations of the study area. The animals’ identification (Ind), distinctiveness (CL) and site fidelity to Madeira (SF; 1–regular visitors, 2–occasional visitors, 3–rare visitors, 0–transients) are presented on the left side of the table, as well as, when it was photo-identified in an area, identified by letters and colours (M – Madeira, green; C – Canary Is., blue; A – Azores, yellow; GU – Guinea, grey; MA – Mauritania, violet; light green - Senegal). On the right side of the table, their “captures” between 2002 and 2021 are presented and also identified with letters and colours. The sampling unit was 2 months (J – January-February; M – March-April; M – May-June, J – July-August, S – September-October, N – November-December) (continuation).

											2002						2003						2004						2005						2006						2007						2008						2009						2010						2011					
Ind	**CL**	**SF**	**M**	**C**	**A**	**AL**	**MA**	**GU**	**SE**	**total**	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N
Be0272	1	0	1							1																																																				
Be0273	1	0	1							1																																																				
Be0274	1	0	1							1																																																				
Be0275	1	0	1							1																																																				
Be0276	1	0	1							1																																																				
Be0278	0	0	1							1																																																				
Be0279	1	-			1					1																																																				
Be0281	1	0	1							1																																																				
Be0282	1	-			1					1																																																				
Be0283	1	-			1					1																																																				
Be0285	1	0	1							1																																																				
Be0287	1	0	1							1																																																				
Be0290	1	0	1							1																																																				
Be0291	0	-	1							1																																																				
Be0292	1	-			1					1																																																				
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Be0294	1	0	1							1																																																				
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Be0297	1	-	1							1																																																				
Be0298	0	0	1							1																																																				
Be0303	1	-				1				1																																																				
Be0305	1	2	1							1																																																				
Be0306	1	0	1							1																																																				
Be0307	1	0	1							1																																																				
Be0308	1	0	1							1																																																				
Be0309	1	0	1							1																																																				
Be0312	1	0	1							1																																																				
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Be0315	1	0	1							1																																																				
Be0319	1	3	1							1																																																				
Be0322	1	0	1							1																																																				
Be0325	1	-	1							1																																																				
Be0326	0	0	1							1																																																				
Be0327	0	0	1							1																																																				
Be0328	1	0	1							1																																																				
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Be0336	0	-		1						1																																																				
Be0337	0	0	1							1																																																				
Be0338	0	-		1						1																																																				
Be0339	1	2	1							1																																																				
Be0340	1	0	1							1																																																				
Be0342	0	0	1							1																																																				
Be0343	0	0	1							1																																																				
Be0344	0	0	1							1																																																				
Be0347	0	0	1							1																																																				
Be0348	1	0	1							1																																																				
Be0349	1	0	1							1																																																				

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Ind	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N
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Table II.4-4 – Table showing the “capture” over time of photo-identified animals seen only once in any of the locations of the study area. The animals’ identification (Ind), distinctiveness (CL) and site fidelity to Madeira (SF; 1–regular visitors, 2–occasional visitors, 3–rare visitors, 0–transients) are presented on the left side of the table, as well as, when it was photo-identified in an area, identified by letters and colours (M – Madeira, green; C – Canary Is., blue; A – Azores, yellow; GU – Guinea, grey; MA – Mauritania, violet; light green - Senegal). On the right side of the table, their “captures” between 2002 and 2021 are presented and also identified with letters and colours. The sampling unit was 2 months (J – January-February; M – March-April; M – May-June, J – July-August, S – September-October, N – November-December) (continuation).

Ind	CL	SF	M	C	A	AL	MA	GU	SE	total
Be0350	0	-		1						1
Be0352	0	0	1							1
Be0354	1	-		1						1
Be0355	0	-		1						1
Be0357	1	0	1							1
Be0358	1	0	1							1
Be0359	0	0	1							1
Be0360	1	0	1							1
Be0361	1	-		1						1
Be0362	0	-			1					1
Be0364	0	-		1						1
Be0365	0	-		1						1
Be0366	0	-			1					1
Be0367	0	-		1						1
Be0368	0	0	1							1
Be0371	1	-			1					1
Be0372	1	0	1							1
Be0373	0	0	1							1
Be0374	0	0	1							1
Be0376	1	0	1							1
Be0377	1	-				1				1
Be0381	1	0	1							1
Be0384	1	0	1							1
Be0386	0	0	1							1
Be0387	0	-		1						1
Be0391	1	-			1					1
Be0392	0	0	1							1
Be0393	1	-		1						1
Be0394	1	-		1						1
Be0395	0	-		1						1
Be0396	0	-			1					1
Be0397	0	-		1						1
Be0398	0	-		1						1
Be0399	1	-		1						1
Be0400	0	0	1							1
Be0402	0	-		1						1
Be0403	0	-						1		1
Be0404	1	-		1						1
Be0405	1	-		1						1
Be0406	1	-		1						1
Be0407	1	-		1						1
Be0408	1	-	1							1
Be0409	1	-			1					1
Be0410	0	-			1					1
Be0411	1	0	1							1
Be0412	0	-		1						1
Be0413	0	-			1					1
Be0414	1	0	1							1
Be0415	1	0	1							1
Be0416	1	0	1							1

	2002						2003						2004						2005						2006					
Ind	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N
Be0350																														
Be0352																														
Be0354																														
Be0355																														
Be0357																														
Be0358																														
Be0359																														
Be0360																														
Be0361																														
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Be0364																														
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Be0381																						M								
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Be0410																														
Be0411																														
Be0412																														
Be0413																														
Be0414																														
Be0415																														
Be0416																														

	2007						2008						2009						2010						2011					
Ind	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N
Be0350																														
Be0352																														
Be0354																														
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Be0365																														
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Be0412																														
Be0413																														
Be0414																														
Be0415																														
Be0416																														

	2012						2013						2014						2015						2016					
Ind	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N
Be0350																	C													
Be0352																						M								
Be0354																											C			
Be0355																										C				
Be0357																														
Be0358																M														
Be0359																M														
Be0360																						M								
Be0361																								C						
Be0362																														
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Be0366																														
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Be0381																														
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Be0386																						M								
Be0387																														
Be0391																														
Be0392																						M								
Be0393																														
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Be0410																														
Be0411																														
Be0412																														
Be0413																														
Be0414																														
Be0415																														
Be0416																	M													

	2017						2018						2019						2020						2021					
Ind	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N	J	M	M	J	S	N
Be0350																														
Be0352																														
Be0354																														
Be0355																														
Be0357																													M	
Be0358																														
Be0359																														
Be0360																														
Be0361																														
Be0362				A																										
Be0364																														
Be0365		C																												
Be0366				A																										
Be0367																														
Be0368					M																									
Be0371																	A													
Be0372																							M							
Be0373																												M		
Be0374																												M		
Be0376																												M		
Be0377																													AL	
Be0381																														
Be0384																														
Be0386																														
Be0387																														
Be0391				A																										
Be0392																														
Be0393					C																									
Be0394					C																									
Be0395																														
Be0396				A																										
Be0397																														
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Be0407																														
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Be0409				A																										
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Be0414					M																									
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II.5. Satellite telemetry – Hidden Markov models

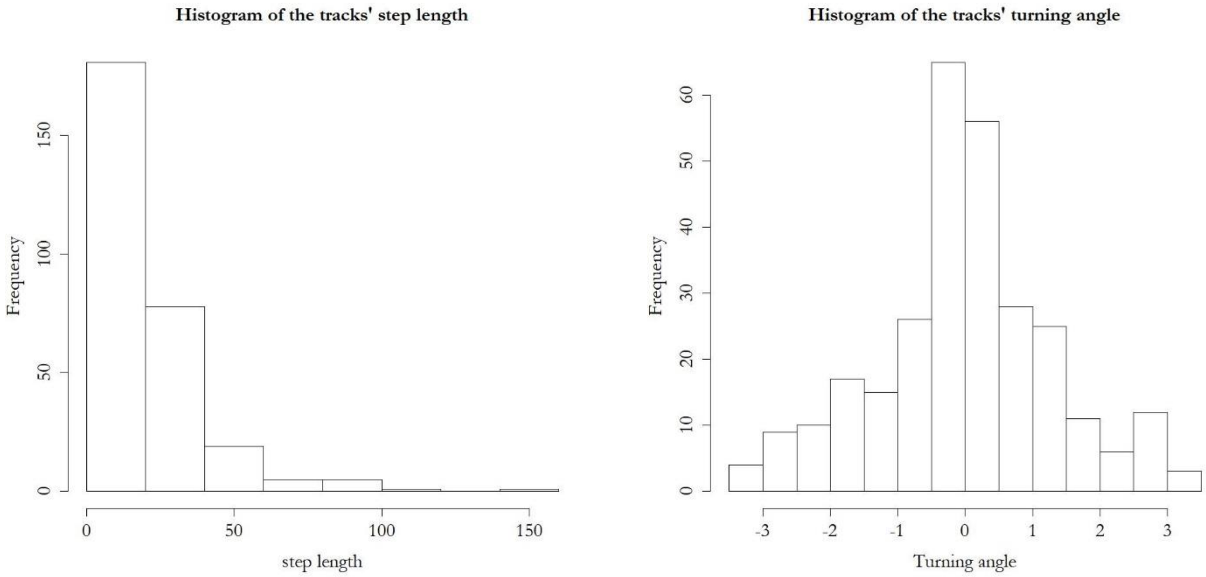


Figure II.5-1 – Histogram of the frequency of distribution of the Bryde's whales tracks observed step lengths (left) and histogram of the frequency of distribution of those tracks observed turning angles (right).

Table II.5-1 – The selected hidden markov model (HMM) parameters fitted to the Bryde's whales tracks.

```
Value of the maximum log-likelihood: -1516.9

step parameters:
----------------
        state1   state2   state3
mean 12.048166 79.58798 32.75089
sd    7.709037 23.26690 10.17560

angle parameters:
-----------------
                 state1  state2   state3
mean          0.0000000  0.0000 0.000000
concentration 0.7299481 13.4178 1.801039

Regression coeffs for the transition probabilities:
---------------------------------------------------
               1 -> 2    1 -> 3    2 -> 1    2 -> 3    3 -> 1    3 -> 2
(Intercept) -5.625105 -2.919961 -25.60568 -1.381903 -1.595108 -2.874593

Transition probability matrix:
------------------------------
             state1      state2     state3
state1 9.455890e-01 0.003409969 0.05100107
state2 6.057644e-12 0.799296467 0.20070353
state3 1.611074e-01 0.044816901 0.79407571

Initial distribution:
---------------------
      state1       state2       state3
5.810950e-01 2.199467e-08 4.189050e-01
```

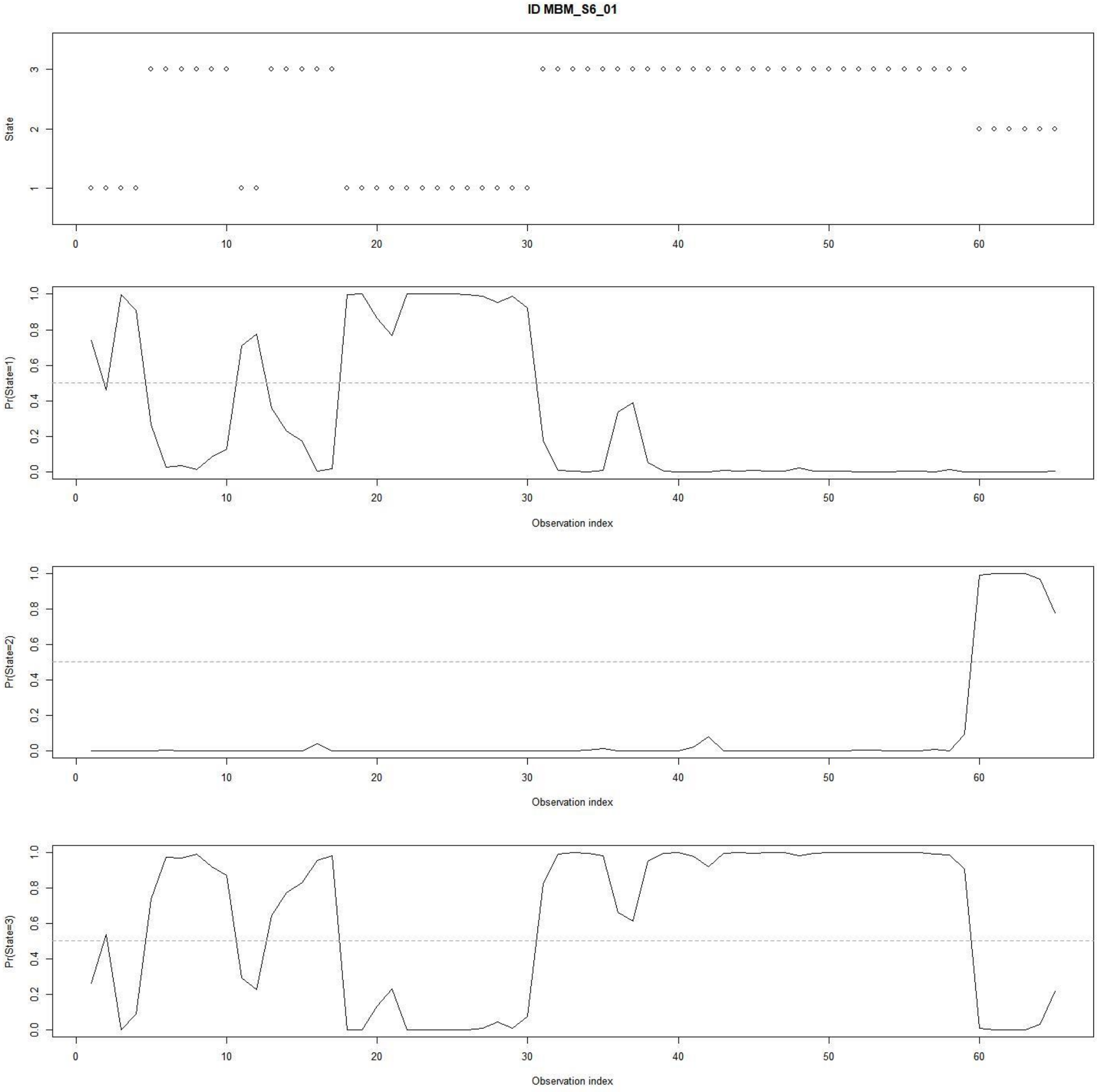


Figure II.5-2 – Graphics representing the probability of change between the states over the sequence of track positions (observation index) for the tag MB_S6_01, predicted by the selected HMM model. The top graph shows the predicted state of the positions and the graphs bellow show the respective probabilities of being in state 1, 2 or 3.

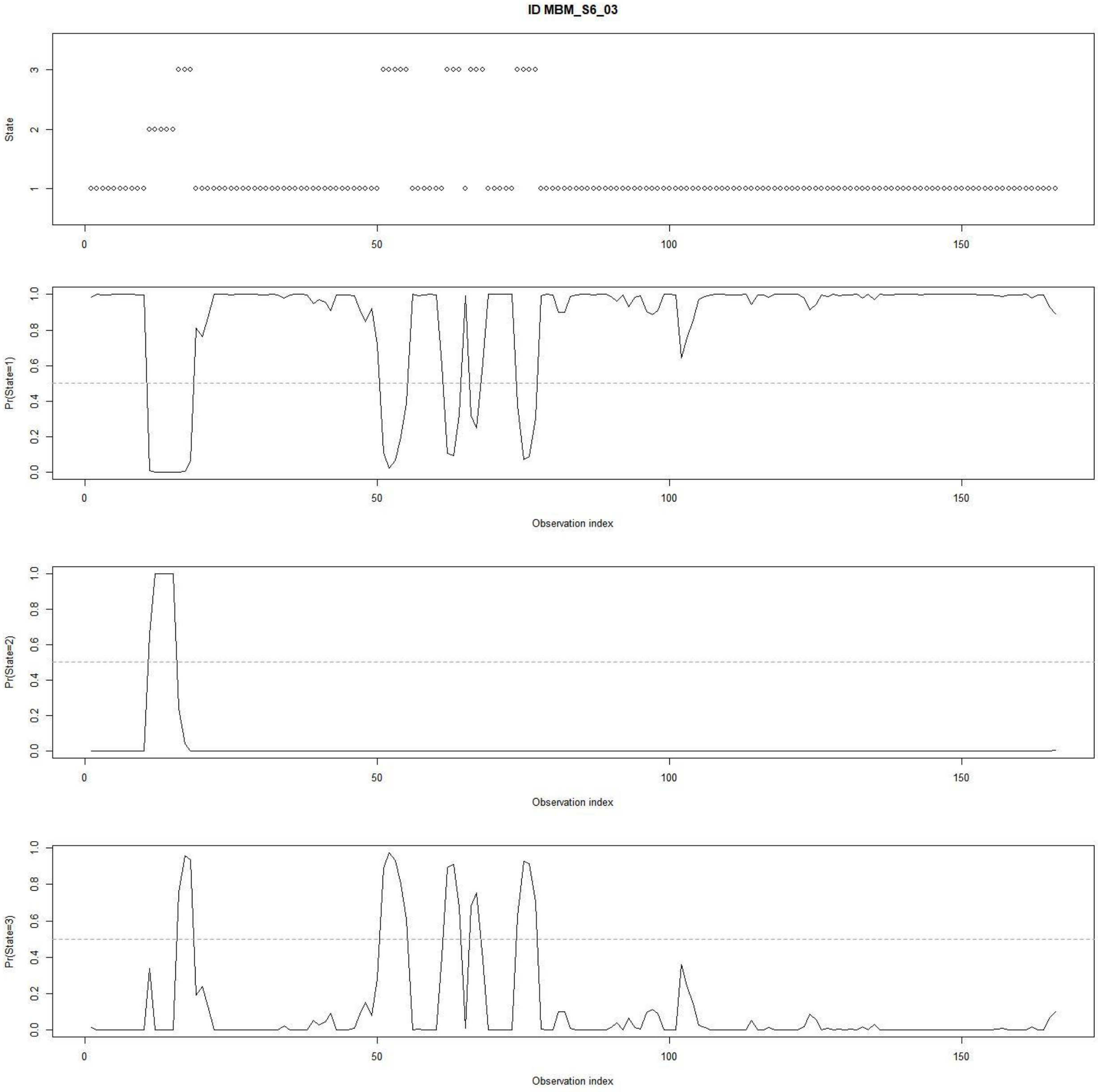


Figure II.5-3 – Graphics representing the probability of change between the states over the sequence of track positions (observation index) for the tag MB_S6_03, predicted by the selected HMM model. The top graph shows the predicted state of the positions and the graphs bellow show the respective probabilities of being in state 1, 2 or 3.

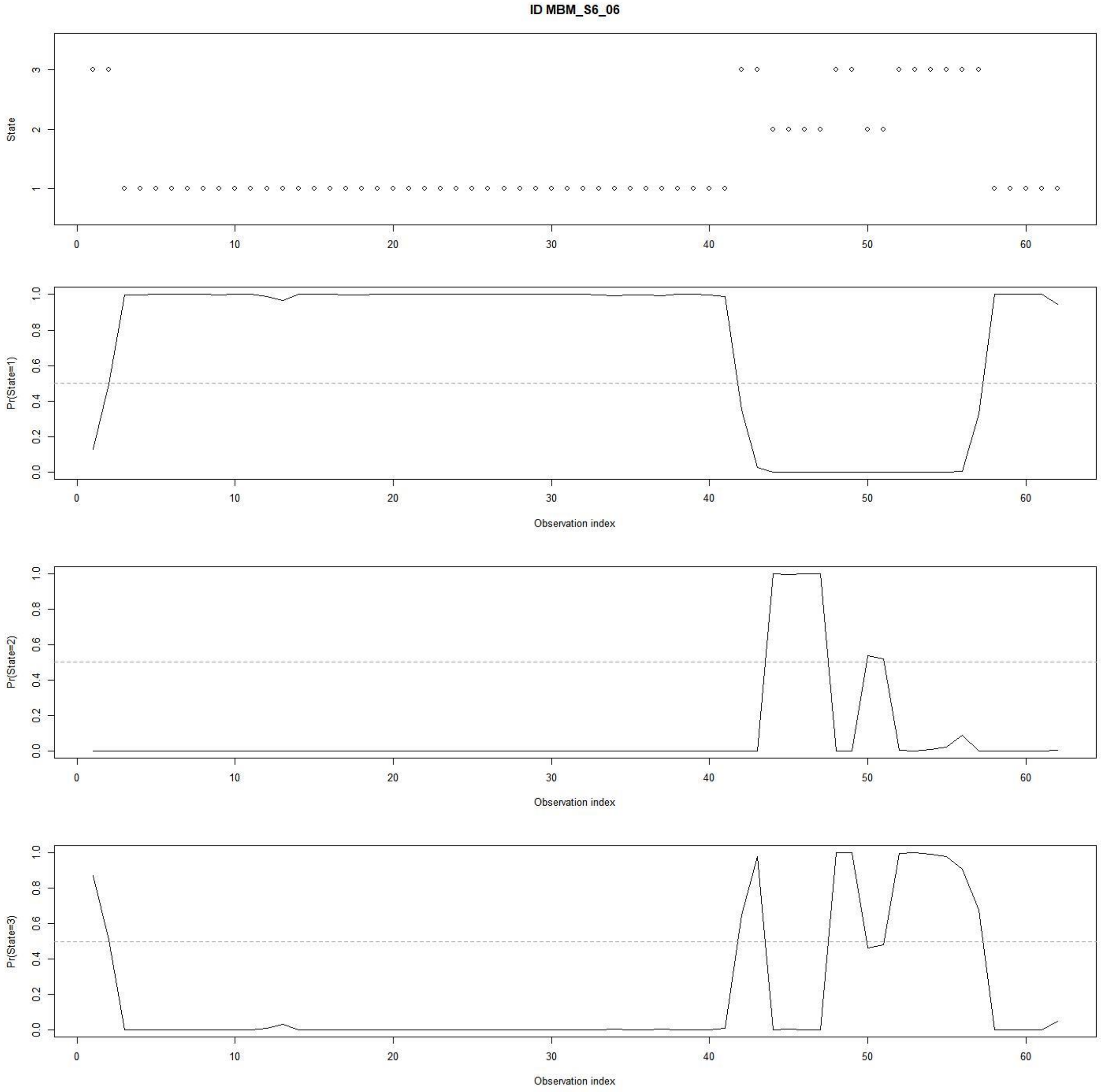


Figure II.5-4 – Graphics representing the probability of change between the states over the sequence of track positions (observation index) for the tag MB_S6_06, predicted by the selected HMM model. The top graph shows the predicted state of the positions and the graphs bellow show the respective probabilities of being in state 1, 2 or 3.

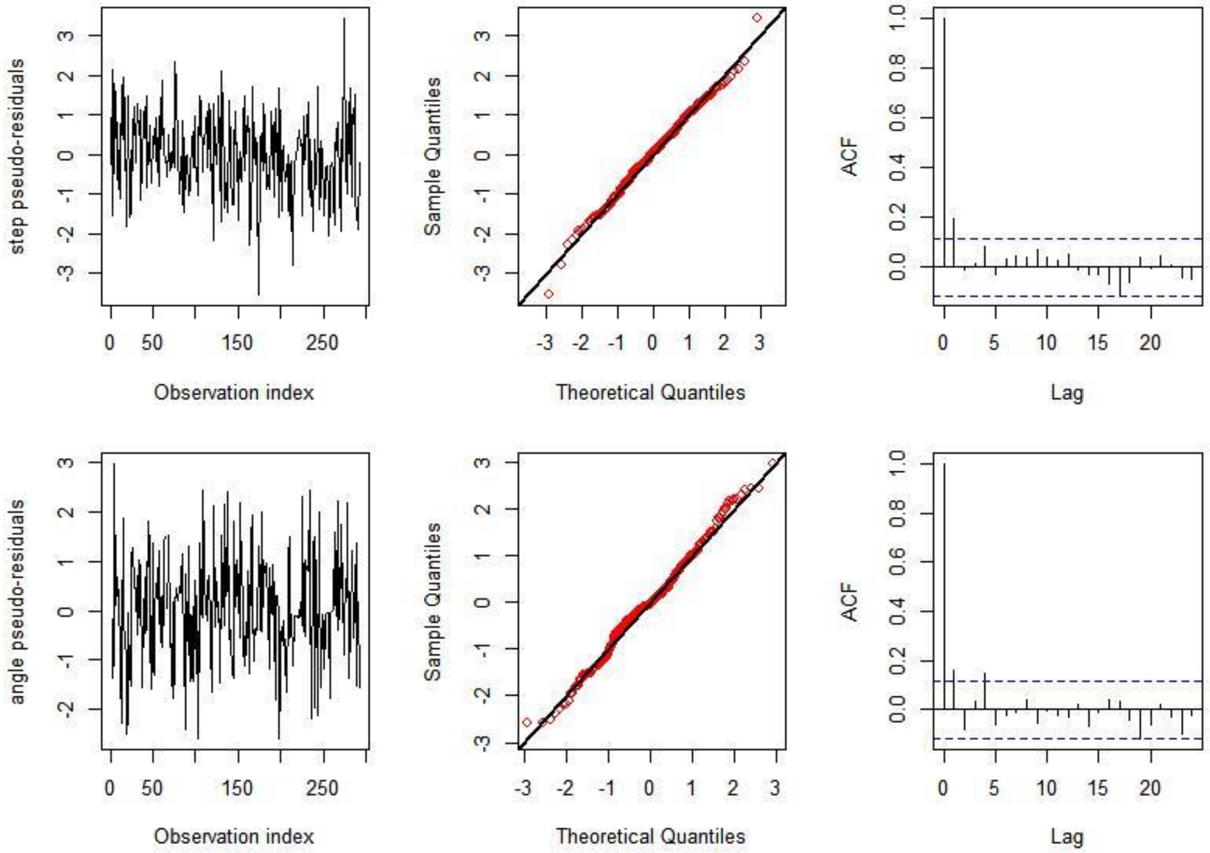


Figure II.5-5 – Diagnostic plots of step length and turning angle predicted by selected HMM model for the tracks of tags MB_S6_01, MB_S6_03 and MB_S6_06.

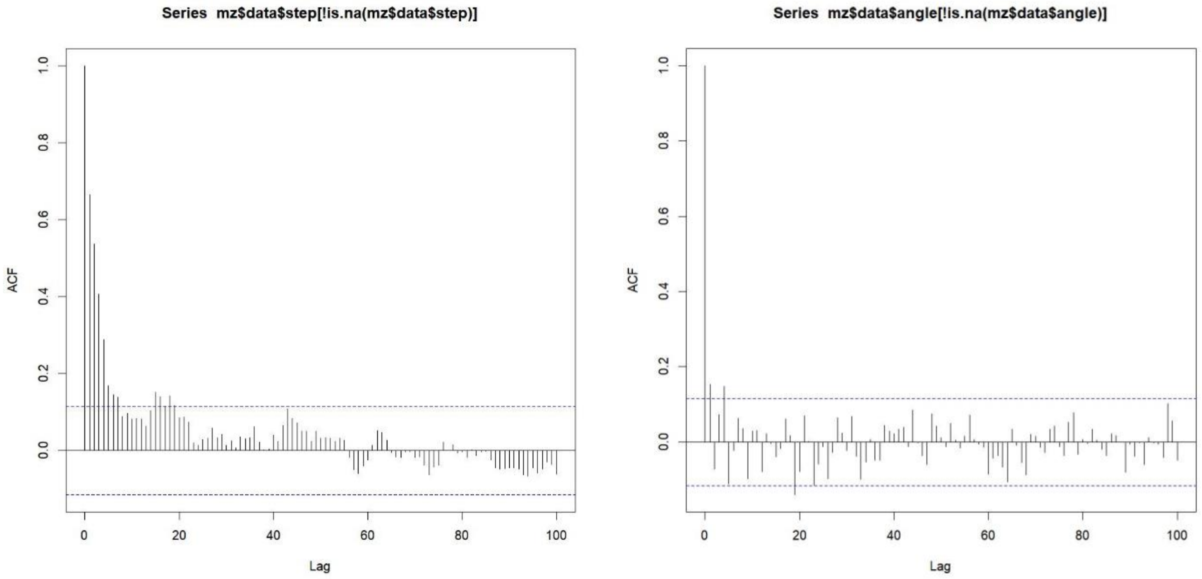


Figure II.5-6 – Auto correlation function (ACF) plots of step length (Left) and turning angle (Right) predicted by selected the HMM model for the tracks of tags MB_S6_01, MB_S6_03 and MB_S6_06.

II.6 Site fidelity indices

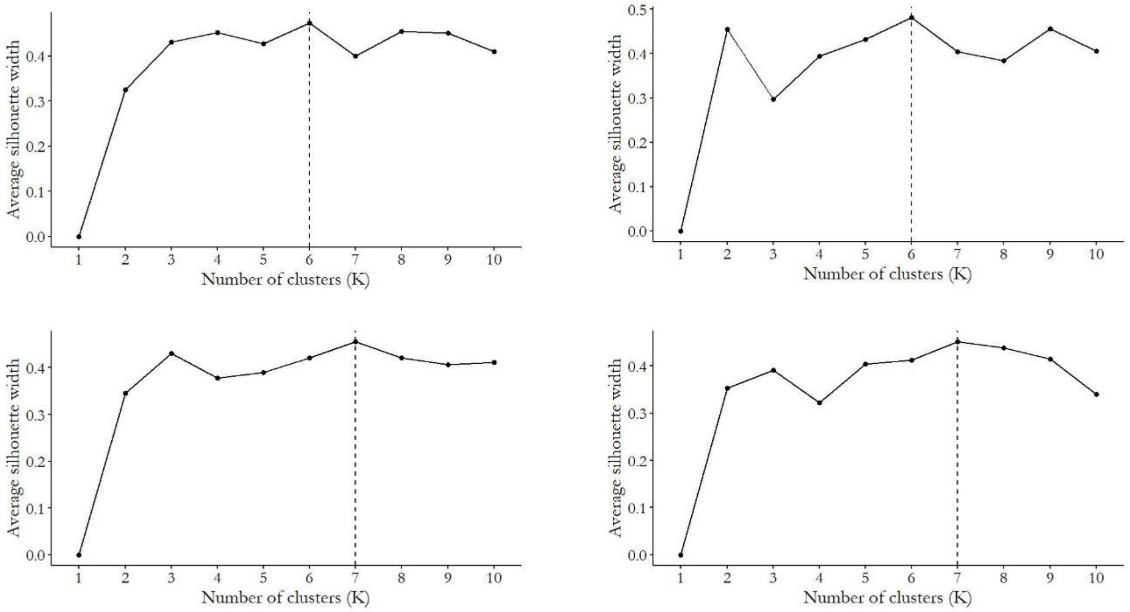


Figure II.6-1 – Results from the Silhouette method with the optimal number of clusters (indicated by the dash line), based on the K-means method, for each of the datasets of Bryde's whales using Madeira inshore waters. Top-left: well-marked and species confirmed Bryde's whales dataset (WM-SC); Top-right: well-marked Bryde's whales dataset, regardless of species cofirmation (WM-SN); bottom-left: all identified animals with species confirmed dataset (ALL-SC), including well marked and with distinctive shaped dorsal fins; bottom-right: all identified animals regardless of species confirmation dataset (ALL-SN), including well marked and with distinctive shaped dorsal fins.

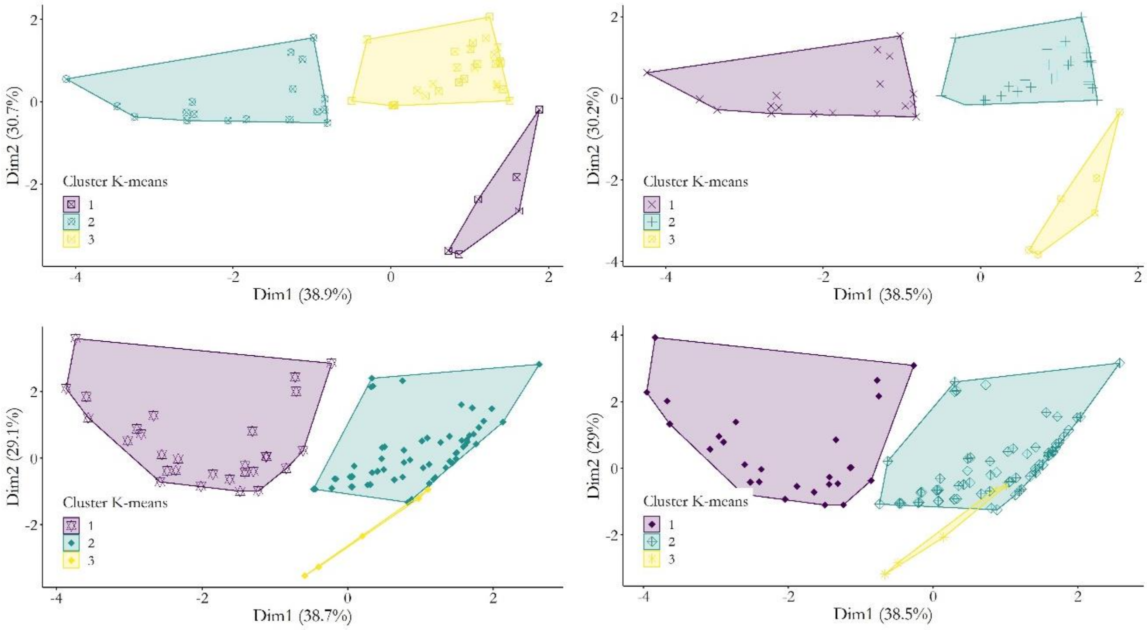


Figure II.6-2 – The graphs show the three clusters of each dataset represented on the two first dimensions of Principal Component Analysis based on six individual Site Fidelity Indices ("IA2","IA1","IA3","IH2","IH3" and "IH4"). Top-left: well-marked and species confirmed Bryde's whales dataset (WM-SC); Top-right: well-marked Bryde's whales dataset, regardless of species cofirmation (WM-SN); bottom-left: all identified animals with species confirmed dataset (ALL-SC), including well marked and with distinctive shaped dorsal fins; bottom-right: all identified animals regardless of species confirmation dataset (ALL-SN), including well marked and with distinctive shaped dorsal fins.

Table II.6-1 – The standard site fidelity index (SSFI) of the Bryde's whale population using Madeira inshore waters, calculated for each of the datasets (WM-SC, WM-SN, ALL-SC, ALL-SN) using the IH4 index (Tschopp et al., 2018). Datasets were obtained combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3; ALL).

Dataset	Cluster	n	SSFI	SD	95% CI
WM-SC	1	18	0.0064	0.0046	0.0000 - 0.0154
	2	29	0.0064	0.0044	0.0000 - 0.0151
	3	8	0.0024	0.0034	0.0000 - 0.0091
WM-SN	1	18	0.0064	0.0046	0.0000 - 0.0154
	2	32	0.0060	0.0044	0.0000 - 0.0147
	3	8	0.0024	0.0034	0.0000 - 0.0091
ALL-SC	1	29	0.0051	0.0042	0.0000 - 0.0133
	2	64	0.0073	0.0052	0.0000 - 0.0174
	3	8	0.0012	0.0013	0.0000 - 0.0036
ALL-SN	1	28	0.0051	0.0043	0.0000 - 0.0135
	2	70	0.0071	0.0051	0.0000 - 0.0171
	3	8	0.0012	0.0013	0.0000 - 0.0036

Table II.6-2 – The results of the comparison among clusters of the SFI values using Kruskal-Wallis tests for all datasets. Datasets were obtained combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3; ALL).

Dataset	SFI	χ^2	df	*p*
WM-SC	IA1	38.69	2	*<0.001*
	IA2	38.41	2	*<0.001*
	IA3	21.96	2	*<0.001*
	IH2	37.29	2	*<0.001*
	IH3	11.99	2	0.002
	IH4	8.21	1	0.016
WM-SN	IA1	39.87	2	*<0.001*
	IA2	39.51	2	*<0.001*
	IA3	23.03	2	*<0.001*
	IH2	38.70	2	*<0.001*
	IH3	12.75	2	0.002
	IH4	7.93	1	0.019
ALL-SC	IA1	70.10	2	*<0.001*
	IA2	68.04	2	*<0.001*
	IA3	21.96	2	*<0.001*
	IH2	55.98	2	*<0.001*
	IH3	7.75	2	0.020
	IH4	18.57	1	0.019
ALL-SN	IA1	70.54	2	<0.001
	IA2	68.16	2	<0.001
	IA3	22.72	2	<0.001
	IH2	56.53	2	<0.001
	IH3	7.39	2	0.020
	IH4	17.46	1	<0.001

Table II.6-3 – The results of the comparison between pairs of clusters of the SFI (IA1, IA2, IA3, IH2, IH3 and IH4) values for all datasets, using post-hoc Dunn tests and applying Benjamini-Hochberg correction. The results presented are only of SFI with pairs of clusters that were not significantly different. The remaining pairs of clusters were significantly or very significantly different (p <0.005 or p < 0.001, respectively). In the case of the IH2, all pairs of clusters in all datasets were significantly or very significantly different. Datasets were obtained combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3; ALL).

Dataset	SFI	Pairs	z	p
WM-SC	IA1	1-3	-0.445	0.656
	IA2	2-3	-1.950	0.057
	IA3	1-2	1.330	0.184
	IH3	1-2	-0.008	0.993
	IH4	1-2	0.038	0.969
WM-SN	IA1	1-3	-0.403	0.687
	IA3	1-2	-1.640	0.101
	IH3	1-2	-0.008	0.993
	IH4	1-2	-0.463	0.644
ALL-SC	IA1	1-3	0.895	0.371
	IA3	1-2	-0.275	0.783
	IH3	1-2	1.410	0.159
	IH3	2-3	-2.100	0.072
	IH4	1-2	1.920	0.055
ALL-SN	IA1	1-3	0.895	0.371
	IA3	1-2	0.538	0.590
	IH3	1-2	-1.010	0.313
	IH4	1-2	-1.680	0.094

Table II.6-4 – Results of a two-sample two-tail z-test for proportions comparing the proportion of females between pairs of clusters of the SFI, including transients. The values significant at *p*<0.05 are highlighted in bold.

	Cluster 1 (n=28)	Cluster 2 (n=70)	Cluster 3 (n=8)	Trans (n=119)
Cluster 1		**0.000**	0.12	**0.000**
Cluster 2			0.87	**0.028**
Cluster 3				**0.010**

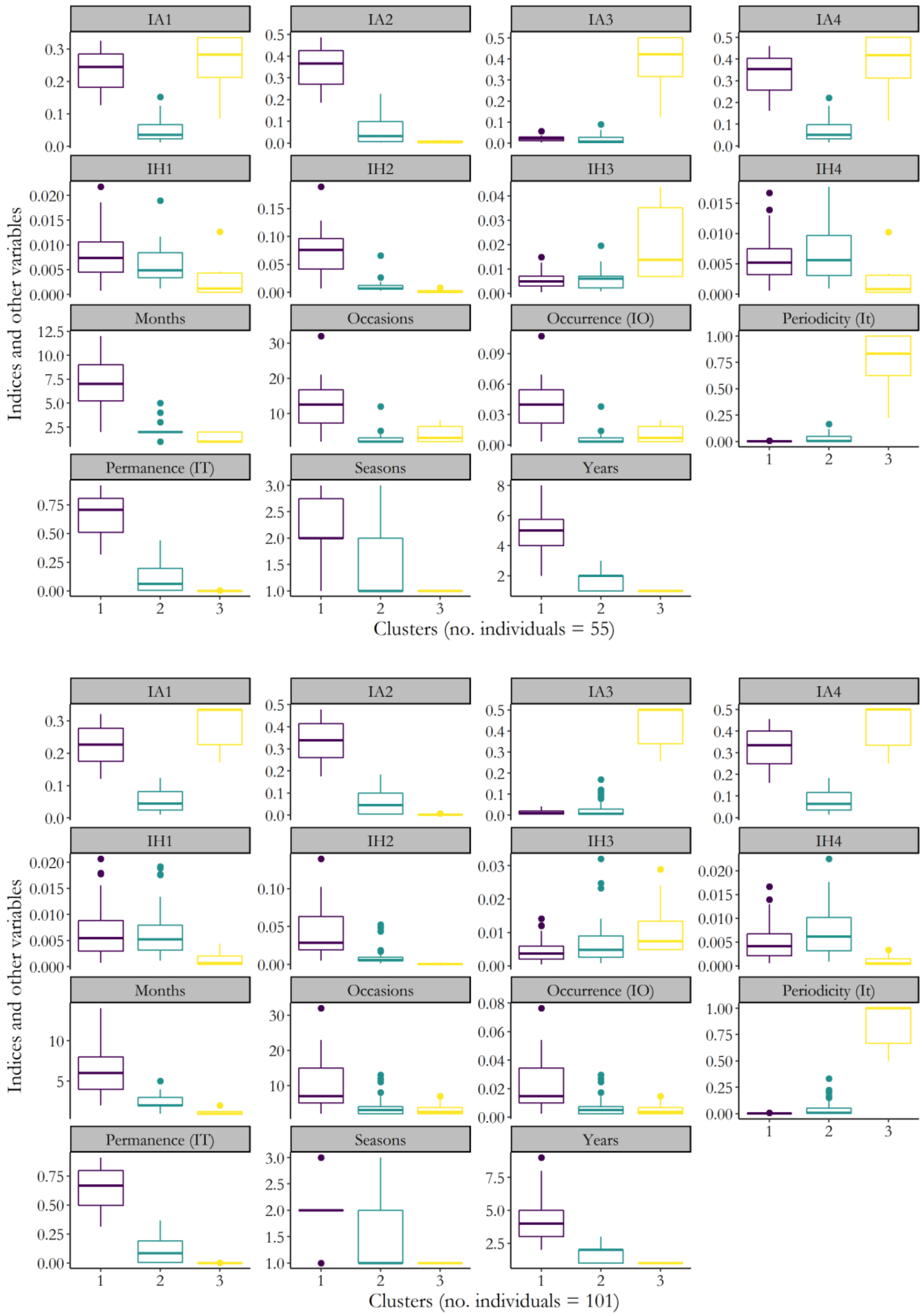


Figure II.6-3. Results of the parameters characterizing each site fidelity cluster, based on K-means, for Bryde's whales population using Madeira inshore waters. The top graphs were based on the WM-SC dataset (55 animals) and the bottom graphs on the ALL-SC dataset (101 animals). WM-SC – well-marked individuals (distinctiveness classes 1-3) confirmed as Bryde's whales; ALL-SC – all identified animals, including well-marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3) confirmed as Bryde's whales.

II.7. Cormack-Jolly-Seber (CJS) models

Table II.7-1 – Results of four components of the goodness-of-fit tests (GOF), the global combined test of overall CJS model fit and the variance inflation factor ($\hat{c}$), calculated as the $\chi2$/degrees of freedom. Datasets with matching uncertainty 3 (certain matches) for which survival estimates were obtained, combining: SC – animals confirmed as Bryde's whale; SN – animals suspected to be Bryde's whales but not confirmed; WM - animals well marked (distinctiveness classes 1-3); ALL: all identified animals, including well marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3).

Dataset	Global test	2.CT	3.SR	2.CL	3.SM	$\hat{c}$
WM-SC.3	$\chi^2 = 38.217$ df=50 p=0.888	χ^2=10.004 df=14 p=0.762	χ^2=20.466 df=12 p=0.059	χ^2=5.949 df=14 p=0.968	χ^2=1.798 df=10 p=0.998	0.764
WM-SN.3	$\chi^2 = 43.691$ df = 51 p = 0.756	$\chi^2 = 8.540$ df = 14 p = 0.859	$\chi^2 = 24.611$ df = 13 p = **0.026**	$\chi^2 = 8.444$ df = 14 p = 0.865	$\chi^2 = 2.096$ df = 10 p = 0.996	0.857
ALL-SC.3	$\chi^2 = 65.811$ df = 56 p = 0.174	$\chi^2 = 9.627$ df = 14 p = 0.789	$\chi^2 = 37.527$ df = 14 p = **0.001**	$\chi^2 = 16.719$ df = 15 p = 0.336	$\chi^2 = 1.938$ df = 13 p = 1.000	1.175
ALL-SN.3	$\chi^2 = 77.595$ df = 57 p = **0.036**	$\chi^2 = 8.417$ df = 14 p = 0.866	$\chi^2 = 48.939$ df = 14 p = **0.000**	$\chi^2 = 18.188$ df = 16 p = 0.313	$\chi^2 = 2.051$ df = 13 p = 1.000	1.361

Table II.7-2 – The best-supported candidate CJS models (≤10 ΔQAICc) for the period 2005-2021 for each of the datasets with matching uncertainty 3, with probability of apparent survival (ϕ) constant (.) or accounting for transience (*trans*) and probability of recapture changing over time (*t*).

Dataset	Model	QAICc	ΔQAICc	QAIC weight	Deviance	Number of parameters
WM-SC.3	$\varphi(trans)\ p(t)$	437.022	0.000	0.969	262.777	18
	$\varphi(.)\ p(t)$	443.890	6.868	0.031	272.211	17
WM-SN.3	$\varphi(trans)\ p(t)$	465.215	0*	1	263.888	18
ALL-SC.3	$\varphi(trans)\ p(t)$	632.387	0**	1	307.399	18
ALL-SN.3	$\varphi(trans)\ p(t)$	580.447	0	0.934	266.565	18
	$\varphi(trans)\ p(.)$	585.746	5.299	0.066	304.060	3

* - The next model had a ΔQAICc of 10.083

** - The next model had a ΔQAICc of 11.314

Table II.7-3 – Apparent survival estimates for the period 2005-2021 for each of the datasets with matching uncertainty 3 (certain matches), and the respective standard error and 95% confidence interval (95% CI). Datasets for which survival estimates were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3; ALL).

Dataset	Parameter	Estimate	Standard error	95% CI
WM-SC.3	non-transients	0.981	0.017	0.900 - 0.997
	transients	0.686	0.105	0.457 - 0.851
WM-SN.3	non-transients	0.984	0.016	0.897 - 0.998
	transients	0.596	0.086	0.423 - 0.748
ALL-SC.3	non-transients	0.993	0.015	0.605 - 1.000
	transients	0.575	0.072	0.431 - 0.707
ALL-SN.3	non-transients	0.996	0.017	0.043 - 1.000
	transients	0.502	0.072	0.364 - 0.639

Table II.7-4 – Results of four components of the goodness-of-fit tests (GOF), the global combined test of overall CJS model fit and the variance inflation factor (ĉ), calculated as the $\chi 2$/degrees of freedom, for clusters of animals with different site fidelity patterns (Regular and Occasional). Datasets with matching uncertain 2-3 (likely and certain matches) for which survival estimates were obtained, combining: SC – animals confirmed as Bryde's whale; SN – animals suspected to be Bryde's whales but not confirmed; WM - animals well marked (distinctiveness classes 1-3); ALL: all identified animals, including well marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3).

Dataset	Site Fidelity	Global test	2.CT	3.SR	2.CL	3.SM	ĉ
WM-SC	Regular	χ^2 = 15.131 df= 33 p= 0.997	χ^2= 6.645 df= 14 p= 0.948	χ^2= 0 df= 1 p= 1	χ^2= 7.778 df= 12 p= 0.802	χ^2= 0.708 df= 6 p= 0.994	0.459
	Occasional	χ^2= 2.986 df= 16 p= 1	χ^2= 0.406 df= 4 p= 0.982	χ^2= 2.580 df= 5 p= 0.764	χ^2= 0 df= 6 p= 1	χ^2= 0 df= 1 p= 1	0.187
WM-SN	Regular	χ^2 = 15.131 df= 33 p= 0.997	χ^2= 6.645 df= 14 p= 0.948	χ^2= 0 df= 1 p= 1	χ^2= 7.778 df= 12 p= 0.802	χ^2= 0.708 df= 6 p= 0.994	0.459
	Occasional	χ^2 =3.11 df= 16 p= 1	χ^2= 0 f= 4 p= 1	χ^2= 2.580 df= 5 p= 0.764	χ^2= 0.530 df= 6 p= 0.997	χ^2= 0 df= 1 p= 1	0.194
ALL-SC	Regular	χ^2 = 25.665 df= 35 p= 0.875	χ^2= 7.908 f= 14 p= 0.894	χ^2= 0 df= 2 p= 1	χ^2= 12.089 df= 13 p= 0.520	χ^2= 5.668 df= 6 p= 0.461	0.733
	Occasional	χ^2 = 14.074 df= 27 p= 0.981	χ^2= 6.074 f= 9 p= 0.732	χ^2= 6.448 df= 8 p= 0.597	χ^2= 0.486 df= 7 p= 0.999	χ^2= 1.06 df= 3 p= 0.785	0.521
ALL-SN	Regular	χ^2 = 25.695 df= 35 p= 0.874	χ^2= 7.877 f= 14 p= 0.896	χ^2= 0 df= 2 p= 1	χ^2= 12.527 df= 13 p= 0.485	χ^2= 5.291 df= 6 p= 0.507	0.734
	Occasional	χ^2 = 15.347 df= 29 p= 0.982	χ^2= 3.940 f= 9 p= 0.915	χ^2= 8.833 df= 8 p= 0.357	χ^2= 1.391 df= 9 p= 0.998	χ^2= 1.183 df= 3 p= 0.757	0.529

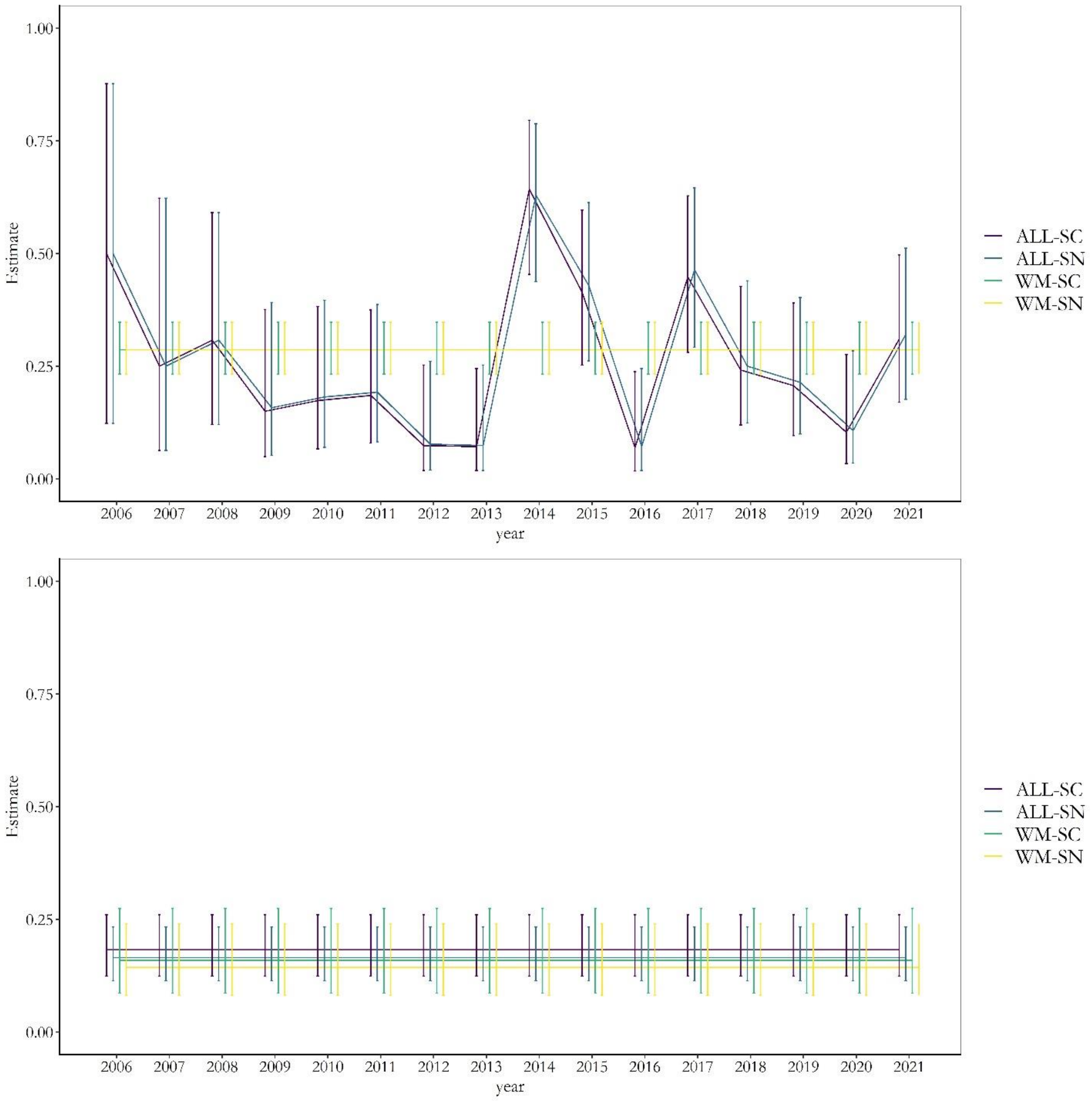


Figure II.7-1. Yearly recapture probability estimates of non-calf Bryde's whales classified as regular visitors – cluster 1 (top) and occasional visitors – cluster 2 (bottom), for the period 2005-2021 for each of the datasets with matching uncertainty 2-3 (likely and certain matches), and the respective 95% confidence intervals. Datasets were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3; ALL).

II.8. Robust Design

Table II.8-1 – Table showing the structure of the data used in the RD analysis of the datasets with matching uncertainty 3 (certain): top - number of captures for datasets of well-marked individuals (WM-SC.3, WM-SN.3) for each secondary occasion within primary occasion (year); bottom - number of captures for datasets of all individuals (ALL-SC.3, ALL-SN.3) for each secondary occasion within primary occasion (year). In each cell, the digit on the left corresponds to the number of captures in the datasets SC (WM or ALL) and the digit on the right to the number of captures in the datasets SN (WM or ALL), for a particular secondary occasion. The tables also show the number and length of secondary occasions for each primary sampling occasion. SC – animals confirmed as Bryde's whale; SN – animals suspected to be Bryde's whales but not confirmed; WM - well-marked animals (distinctiveness classes 1-3); ALL – all identified animals, including well marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3).

Primary occasion (Year)	**Secondary occasion length**	**Number of secondary occasions by primary occasion**					
		1	**2**	**3**	**4**	**5**	**6**
2006	month	1, 1	2, 2	3, 3	1, 1		
2007	month	4, 4	1, 2				
2008	bimonth	7, 7	5, 5				
2009	bimonth	1, 1	3, 3				
2010	bimonth	6, 6	1, 2	1, 1			
2011	bimonth	2, 3	2, 2				
2012	month	5, 5	1, 1				
2013	-	-	-	-	-	-	-
2014	month	4, 5	14, 16	17, 18	9, 10	5, 5	3, 3
2015	month	1, 1	10, 10	7, 8	2, 2		
2016	-	-	-	-	-	-	-
2017	month	1, 1	2, 4	11, 11	10, 10	4, 4	
2018	month	9, 9	2, 2	3, 3	2, 2	1, 2	
2019	month	8, 8	1, 1	6, 7	6, 6	1, 1	
2020	month	2, 2	2, 2	4, 4	2, 2		
2021	month	3, 3	6, 8	5, 5	2, 2		

Primary occasion (Year)	**Secondary occasion length**	**Number of secondary occasions by primary occasion**					
		1	**2**	**3**	**4**	**5**	**6**
2006	month	1, 1	3, 3	3, 3	2, 2		
2007	bimonth	6, 6	3, 4				
2008	bimonth	8, 8	9, 9				
2009	bimonth	2, 2	4, 4				
2010	trimester	7, 7	2, 3	1, 1			
2011	bimonth	3, 4	4, 4				
2012	bimonth	8, 8	1, 1	0, 1			
2013	-	-	-	-	-	-	-
2014	month	6, 7	20, 24	26, 32	17, 20	10, 10	6, 6
2015	month	1, 1	16, 18	18, 21	3, 3	1, 1	1, 1
2016	-	-	-	-	-	-	-
2017	month	2, 2	5, 7	22, 22	32, 36	17, 18	
2018	month	15, 15	3, 3	4, 5	3, 3	3, 4	
2019	month	16, 16	3, 3	10, 12	7, 8	1, 1	
2020	month	2, 2	4, 4	6, 6	3, 3		
2021	month	12, 15	14, 16	1, 1			

Table II.8-2 – The best-supported candidate RD models (ΔAICc ≤10) for the study period (2006-2012, 2014-2015, 2017-2021) and study area (Madeira inshore waters), for each of the datasets with matching uncertainty 3. The models included the probability of survival (*S*) as constant (.) or accounting for transience (*trans*), with no temporary emigration ($\gamma''(.)=\gamma'(.)=0$) and probability of capture/recapture changing by primary sampling occasion (*s*) or by primary and secondary sampling occasion (*s:t*), The probability of capture and recapture were assumed to be equal in all models (p(s)=c(s)). Datasets for which abundance was estimated, combined animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well-marked and with distinctive shaped dorsal fins (ALL).

Dataset	Model	AICc	ΔAICc	AIC weight	Deviance	Number of parameters
WM-SC.3	$S(trans)\ \gamma''(.)=\gamma'(.)=0\ \ p(s)=c(s)$	623.361	0.000	0.988	440.774	30
	$S(.)\ \gamma''(.)=\gamma'(.)=0\ \ p(s)=c(s)$	632.259	8.898	0.012	452.392	29
WM-SN.3	$S(trans)\ \gamma''(.)=\gamma'(.)=0\ \ p(s)=c(s)$	622.253	0.000	1.000	393.805	30
ALL-SC.3	$S(trans)\ \gamma''(.)=\gamma'(.)=0\ \ p(s{:}t)=c(s{:}t)$	531.683	0.000	1.000	231.316	67
ALL-SN.3	$S(trans)\ \gamma''(.)=\gamma'(.)=0\ \ p(s{:}t)=c(s{:}t)$	419.568	0.000	1.000	94.038	68

Table II.8-3 – Robust Design analysis estimates of abundance corrected for the proportion of unmarked animals and the respective standard error, 95% confidence intervals and coefficient of variation (CV), for datasets of well-marked animals (WM) with likely and certain matches (matching uncertainty level 2 – 3), for both animals confirmed as Bryde's whales (WM-SC) and confirmed or suspected to be Bryde's whales (WM-SN).

Dataset	Year	Estimate	Standard error	95% CI	CV
WM-SC	2006	18	12	8 - 41	69%
	2007	33	13	20 - 54	40%
	2008	27	9	17 - 41	34%
	2009	30	18	15 - 62	61%
	2010	36	14	22 - 59	39%
	2011	26	16	13 - 54	59%
	2012	44	26	22 - 90	59%
	2013	-	-	-	-
	2014	50	9	40 - 63	17%
	2015	65	15	48 - 88	24%
	2016	-	-	-	-
	2017	163	32	126 - 209	20%
	2018	131	39	90 - 191	30%
	2019	128	32	94 - 176	25%
	2020	117	53	67 - 205	45%
	2021	110	37	72 - 167	33%
WM-SN	2006	18	12	8 - 41	69%
	2007	35	14	21 - 57	39%
	2008	27	9	18 - 41	34%
	2009	30	18	15 - 62	61%
	2010	40	16	25 - 65	38%
	2011	32	18	17 - 63	55%
	2012	54	31	27 - 109	58%
	2013	-	-	-	-
	2014	65	10	53 - 80	16%
	2015	79	18	60 - 106	22%
	2016	-	-	-	-
	2017	184	36	144 - 236	19%
	2018	154	45	107 - 223	29%
	2019	139	34	103 - 189	24%
	2020	125	57	71 - 218	46%
	2021	125	39	85 - 186	31%

Table II.8-4 – Robust Design analysis estimates of abundance corrected for the proportion of unmarked animals and the respective standard error, 95% confidence intervals and coefficient of variation (CV), for datasets of well-marked animals and animals with distinctive dorsal fin shapes (ALL), with likely and certain matches (matching uncertainty level 2 – 3), for both animals confirmed as Bryde's whales (ALL-SC) and confirmed or suspected to be Bryde's whales (ALL-SN).

Dataset	Year	Estimate	Standard error	95% CI	CV
ALL-SC	2006	25	20	10 - 63	80%
	2007	34	15	19 - 59	46%
	2008	42	13	29 - 62	31%
	2009	42	28	19 - 92	66%
	2010	36	15	21 - 60	42%
	2011	39	21	20 - 75	54%
	2012	84	53	39 - 177	63%
	2013	-	-	-	-
	2014	82	9	71 - 93	10%
	2015	73	14	57 - 93	19%
	2016	-	-	-	-
	2017	118	17	98 - 143	15%
	2018	131	34	95 - 183	26%
	2019	185	44	137 - 251	24%
	2020	167	65	103 - 271	39%
	2021	173	53	117 - 255	31%
ALL-SN	2006	25	20	10 - 63	80%
	2007	36	16	20 - 62	45%
	2008	42	13	29 - 62	31%
	2009	42	28	19 - 92	66%
	2010	40	17	24 - 68	41%
	2011	45	24	24 - 86	52%
	2012	97	61	46 - 203	63%
	2013	-	-	-	-
	2014	106	11	93 - 120	10%
	2015	93	17	73 - 118	19%
	2016	-	-	-	-
	2017	145	21	121 - 175	15%
	2018	155	40	111 - 215	26%
	2019	210	49	156 - 283	23%
	2020	182	71	112 - 296	39%
	2021	213	63	147 - 310	29%

Table II.8-5 – Robust Design analysis estimates of abundance corrected for the proportion of unmarked animals and the respective standard error, 95% confidence intervals and coefficient of variation (CV), for datasets of well-marked animals (WM) with likely and certain matches (matching uncertainty level 3), for both animals confirmed as Bryde's whales (WM-SC.3) and confirmed or suspected to be Bryde's whales (WM-SN.3).

Dataset	Year	Estimate	Standard error	95% CI	CV
WM-SC.3	2006	17	12	7 - 39	72%
	2007	58	22	36 - 92	38%
	2008	22	8	14 - 35	35%
	2009	17	11	9 - 38	69%
	2010	25	12	14 - 44	47%
	2011	21	13	10 - 43	61%
	2012	44	24	22 - 85	55%
	2013	-	-	-	-
	2014	46	8	36 - 57	18%
	2015	98	21	75 - 129	21%
	2016	-	-	-	-
	2017	153	30	119 - 197	20%
	2018	105	33	71 - 156	31%
	2019	115	30	83 - 160	26%
	2020	146	67	83 - 256	46%
	2021	98	33	64 - 150	34%
WM-SN.3	2006	19	12	8 - 41	67%
	2007	39	18	22 - 69	46%
	2008	29	11	19 - 46	36%
	2009	21	11	11 - 39	53%
	2010	52	25	29 - 93	48%
	2011	35	20	18 - 69	57%
	2012	47	42	17 - 126	89%
	2013	-	-	-	-
	2014	56	9	46 - 69	16%
	2015	73	18	54 - 99	24%
	2016	-	-	-	-
	2017	169	33	132 - 217	20%
	2018	126	37	86 - 183	30%
	2019	125	31	91 - 170	24%
	2020	138	65	78 - 246	47%
	2021	110	34	74 - 163	31%

Table II.8-6 – Robust Design analysis estimates of abundance corrected for the proportion of unmarked animals and the respective standard error, 95% confidence intervals and coefficient of variation (CV), for datasets of well-marked animals and animals with distinctive dorsal fin shapes (ALL), with certain matches (matching uncertainty level 3), for both animals confirmed as Bryde's whales (ALL-SC.3) and confirmed or suspected to be Bryde's whales (ALL-SN.3).

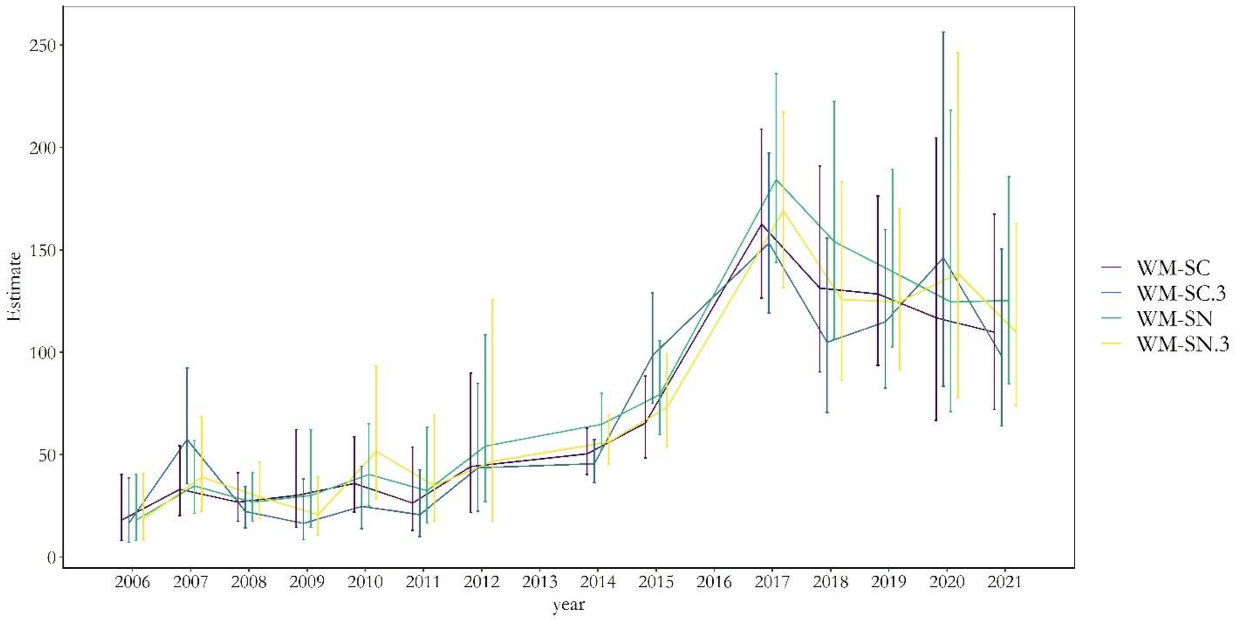
Dataset	Year	Estimate	Standard error	95% CI	CV
ALL.SC.3	2006	23	20	9 - 60	84%
	2007	38	27	17 - 86	69%
	2008	32	10	21 - 48	33%
	2009	34	22	16 - 73	65%
	2010	28	13	16 - 49	47%
	2011	33	18	17 - 63	53%
	2012	68	43	32 - 143	63%
	2013	-	-	-	-
	2014	69	8	60 - 80	11%
	2015	65	13	51 - 84	20%
	2016	-	-	-	-
	2017	106	16	87 - 128	15%
	2018	115	33	80 - 166	29%
	2019	157	41	113 - 219	26%
	2020	143	60	85 - 240	42%
	2021	154	49	104 - 230	32%
ALL-SN.3	2006	23	20	9 - 60	84%
	2007	45	31	20 - 100	69%
	2008	35	11	23 - 53	32%
	2009	34	22	16 - 73	65%
	2010	36	16	21 - 62	44%
	2011	39	20	21 - 72	52%
	2012	79	49	38 - 166	62%
	2013	-	-	-	-
	2014	93	10	81 - 106	11%
	2015	82	16	64 - 106	20%
	2016	-	-	-	-
	2017	130	20	107 - 158	15%
	2018	134	39	93 - 192	29%
	2019	173	44	125 - 239	26%
	2020	154	64	92 - 258	42%
	2021	184	55	126 - 269	30%

Table II.8-7 – Proportion of marked animals and respective standard error (SE) and coefficient of variation (CV), for datasets of well-marked animals (WM) and datasets of well-marked animals and animals with distinctive dorsal fin shapes (ALL), with likely and certain matches (matching uncertainty level 2 – 3), for both animals confirmed as Bryde's whales (WM-SC and ALL-SC) and confirmed or suspected to be Bryde's whales (WM-SN and ALL-SN), used in the RD analysis. These proportions were used to correct the RD abundance estimates for Madeira.

dataset	Year	Proportion	SE(P)	CV(P)	dataset	Year	Proportion	SE(P)	CV(P)
WM-SC	2006	0.7692	0.1169	0.1519	WM-SN	2006	0.7692	0.1169	0.1519
	2007	0.4667	0.1288	0.2760		2007	0.5294	0.1211	0.2287
	2008	0.5806	0.0886	0.1526		2008	0.5806	0.0886	0.1526
	2009	0.6364	0.1450	0.2279		2009	0.6364	0.1450	0.2279
	2010	0.6500	0.1067	0.1641		2010	0.6667	0.1029	0.1543
	2011	0.6667	0.1571	0.2357		2011	0.7000	0.1449	0.2070
	2012	0.8125	0.0976	0.1201		2012	0.8235	0.0925	0.1123
	2014	0.6130	0.0301	0.0492		2014	0.5978	0.0295	0.0494
	2015	0.4783	0.0521	0.1089		2015	0.4694	0.0504	0.1074
	2017	0.3205	0.0374	0.1166		2017	0.3450	0.0364	0.1054
	2018	0.5652	0.0731	0.1293		2018	0.5625	0.0716	0.1273
	2019	0.5091	0.0674	0.1324		2019	0.5000	0.0657	0.1313
	2020	0.6429	0.0906	0.1409		2020	0.6429	0.0906	0.1409
	2021	0.6195	0.0457	0.0737		2021	0.6102	0.0449	0.0736
ALL-SC	2006	0.9231	0.0739	0.0801	ALL-SN	2006	0.9231	0.0739	0.0801
	2007	0.8000	0.1033	0.1291		2007	0.8235	0.0925	0.1123
	2008	0.8065	0.0710	0.0880		2008	0.8065	0.0710	0.0880
	2009	1.0000	0.0000	0.0000		2009	1.0000	0.0000	0.0000
	2010	0.9000	0.0671	0.0745		2010	0.9048	0.0641	0.0708
	2011	1.0000	0.0000	0.0000		2011	1.0000	0.0000	0.0000
	2012	1.0000	0.0000	0.0000		2012	1.0000	0.0000	0.0000
	2014	0.8927	0.0192	0.0215		2014	0.8986	0.0182	0.0202
	2015	0.9457	0.0236	0.0250		2015	0.9490	0.0222	0.0234
	2017	0.9167	0.0221	0.0241		2017	0.9240	0.0203	0.0219
	2018	0.9565	0.0301	0.0314		2018	0.9583	0.0288	0.0301
	2019	0.8727	0.0449	0.0515		2019	0.8793	0.0428	0.0486
	2020	0.8214	0.0724	0.0881		2020	0.8214	0.0724	0.0881
	2021	0.9646	0.0174	0.0180		2021	0.9661	0.0167	0.0172

Table II.8-8 – Proportion of marked animals and respective standard error (SE) and coefficient of variation (CV), for datasets of well-marked animals (WM) and datasets of well-marked animals and animals with distinctive dorsal fin shapes (ALL), with certain matches (matching uncertainty level 3), for both animals confirmed as Bryde's whales (WM-SC and ALL-SC) and confirmed or suspected to be Bryde's whales (WM-SN and ALL-SN), used in the RD analysis. These proportions were used to correct the RD abundance estimates for Madeira.

dataset	Year	Proportion	SE(P)	CV(P)	dataset	Year	Proportion	SE(P)	CV(P)
WM-SC.C3	2006	0.8333	0.1521	0.1826	WM-SN.C3	2006	0.7500	0.1250	0.1667
	2007	0.2500	0.2165	0.8660		2007	0.4615	0.1383	0.2996
	2008	0.6667	0.1361	0.2041		2008	0.6071	0.0923	0.1520
	2009	0.0000	0.0003	624.1935		2009	0.6250	0.1712	0.2739
	2010	0.8571	0.1323	0.1543		2010	0.6667	0.1111	0.1667
	2011	0.7500	0.2165	0.2887		2011	0.7778	0.1386	0.1782
	2012	0.7273	0.1343	0.1846		2012	0.8235	0.0925	0.1123
	2014	0.6036	0.0464	0.0769		2014	0.6229	0.0315	0.0507
	2015	0.3077	0.0905	0.2942		2015	0.4756	0.0552	0.1160
	2017	0.3307	0.0417	0.1262		2017	0.3580	0.0377	0.1052
	2018	0.6471	0.0820	0.1267		2018	0.6047	0.0746	0.1233
	2019	0.5625	0.0716	0.1273		2019	0.5273	0.0673	0.1277
	2020	0.5909	0.1048	0.1774		2020	0.6296	0.0929	0.1476
	2021	0.6477	0.0509	0.0786		2021	0.6182	0.0463	0.0749
ALL-SC.C3	2006	1.0000	0.0000	0.0000	ALL-SN.C3	2006	1.0000	0.0000	0.0000
	2007	1.0000	0.0000	0.0000		2007	1.0000	0.0000	0.0000
	2008	0.9091	0.0867	0.0953		2008	0.8148	0.0748	0.0917
	2009	1.0000	0.0000	0.0000		2009	1.0000	0.0000	0.0000
	2010	1.0000	0.0000	0.0000		2010	0.8889	0.0741	0.0833
	2011	1.0000	0.0000	0.0000		2011	1.0000	0.0000	0.0000
	2012	1.0000	0.0000	0.0000		2012	1.0000	0.0000	0.0000
	2014	0.8972	0.0294	0.0327		2014	0.9123	0.0187	0.0205
	2015	0.9600	0.0392	0.0408		2015	0.9747	0.0177	0.0181
	2017	0.9748	0.0144	0.0147		2017	0.9739	0.0129	0.0132
	2018	1.0000	0.0000	0.0000		2018	1.0000	0.0000	0.0000
	2019	0.9545	0.0314	0.0329		2019	0.9600	0.0277	0.0289
	2020	0.9000	0.0671	0.0745		2020	0.8800	0.0650	0.0739
	2021	0.9767	0.0163	0.0166		2021	0.9815	0.0130	0.0132



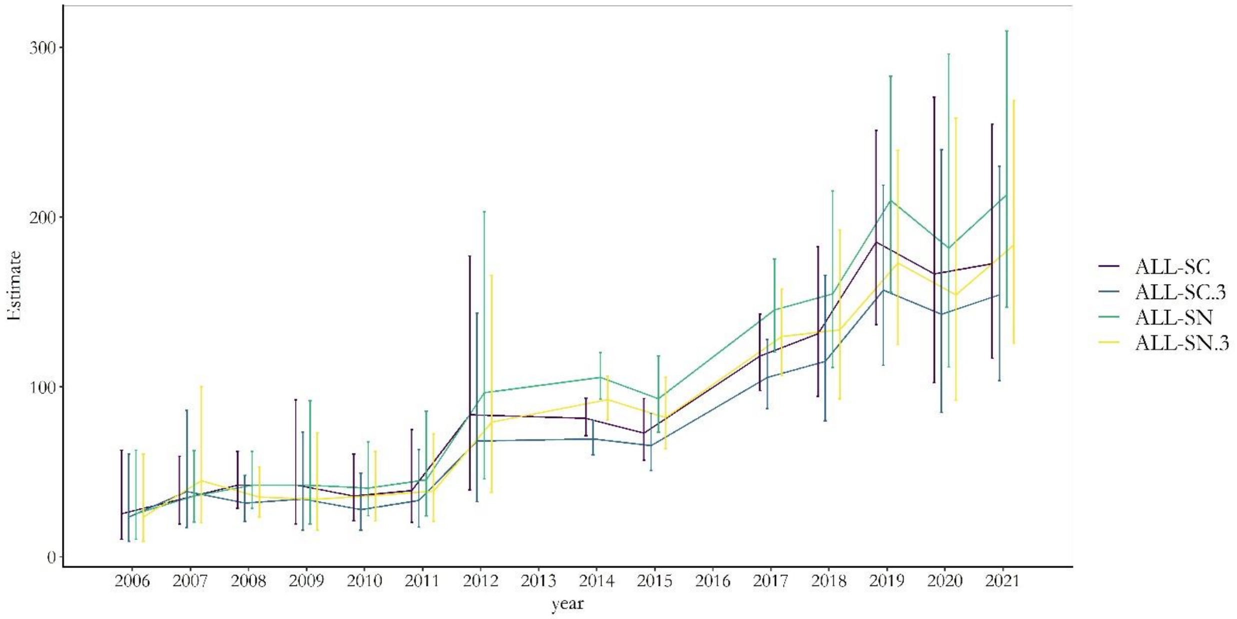


Figure II.8-1. Robust Design yearly abundance estimates for Madeira inshore waters for the study period (2006-2012, 2014-2015, 2017-2021), corrected for the proportion of unmarked animals. Top: well-marked individuals (distinctiveness classes 1-3) confirmed as Bryde's whales (SC) or suspected to be Bryde's whales (SN), with matching uncertainty 2-3 (WM-SC and WM-SN) or with matching uncertainty 3 (WM-SC.3 and WM-SN.3). Bottom: all identified individuals, including well-marked individuals and individuals with distinctive shape dorsal fins (distinctiveness classes 0-3), confirmed as Bryde's whales (SC) or suspected to be Bryde's whales (SN), with matching uncertainty 2-3 (ALL-SC and ALL-SN) or with matching uncertainty 3 (ALL-SC.3 and ALL-SN.3).

II.9. POPAN

Table II.9-1 – Results of four the components of the goodness-of-fit tests (GOF), the global combined test of overall CJS model fit and the variance inflation factor (ĉ), calculated as the χ^2/degrees of freedom, applied to the "Madeira" datasets with matching uncertainty 3 used in the POPAN analysis (2006 – 2021). Datasets for which survival estimates were obtained, combining: SC – animals confirmed as Bryde's whale; SN – animals suspected to be Bryde's whales but not confirmed; WM - animals well marked (distinctiveness classes 1-3); ALL: all identified animals, including well marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3).

Dataset	Global test	2.CT	3.SR	2.CL	3.SM	ĉ
WM-SC.3	$\chi^2 = 33.552$ df=46 p=0.867	χ^2=+.659 df=13 p=0.722	χ^2=17.982 df=11 p=0.082	χ^2=5.839 df=13 p=0.952	χ^2=2.072 df=9 p=0.990	0.773
WM-SN.3	$\chi^2 = 40.631$ df = 47 p = 0.732	$\chi^2 = 8.195$ df = 13 p = 0.831	$\chi^2 = 22.290$ df = 12 p = **0.034**	$\chi^2 = 8.334$ df = 13 p = 0.821	$\chi^2 = 1.812$ df = 9 p = 0.994	0.864
ALL-SC.3	$\chi^2 = 69.730$ df = 52 p = 0.051	$\chi^2 = 10.004$ df = 13 p = 0.694	$\chi^2 = 40.287$ df = 13 **p = 0.000**	$\chi^2 = 17.286$ df = 14 p = 0.241	2.153 df = 12 p = 0.999	1.341
ALL-SN.3	$\chi^2 = 81.049$ df = 53 p = **0.008**	$\chi^2 = 8.794$ df = 13 p = 0.788	$\chi^2 = 51.582$ df = 13 p = **0.000**	$\chi^2 = 18.755$ df = 15 p = 0.225	$\chi^2 = 1.918$ df = 12 p = 1.000	1.529

Table II.9-2 – Results of four the components of the goodness-of-fit tests (GOF), the global combined test of overall CJS model fit and the variance inflation factor (ĉ), calculated as the χ^2/degrees of freedom, applied to the "Madeira – Canary Islands" datasets with matching uncertainty 3 used in the POPAN analysis (2006 – 2021). Datasets for which survival estimates were obtained, combining: SC – animals confirmed as Bryde's whale; SN – animals suspected to be Bryde's whales but not confirmed; WM - animals well marked (distinctiveness classes 1-3); ALL: all identified animals, including well marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3).

Dataset	Global test	2.CT	3.SR	2.CL	3.SM	ĉ
WM-SC.3	$\chi^2 = 43.402$ df = 46 p= 0.582	$\chi^2 = 12.583$ df = 13 p = 0.481	$\chi^2 = 14.299$ df = 10 p = 0.160	$\chi^2 = 11.188$ df = 13 p = 0.595	$\chi^2 = 5.332$ df = 10 p = 0.868	0.944
WM-SN.3	$\chi^2 = 54.938$ df = 46 p = 0.172	$\chi^2 = 14.462$ df = 13 p = 0.342	$\chi^2 = 17.760$ df = 11 p = 0.087	$\chi^2 = 16.102$ df = 12 p = 0.187	$\chi^2 = 6.614$ df = 10 p = 0.761	1.194
ALL-SC.3	$\chi^2 = 64.416$ df = 55 p = 0.180	$\chi^2 = 10.592$ df = 13 p = 0.645	$\chi^2 = 21.134$ df = 13 p = 0.070	$\chi^2 = 19.978$ df = 15 p = 0.173	$\chi^2 = 12.712$ df = 14 p = 0.549	1.171
ALL-SN.3	$\chi^2 = 82.434$ df = 54 **p = 0.008**	$\chi^2 = 11.105$ df = 13 p = 0.602	$\chi^2 = 33.861$ df = 13 **p = 0.001**	$\chi^2 = 21.215$ df = 14 p = 0.096	$\chi^2 = 16.253$ df = 14 p = 0.298	1.527

Table II.9-3 – The best-supported candidate POPAN models (≤10 ΔQAICc) for the period 2006-2021 for each "Madeira" dataset with matching uncertainty 3, with probability of apparent survival (ϕ) constant (.) or accounting for transience (*trans*), probability of recapture changing over time (t) and probability of recruitment from the super-population into the study area (pent) with a trend over time (T). Datasets for which superpopulation estimates were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3; ALL).

Dataset	Model	QAICc	ΔQAICc	QAIC weight	Deviance	Number of parameters
WM-SC.3	*φ(.) p(t) pent(T)*	490.815	0.000	0.776	-99.557	20
	φ(trans) p(t) pent(T)	493.301	2.486	0.224	-99.718	21
WM-SN.3	*φ(.) p(t) pent(T)*	528.798	0.000	0.762	-160.078	20
	φ(trans) p(t) pent(T)	531.370	2.572	0.210	-160.082	21
	φ(.) p(t) pent(.)	535.903	7.105	0.022	-150.429	19
	φ(trans) p(t) pent(.)	538.443	9.645	0.006	-150.433	20
ALL-SC.3	*φ(.) p(t) pent(T)*	617.098	0.000	0.695	-337.223	20
	φ(trans) p(t) pent(T)	619.200	2.102	0.243	-337.431	21
	φ(.) p(t) pent(.)	622.536	5.438	0.046	-329.492	19
	φ(trans) p(t) pent(.)	624.617	7.519	0.016	-329.704	20
ALL-SN.3	*φ(.) p(t) pent(T)*	581.460	0.000	0.635	-390.002	20
	φ(trans) p(t) pent(T)	583.490	2.030	0.230	-390.243	21
	φ(.) p(t) pent(.)	585.197	3.737	0.098	-384.008	19
	φ(trans) p(t) pent(.)	587.191	5.732	0.036	-384.271	20

Table II.9-4 – The best-supported candidate POPAN models (≤10 ΔQAICc) for the period 2006-2021 for each "Madeira – Canary Islands" dataset with matching uncertainty 3, with probability of apparent survival (ϕ) constant (.) or accounting for transience (*trans*), probability of recapture changing over time (*t*) and probability of recruitment from the super-population into the study area (pent) with a trend over time (T). Datasets for which superpopulation estimates were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3; ALL).

Dataset	Model	QAICc	ΔQAICc	QAIC weight	Deviance	Number of parameters
WM-SC.3	*φ(.) p(t) pent(T)*	633.710	0.000	0.684	-108.179	20
	φ(trans) p(t) pent(T)	635.257	1.547	0.316	-109.121	21
WM-SN.3	*φ(.) p(t) pent(T)*	590.116	0.000	0.664	-165.621	20
	φ(trans) p(t) pent(T)	592.226	2.110	0.231	-165.935	21
	φ(.) p(t) pent(.)	594.385	4.269	0.079	-158.952	19
	φ(trans) p(t) pent(.)	596.551	6.435	0.027	-159.187	20
ALL-SC.3	*φ(.) p(t) pent(T)*	890.087	0.000	0.830	-452.225	20
	φ(.) p(t) pent(.)	893.258	3.171	0.170	-446.821	19
ALL-SN.3	*φ(.) p(t) pent(T)*	766.023	0.000	0.604	-524.168	20
	φ(.) p(t) pent(.)	767.538	1.515	0.283	-520.461	19
	φ(trans) p(t) pent(.)	769.440	3.417	0.109	-520.751	20
	φ(.) p(t) pent(t)	775.984	9.960	0.004	-543.678	33

Table II.9-5 – Table with the abundance estimates, corrected for the proportion of unmarked animals, for the "Madeira" and "Madeira – Canary Islands" super-populations for the period 2006-2021, and the respective statistics, based on datasets with matching uncertainty 2-3. Datasets for which superpopulation estimates were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3; ALL).

Dataset	Area	Estimate	Standard error	95% CI	CV
WM-SC	Madeira	330	39	283 - 383	18%
	Madeira - Canaries	371	43	320 - 430	19%
WM-SN	Madeira	367	40	319 - 423	17%
	Madeira - Canaries	422	51	362 - 492	20%
ALL-SC	Madeira	417	58	350 - 499	15%
	Madeira - Canaries	415	50	356 - 485	12%
ALL-SN	Madeira	519	75	431 - 625	16%
	Madeira - Canaries	592	73	506 - 694	13%

Table II.9-6 – Table with the abundance estimates, corrected for the proportion of unmarked animals, for the "Madeira" and "Madeira – Canary Islands" super-populations for the period 2006-2021, and the respective statistics, based on datasets with matching uncertainty 3. Datasets for which superpopulation estimates were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3; ALL).

Dataset	Area	Estimate	Standard error	95% CI	CV
WM-SC.3	Madeira	366	44	314 - 427	20%
	Madeira - Canaries	395	43	343 - 455	17%
WM-SN.3	Madeira	385	44	333 - 446	18%
	Madeira - Canaries	451	54	387 - 526	19%
ALL-SC.3	Madeira	450	72	366 - 553	17%
	Madeira - Canaries	471	63	396 - 560	14%
ALL-SN.3	Madeira	571	96	460 - 708	18%
	Madeira - Canaries	655	92	547 - 784	15%

Table II.9-7 – Proportion of marked animals and respective standard error (SE) and coefficient of variation (CV), for datasets of well-marked animals (WM) and datasets of well-marked animals and animals with distinctive dorsal fin shapes

(ALL), with likely and certain matches (matching uncertainty level 2 – 3), for both animals confirmed as Bryde's whales (WM-SC and ALL-SC) and confirmed or suspected to be Bryde's whales (WM-SN and ALL-SN), used in the POPAN analysis. These proportions were used to correct the POPAN abundance estimates for Madeira.

dataset	Year	Proportion	SE(P)	CV(P)	dataset	Year	Proportion	SE(P)	CV(P)
WM-SC	2006	0.7692	0.1169	0.1519	WM-SN	2006	0.7692	0.1169	0.1519
	2007	0.4667	0.1288	0.2760		2007	0.5294	0.1211	0.2287
	2008	0.5806	0.0886	0.1526		2008	0.5806	0.0886	0.1526
	2009	0.6364	0.1450	0.2279		2009	0.6364	0.1450	0.2279
	2010	0.6500	0.1067	0.1641		2010	0.6667	0.1029	0.1543
	2011	0.6667	0.1571	0.2357		2011	0.7000	0.1449	0.2070
	2012	0.8125	0.0976	0.1201		2012	0.8235	0.0925	0.1123
	2013	0.5000	0.2500	0.5000		2013	0.5000	0.2500	0.5000
	2014	0.6130	0.0301	0.0492		2014	0.5978	0.0295	0.0494
	2015	0.4783	0.0521	0.1089		2015	0.4694	0.0504	0.1074
	2016	0.2143	0.1097	0.5118		2016	0.2143	0.1097	0.5118
	2017	0.3205	0.0374	0.1166		2017	0.3450	0.0364	0.1054
	2018	0.5652	0.0731	0.1293		2018	0.5625	0.0716	0.1273
	2019	0.5091	0.0674	0.1324		2019	0.5000	0.0657	0.1313
	2020	0.6429	0.0906	0.1409		2020	0.6429	0.0906	0.1409
	2021	0.6195	0.0457	0.0737		2021	0.6102	0.0449	0.0736
ALL-SC	2006	0.9231	0.0739	0.0801	ALL-SN	2006	0.9231	0.0739	0.0801
	2007	0.8000	0.1033	0.1291		2007	0.8235	0.0925	0.1123
	2008	0.8065	0.0710	0.0880		2008	0.8065	0.0710	0.0880
	2009	1.0000	0.0000	0.0000		2009	1.0000	0.0000	0.0000
	2010	0.9000	0.0671	0.0745		2010	0.9048	0.0641	0.0708
	2011	1.0000	0.0000	0.0000		2011	1.0000	0.0000	0.0000
	2012	1.0000	0.0000	0.0000		2012	1.0000	0.0000	0.0000
	2013	1.0000	0.0000	0.0000		2013	1.0000	0.0000	0.0000
	2014	0.8927	0.0192	0.0215		2014	0.8986	0.0182	0.0202
	2015	0.9457	0.0236	0.0250		2015	0.9490	0.0222	0.0234
	2016	0.9286	0.0688	0.0741		2016	0.9286	0.0688	0.0741
	2017	0.9167	0.0221	0.0241		2017	0.9240	0.0203	0.0219
	2018	0.9565	0.0301	0.0314		2018	0.9583	0.0288	0.0301
	2019	0.8727	0.0449	0.0515		2019	0.8793	0.0428	0.0486
	2020	0.8214	0.0724	0.0881		2020	0.8214	0.0724	0.0881
	2021	0.9646	0.0174	0.0180		2021	0.9661	0.0167	0.0172

Table II.9-8 – Proportion of marked animals and respective standard error (SE) and coefficient of variation (CV), for datasets of well-marked animals (WM) and datasets of well-marked animals and animals with distinctive dorsal fin shapes (ALL), with likely and certain matches (matching uncertainty level 2 – 3), for both animals confirmed as Bryde's whales (WM-SC and ALL-SC) and confirmed or suspected to be Bryde's whales (WM-SN and ALL-SN), used in the POPAN analysis. These proportions were used to correct the POPAN abundance estimates for Madeira – Canary Islands.

dataset	**Year**	**Proportion**	**SE(P)**	**CV(P)**	**dataset**	**Year**	**Proportion**	**SE(P)**	**CV(P)**
WM-SC	2006	0.8333	0.1521	0.1826	WM-SN	2006	0.7692	0.1169	0.1519
	2007	0.3333	0.1925	0.5774		2007	0.5238	0.1090	0.2081
	2008	0.6923	0.1280	0.1849		2008	0.6786	0.0883	0.1301
	2009	0.2500	0.2165	0.8660		2009	0.6667	0.1361	0.2041
	2010	0.7000	0.1449	0.2070		2010	0.6667	0.0962	0.1443
	2011	0.8333	0.1521	0.1826		2011	0.8333	0.1076	0.1291
	2012	0.5333	0.1288	0.2415		2012	0.6923	0.0905	0.1307
	2013	0.3333	0.2722	0.8165		2013	0.5000	0.2500	0.5000
	2014	0.6320	0.0431	0.0683		2014	0.6413	0.0289	0.0450
	2015	0.3333	0.0821	0.2462		2015	0.4811	0.0485	0.1009
	2016	0.4286	0.0707	0.1650		2016	0.4384	0.0581	0.1325
	2017	0.3699	0.0400	0.1080		2017	0.3902	0.0341	0.0873
	2018	0.5682	0.0747	0.1314		2018	0.5370	0.0679	0.1263
	2019	0.5294	0.0699	0.1320		2019	0.5085	0.0651	0.1280
	2020	0.6667	0.1029	0.1543		2020	0.7308	0.0870	0.1190
	2021	0.6452	0.0496	0.0769		2021	0.6207	0.0451	0.0726
ALL-SC	2006	1.0000	0.0000	0.0000	ALL-SN	2006	0.9231	0.0739	0.0801
	2007	0.8333	0.1521	0.1826		2007	0.8571	0.0764	0.0891
	2008	0.9231	0.0739	0.0801		2008	0.9643	0.0351	0.0364
	2009	1.0000	0.0000	0.0000		2009	1.0000	0.0000	0.0000
	2010	1.0000	0.0000	0.0000		2010	1.0000	0.0000	0.0000
	2011	1.0000	0.0000	0.0000		2011	1.0000	0.0000	0.0000
	2012	1.0000	0.0000	0.0000		2012	1.0000	0.0000	0.0000
	2013	1.0000	0.0000	0.0000		2013	1.0000	0.0000	0.0000
	2014	0.9680	0.0157	0.0163		2014	0.9710	0.0101	0.0104
	2015	0.9697	0.0298	0.0308		2015	0.9717	0.0161	0.0166
	2016	1.0000	0.0000	0.0000		2016	0.9863	0.0136	0.0138
	2017	0.9315	0.0209	0.0224		2017	0.9415	0.0164	0.0174
	2018	0.9773	0.0225	0.0230		2018	0.9630	0.0257	0.0267
	2019	0.9216	0.0376	0.0409		2019	0.9153	0.0363	0.0396
	2020	0.9048	0.0641	0.0708		2020	0.9231	0.0523	0.0566
	2021	0.9785	0.0150	0.0154		2021	0.9828	0.0121	0.0123

Table II.9-9 – Proportion of marked animals and respective standard error (SE) and coefficient of variation (CV), for datasets of well-marked animals (WM) and datasets of well-marked animals and animals with distinctive dorsal fin shapes (ALL), with certain matches (matching uncertainty level 3), for both animals confirmed as Bryde's whales (WM-SC and ALL-SC) and confirmed or suspected to be Bryde's whales (WM-SN and ALL-SN), used in the POPAN analysis. These proportions were used to correct the POPAN abundance estimates for Madeira.

dataset	Year	Proportion	SE(P)	CV(P)	dataset	Year	Proportion	SE(P)	CV(P)
WM-SC.C3	2006	0.8333	0.1521	0.1826	WM-SN.C3	2006	0.7500	0.1250	0.1667
	2007	0.2500	0.2165	0.8660		2007	0.4615	0.1383	0.2996
	2008	0.6667	0.1361	0.2041		2008	0.6071	0.0923	0.1520
	2009	0.0000	0.0003	624.1935		2009	0.6250	0.1712	0.2739
	2010	0.8571	0.1323	0.1543		2010	0.6667	0.1111	0.1667
	2011	0.7500	0.2165	0.2887		2011	0.7778	0.1386	0.1782
	2012	0.7273	0.1343	0.1846		2012	0.8235	0.0925	0.1123
	2013	0.3333	0.2722	0.8165		2013	0.5000	0.2500	0.5000
	2014	0.6036	0.0464	0.0769		2014	0.6229	0.0315	0.0507
	2015	0.3077	0.0905	0.2942		2015	0.4756	0.0552	0.1160
	2016	0.1818	0.1163	0.6396		2016	0.1538	0.1001	0.6504
	2017	0.3307	0.0417	0.1262		2017	0.3580	0.0377	0.1052
	2018	0.6471	0.0820	0.1267		2018	0.6047	0.0746	0.1233
	2019	0.5625	0.0716	0.1273		2019	0.5273	0.0673	0.1277
	2020	0.5909	0.1048	0.1774		2020	0.6296	0.0929	0.1476
	2021	0.6477	0.0509	0.0786		2021	0.6182	0.0463	0.0749
ALL-SC.C3	2006	1.0000	0.0000	0.0000	ALL-SN.C3	2006	1.0000	0.0000	0.0000
	2007	1.0000	0.0000	0.0000		2007	1.0000	0.0000	0.0000
	2008	0.9091	0.0867	0.0953		2008	0.8148	0.0748	0.0917
	2009	1.0000	0.0000	0.0000		2009	1.0000	0.0000	0.0000
	2010	1.0000	0.0000	0.0000		2010	0.8889	0.0741	0.0833
	2011	1.0000	0.0000	0.0000		2011	1.0000	0.0000	0.0000
	2012	1.0000	0.0000	0.0000		2012	1.0000	0.0000	0.0000
	2013	1.0000	0.0000	0.0000		2013	1.0000	0.0000	0.0000
	2014	0.8972	0.0294	0.0327		2014	0.9123	0.0187	0.0205
	2015	0.9600	0.0392	0.0408		2015	0.9747	0.0177	0.0181
	2016	1.0000	0.0000	0.0000		2016	0.9231	0.0739	0.0801
	2017	0.9748	0.0144	0.0147		2017	0.9739	0.0129	0.0132
	2018	1.0000	0.0000	0.0000		2018	1.0000	0.0000	0.0000
	2019	0.9545	0.0314	0.0329		2019	0.9600	0.0277	0.0289
	2020	0.9000	0.0671	0.0745		2020	0.8800	0.0650	0.0739
	2021	0.9767	0.0163	0.0166		2021	0.9815	0.0130	0.0132

Table II.9-10 – Proportion of marked animals and respective standard error (SE) and coefficient of variation (CV), for datasets of well-marked animals (WM) and datasets of well-marked animals and animals with distinctive dorsal fin shapes (ALL), with certain matches (matching uncertainty level 3), for both animals confirmed as Bryde's whales (WM-SC and ALL-SC) and confirmed or suspected to be Bryde's whales (WM-SN and ALL-SN), used in the POPAN analysis. These proportions were used to correct the POPAN abundance estimates for Madeira – Canary Islands.

dataset	Year	Proportion	SE(P)	CV(P)	dataset	Year	Proportion	SE(P)	CV(P)
WM-SC.C3	2006	0.8333	0.1521	0.1826	WM-SN.C3	2006	0.7500	0.1250	0.1667
	2007	0.2000	0.1789	0.8944		2007	0.4706	0.1211	0.2572
	2008	0.7273	0.1343	0.1846		2008	0.7200	0.0898	0.1247
	2009	0.3333	0.2722	0.8165		2009	0.6667	0.1571	0.2357
	2010	0.8750	0.1169	0.1336		2010	0.6842	0.1066	0.1559
	2011	0.8333	0.1521	0.1826		2011	0.8333	0.1076	0.1291
	2012	0.5714	0.1323	0.2315		2012	0.7083	0.0928	0.1310
	2013	0.3333	0.2722	0.8165		2013	0.5000	0.2500	0.5000
	2014	0.6699	0.0463	0.0692		2014	0.6752	0.0306	0.0453
	2015	0.3214	0.0883	0.2746		2015	0.4831	0.0530	0.1096
	2016	0.4000	0.0775	0.1936		2016	0.4500	0.0642	0.1427
	2017	0.3759	0.0408	0.1085		2017	0.3969	0.0351	0.0885
	2018	0.6154	0.0779	0.1266		2018	0.5714	0.0707	0.1237
	2019	0.5625	0.0716	0.1273		2019	0.5357	0.0666	0.1244
	2020	0.6667	0.1029	0.1543		2020	0.7200	0.0898	0.1247
	2021	0.6628	0.0510	0.0769		2021	0.6296	0.0465	0.0738
ALL-SC.C3	2006	1.0000	0.0000	0.0000	ALL-SN.C3	2006	0.9167	0.0798	0.0870
	2007	0.8000	0.1789	0.2236		2007	0.8235	0.0925	0.1123
	2008	0.9091	0.0867	0.0953		2008	0.9600	0.0392	0.0408
	2009	1.0000	0.0000	0.0000		2009	1.0000	0.0000	0.0000
	2010	1.0000	0.0000	0.0000		2010	1.0000	0.0000	0.0000
	2011	1.0000	0.0000	0.0000		2011	1.0000	0.0000	0.0000
	2012	1.0000	0.0000	0.0000		2012	1.0000	0.0000	0.0000
	2013	1.0000	0.0000	0.0000		2013	1.0000	0.0000	0.0000
	2014	0.9612	0.0190	0.0198		2014	0.9658	0.0119	0.0123
	2015	0.9643	0.0351	0.0364		2015	0.9663	0.0191	0.0198
	2016	1.0000	0.0000	0.0000		2016	0.9833	0.0165	0.0168
	2017	0.9291	0.0216	0.0233		2017	0.9381	0.0173	0.0184
	2018	0.9744	0.0253	0.0260		2018	0.9592	0.0283	0.0295
	2019	0.9167	0.0399	0.0435		2019	0.9107	0.0381	0.0418
	2020	0.9048	0.0641	0.0708		2020	0.9200	0.0543	0.0590
	2021	0.9767	0.0163	0.0166		2021	0.9815	0.0130	0.0132

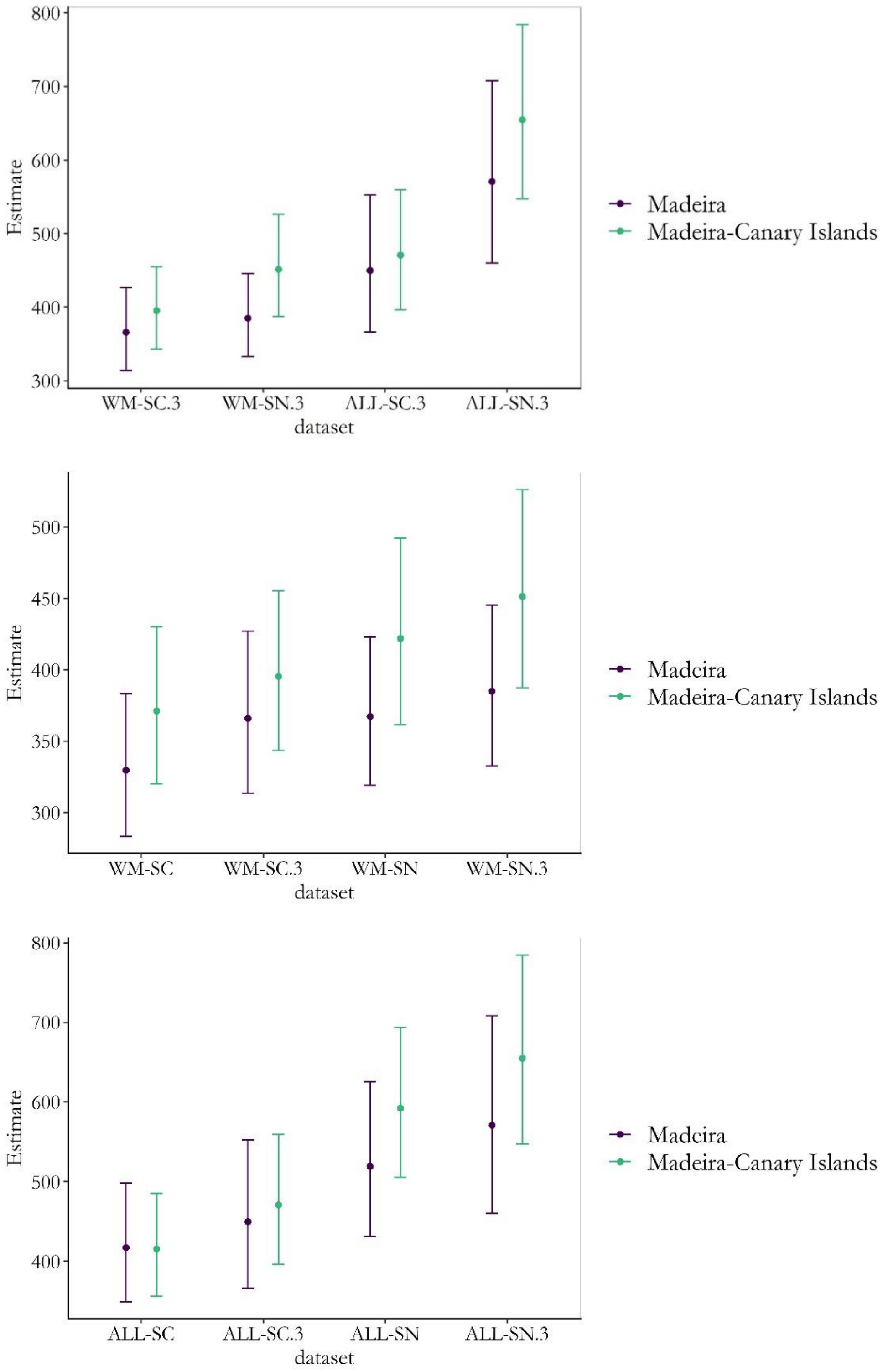
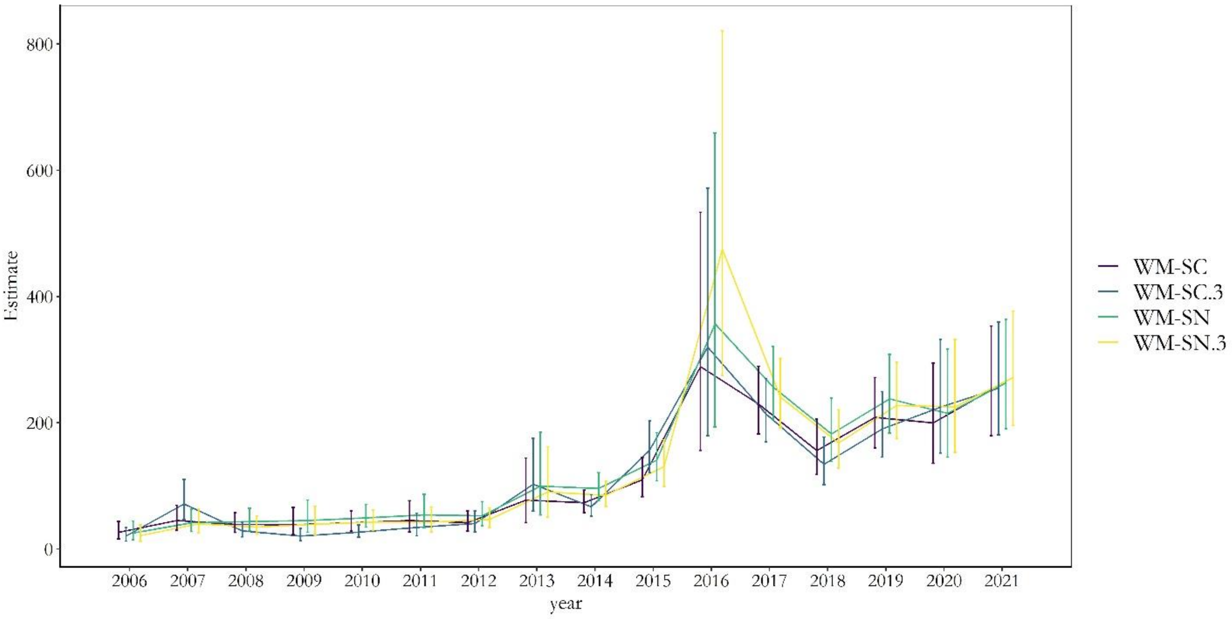


Figure II.9-1. Comparison of POPAN abundance estimates of "Madeira" and "Madeira-Canary Islands" super-populations for the period 2006-2021, based on: top - datasets with only certain matches (WM-SC.3; WM-SN.3; ALL-SC.3 and ALL-SN.3); centre – well-marked individuals with likely or certain matches (WM-SC and WM-SN) or with only certain matches (WM-SC.3 and WM-SN.3); bottom – all identified individuals, with likely or certain matches (ALL-SC and ALL-SN) or with only certain matches (ALL-SC.3 and ALL-SN.3). Datasets for which super-population estimates were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well-marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3; ALL).



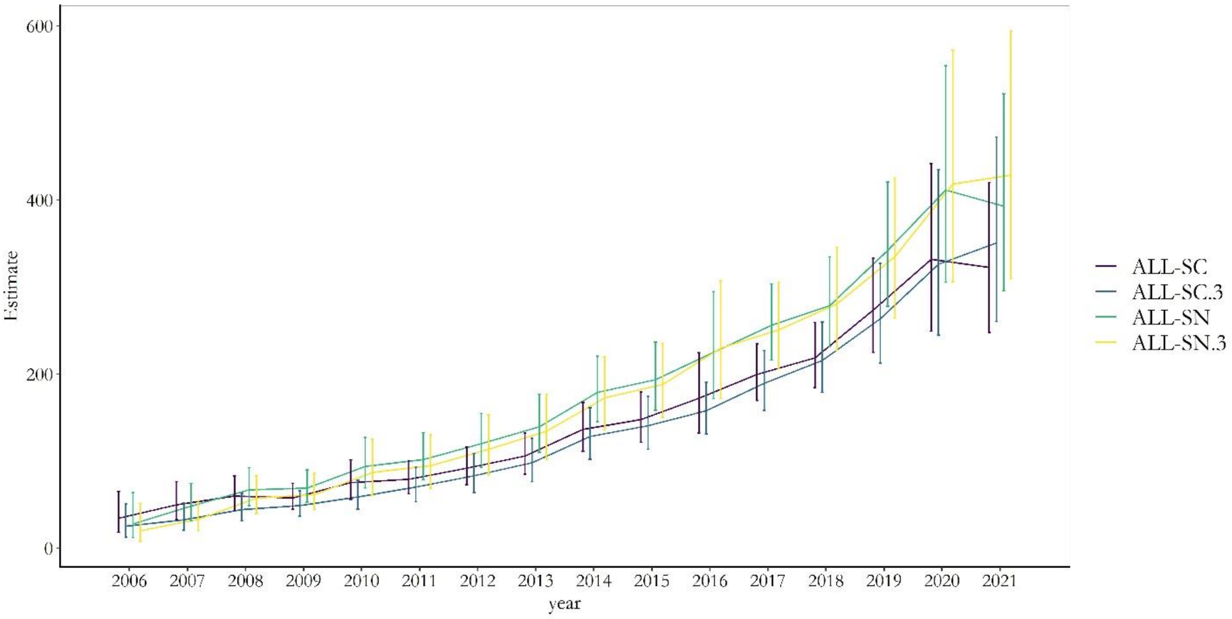


Figure II.9-2. POPAN yearly abundance estimates of the "Madeira" super-population, based on: top – datasets of well-marked individuals with likely or certain matches (WM-SC and WM-SN) or with only certain matches (WM-SC.3 and WM-SN.3); bottom – datasets of all identified individuals with likely or certain matches (ALL-SC and ALL-SN) or with only certain matches (ALL-SC.3 and ALL-SN.3). Datasets for which super-population estimates were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well-marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3; ALL).

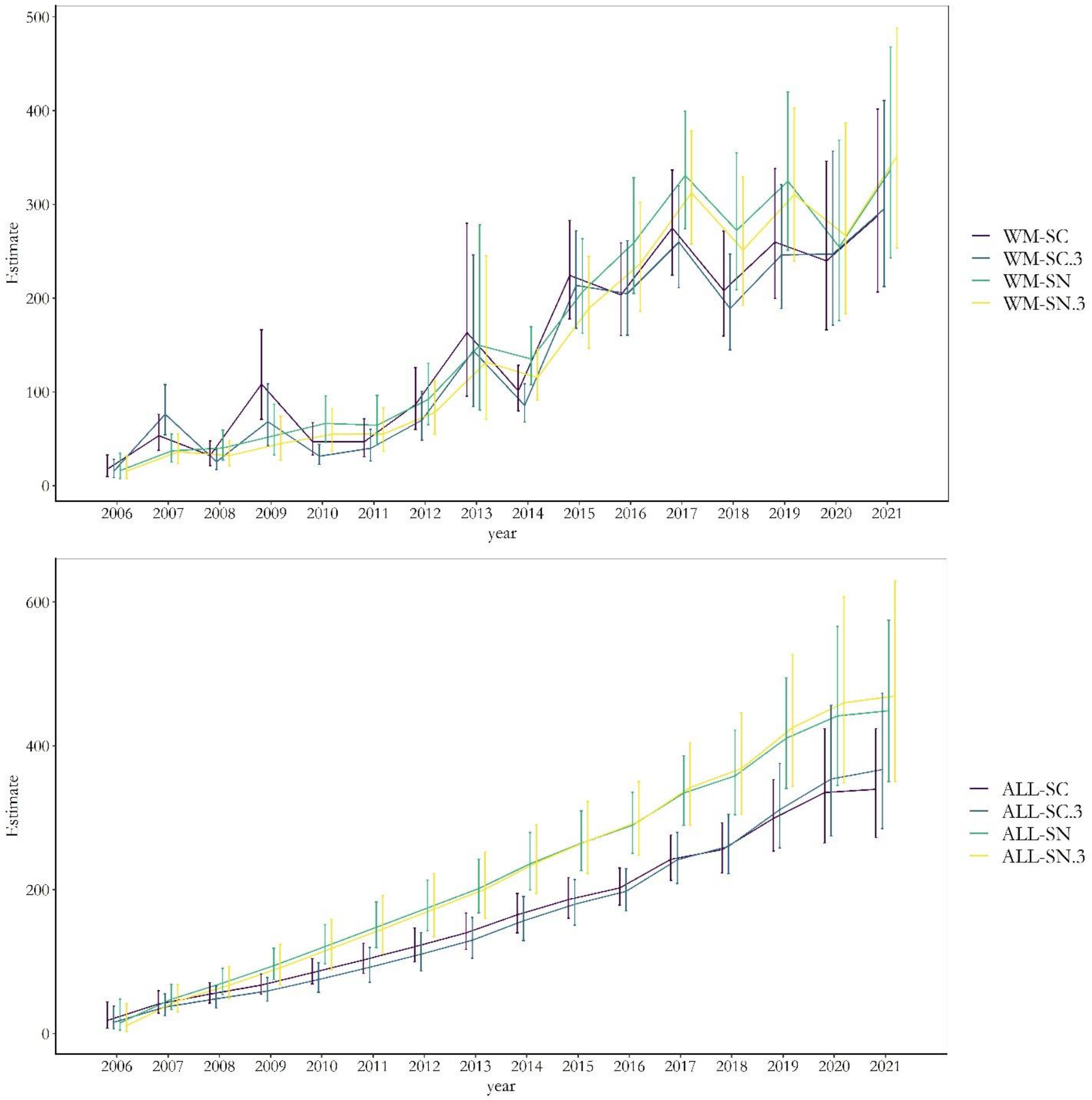


Figure II.9-3. POPAN yearly abundance estimates of the "Madeira-Canary Islands" super-population, based on: top – datasets of well-marked individuals with likely or certain matches (WM-SC and WM-SN) or with only certain matches (WM-SC.3 and WM-SN.3); bottom – datasets of all identified individuals with likely or certain matches (ALL-SC and ALL-SN) or with only certain matches (ALL-SC.3 and ALL-SN.3). Datasets for which super-population estimates were obtained, combining animals confirmed as Bryde's whale (SC), animals confirmed or suspected to be Bryde's whales (SN), animals well marked (distinctiveness classes 1-3; WM) and all identified animals, including well-marked and with distinctive shaped dorsal fins (distinctiveness classes 0-3; ALL).

II.10. Female-calf association and calving rates

Table II.10-1 – Table with the female-calf associations identified through photo-identification in Madeira, Azores and the Canary Islands for the period 2002-2021, including: female ID code, year it was first captured, respective location, and age class at the first sighting (C – calf; A – Adult); calf ID code (NID – non-identified), the year the calf was first and last seen with the female, respective locations (MAD – Madeira; Canary Islands: CEH – El Hierro; CTN – Tenerife; CGC – Gran Canaria; CLP – La Palma; CFV – Fuerteventura; CLG – La Gomera; Azores: ASM – São Miguel; AZF - Faial), and number of days between these two events; information on the recapture of the calf after it left the progenitor.

Female				Calves with female						Calf seen afterwards
ID	1st year	Location	Age	ID	First seen	Location	Last seen	Location	first and last seen (days)	
Be0003	2003	MAD	A	Be0015	2005	MAD	2006	MAD	378	
				Be0036	2007	MAD	2008	MAD	129	
				Be0059	2010	MAD	2010	MAD	42	Seen in 2017 in Madeira with a calf
Be0004	2004	CGC	A	Be0280	2018	MAD	2018	MAD	1	
Be0016	2006	MAD	A	Be0125	2015	MAD	2016	MAD	374	Seen alone in 2016 and 2017 in Madeira
Be0017	2005	MAD	A	NID	2005	MAD	2005	MAD	1	
Be0018	2005	MAD	A	NID	2016	CEH	2016	CEH	1	
Be0021	2005	MAD	A	NID	2005	MAD	2005	MAD	1	
Be0023	2017	CTN	A	NID	2017	CTN	2017	CTN	1	
				Be0382	2018	MAD	2018	MAD	1	
Be0024	2006	MAD	A	Be0302	2020	MAD	2020	MAD	1	
Be0026	2006	MAD	A	Be0041	2007	MAD	2008	MAD	141	Seen alone in 2008 and 2015 in Madeira
				NID	2009	MAD	2009	MAD	1	
				Be0097	2014	CTN	2014	CTN	1	Seen alone in 2018 in Madeira
				Be0311	2019	MAD	2019	MAD	2	
Be0030	2008	MAD	A	Be0045	2008	MAD	2008	MAD	1	
				Be0061	2011	MAD	2011	MAD	18	
Be0031	2007	CGC	C/A	NID	2017	MAD	2017	MAD	1	
Be0032	2007	CGC	A	Be0031	2007	CGC	2007	CGC	1	Seen in 2017 in Madeira with a calf
Be0035	2007	MAD	A	Be0243	2017	MAD	2017	MAD	15	
Be0046	2008	MAD	A	NID	2008	MAD	2008	MAD	1	
				Be0104	2009	MAD	2009	MAD	2	
				Be0086	2014	MAD	2014	MAD	32	
				Be0277	2018	MAD	2018	MAD	5	
Be0047	2008	MAD	A	Be0214	2017	MAD	2017	MAD	10	
Be0050	2008	MAD	A	Be0064	2014	MAD	2014	MAD	7	Seen alone in 2021 in Madeira
Be0052	2008	MAD	A	Be0191	2017	MAD	2017	MAD	2	
				Be320	2021	MAD	2021	MAD	1	
Be0054	2007	MAD	A	Be0289	2019	CLP	2019	CLP	60	
Be0056	2008	CGC	A	Be0205	2014	CTN	2014	CTN	1	
				Be0230	2017	CLP	2017	CLP	1	
Be0057	2009	MAD	A	NID	2009	MAD	2009	MAD	1	
				NID	2014	MAD	2014	MAD	1	
				Be0380	2021	MAD	2021	MAD	1	
Be0059	2010	MAD	C/A	Be0401	2017	MAD	2017	MAD	2	
Be0062	2017	CEH	A	Be0168	2017	CEH	2017	CEH	1	

Table II.10-2 – Table with the female-calf associations identified through photo-identification in Madeira, Azores and the Canary Islands for the period 2002-2021, including: female ID code, year it was first captured, respective location, and age class at the first sighting (C – calf; A – Adult); calf ID code (NID – non-identified), the year the calf was first and last seen with the female, respective locations (MAD – Madeira and Porto Santo; Canary Islands: CEH – El Hierro; CTN – Tenerife; CGC – Gran Canaria; CLP – La Palma; CFV – Fuerteventura; CLG – La Gomera; Azores: ASM – São Miguel; AZF - Faial), and number of days between these two events; information on the recapture of the calf after it left the progenitor (continuation).

Female				Calves with female						Calf seen afterwards
ID	1st year	Location	Age	ID	First seen	Location	Last seen	Location	first and last seen (days)	
Be0065	2004	MAD	A	Be0020	2005	MAD	2005	MAD	1	Seen in 2014 alone and in a group with the female; seen alone in 2015 and 2020; always in Madeira
				Be0221	2017	MAD	2017	MAD	35	
				Be0310	2019	MAD	2019	MAD	88	
Be0066	2011	MAD	A	Be0204	2011	MAD	2011	MAD	1	Seen alone in 2014 in Madeira
Be0072	2012	CGC	A	Be0229	2017	MAD	2017	CTN	67	Seen mulitple times with female in Madeira in Summer and last sight in November, Tenerife, Canary Islands
Be0078	2013	CTN	A	Be0182	2017	MAD	2017	MAD	1	
Be0084	2007	MAD	A	Be0029	2007	MAD	2007	MAD	1	
				Be0301	2020	MAD	2020	MAD	1	
Be0087	2010	MAD	A	Be0218	2017	CEH	2018	MAD	426	Seen alone in 2019 in Madeira
Be0098	2014	MAD	A	Be0207	2015	MAD	2015	MAD	1	
Be0099	2014	MAD	A	Be0152	2016	CTN	2017	MAD	458	
				Be0304	2020	MAD	2020	MAD	1	
Be0101	2009	MAD	A	Be0241	2017	MAD	2017	MAD	1	
Be0108	2012	MAD	A	Be0107	2014	MAD	2014	MAD	2	Seen alone in 2018 in Madeira
Be0118	2015	CTN	A	Be0117	2015	CTN	2016	CTN	416	
Be0122	2004	MAD	A	Be0169	2017	MAD	2017	MAD	76	
Be0127	2015	CTN	A	Be0208	2015	CTN	2015	CTN	1	
Be0128	2016	MAD	A	Be0209	2016	MAD	2016	MAD	1	
				Be0262	2018	CLG	2018	CLG	1	Seen alone in 2018 in Porto Santo
Be0131	2014	MAD	A	Be0132	2015	CTN	2016	CTN	434	Seen alone in 2016 in Tenerife, Canary Islands
Be0148	2016	MAD	A	Be0147	2016	MAD	2016	MAD	1	
Be0154	2016	CEH	A	Be0189	2016	CEH	2016	CEH	1	Seen alone in 2017 and 2021 in Madeira
Be0159	2004	MAD	A	Be0160	2017	CTN	2017	CTN	23	
Be0174	2017	AZSM	A	Be0175	2017	ASM	2017	ASM	53	
Be0178	2017	AZF	A	Be0199	2017	AZF	2017	MAD	60	
Be0188	2017	MAD	A	NID	2017	MAD	2017	MAD	1	
Be0195	2017	MAD	A	Be0372	2020	MAD	2020	MAD	1	
Be0198	2016	CFV	A	Be0142	2016	CFV	2016	CFV	1	
Be0223	2017	MAD	A	Be0225	2017	MAD	2017	CFV	1	
Be0231	2017	CLP	A	Be0232	2017	CLP	2017	CLP	1	
Be0233	2017	CFV	A	NID	2017	CFV	2017	CFV	1	Female seen without the calf in Sept 2017
Be0234	2017	CLP	A	Be0235	2017	CLP	2017	CLP	1	
Be0239	2017	MAD	A	Be0284	2019	MAD	2019	MAD	1	
Be0266	2018	MAD	A	Be0267	2018	MAD	2018	MAD	3	
Be0274	2017	MAD	A	NID	2017	MAD	2017	MAD	1	
Be0276	2019	MAD	A	Be0370	2019	MAD	2019	MAD	1	
Be0321	2018	MAD	A	Be0318	2020	MAD	2020	MAD	1	
Be0374	2021	MAD	A	Be0375	2021	MAD	2021	MAD	1	
Be0393	2017	CLP	A	NID	2017	CLP	2017	CLP	1	

Table II.10-3 – Time series of the years Bryde's whales identified as females (accompanied by a calf) were observed in Madeira, Azores or the Canary Islands with or without a calf between 2003 and 2021. A – Animal considered adult at a particular year based on size; C – animal considered a calf at a particular year based on size. The numbers identify the sequence of identified calves a particular female had throughout the time series the animal was photo-identified. The column site fidelity indicates the site fidelity each animals to Madeira inshore waters, excluding transient animals and animals only identified in the Canary Islands or Azores.

Female	Site fidelity	Years with captures	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	Total Calves
Be0003	Regular	8	A	A	1	1	2	A	A	3												3
Be0004	Regular	6		A				A				A		A	A			1				1
Be0016	Regular	9				A		A			A			A	1	1	A	A			A	1
Be0017	-	2			1			A														1
Be0018	Occasional	4			A			A			A					1						1
Be0021	Occasional	4			1									A		A		2				2
Be0023	-	2															1	1?				1
Be0024	Regular	4				A						A		A						1		1
Be0026	Regular	10				A	1	1	2	A	A			3	A		A		4			4
Be0030	Occasional	4						1		A	2				A							2
Be0031	-	2					C										1					1
Be0032	-	1					1															1
Be0035	Regular	3					A							A			1					1
Be0046	Regular	8						1	2	A		A		3	A			4			A	4
Be0047	Regular	2						A									1					1
Be0050	Regular	5						A	A			A		1							A	1
Be0052	Regular	4						A						A			1				2	2
Be0054	Regular	4					A								A		A		1			1
Be0056	-	4						A						1		A	2					2
Be0057	Regular	4							1	A				2							3	3
Be0059	Regular	3								C							1	A				1
Be0062	-	2															1	A				1
Be0065	Regular	10		A	1	A	A	A			A			A	A		2		3			3
Be0066	-	3									1			A	A							1
Be0072	Occasional	2										A					1					1
Be0078	-	2											A				1					1
Be0084	Occasional	3					1							A						2		2
Be0087	Regular	6								A				A	A	A	1	1				1
Be0098	Occasional	2												A	1							1
Be0099	Regular	5												A	A	1	1			2		2
Be0101	Regular	3							A								1	A				1
Be0108	Rare	3										A		1		A						1
Be0118	Rare	3													1	1					A	1
Be0122	Occasional	5		A											A		1	A	A			1
Be0127	-	1													1							1
Be0128	-	3														1	A	2				2
Be0131	Occasional	5												A	1	1	A		A			1
Be0148	-	1														1						1
Be0154	-	2														1					A	1
Be0159	-	2		A													1					1
Be0174	-	1															1					1
Be0178	Occasional	1															1					1
Be0188	Occasional	1															1					1
Be0195	Occasional	3															A		A	1		1
Be0198	-	1														1						1
Be0223	-	1															1					1
Be0231	-	1															1					1
Be0233	Occasional	3												A			1				A	1
Be0234	-	1															1					1
Be0239	Occasional	2															A		1			1
Be0266	Rare	1																1				1
Be0274	-	1															1					1
Be0276	-	1																	1			1
Be0321	Occasional	3																A		1	A	1
Be0374	-	1																			1	1
Be0393	-	1															1					1

APPENDIX III

APPENDIX III.

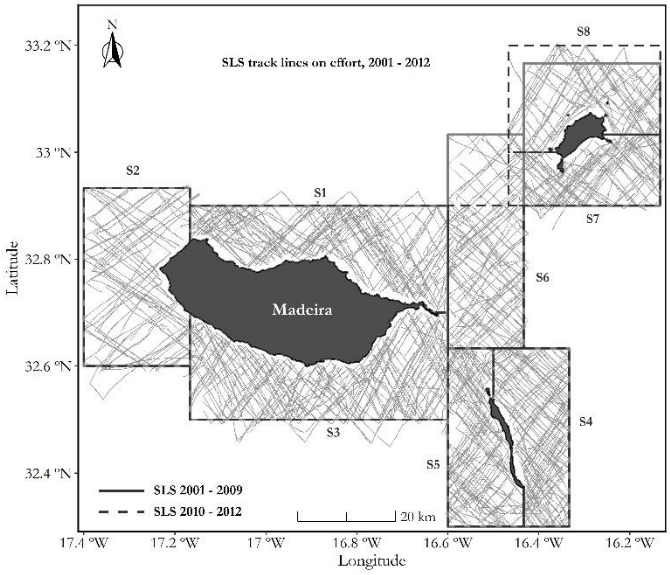
III.1 Table with areas of the overall area and survey blocks

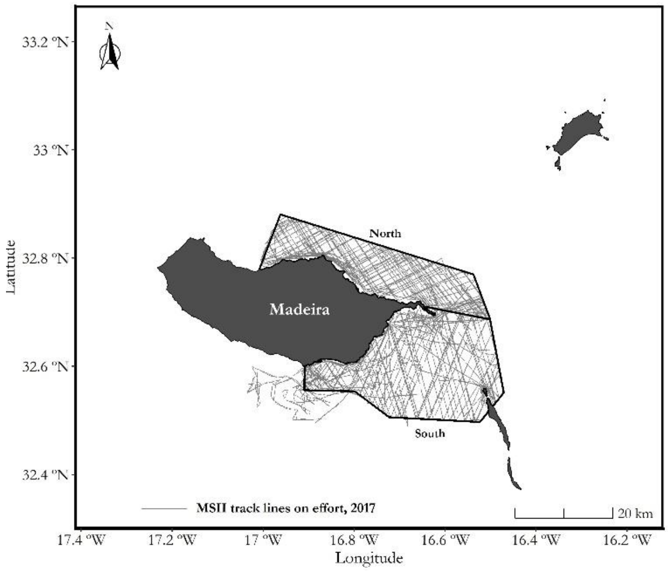
Table III.1-1 – Table with areas and perimeters of the blocks covered in the different types of surveys and the respective totals. The area of the FO 2010-12 corresponds to the total area covered by all types of surveys (Madeira extended area). SLS – shipboard line-transect surveys; SLS-RD – shipboard line-transect surveys for photo-id robust design study; ALS – Aerial line transect surveys; NSS – non-systematic surveys for photo-identification and biopsy sampling studies; WWO – whale-watching observers program; and FO – fisheries observers program.

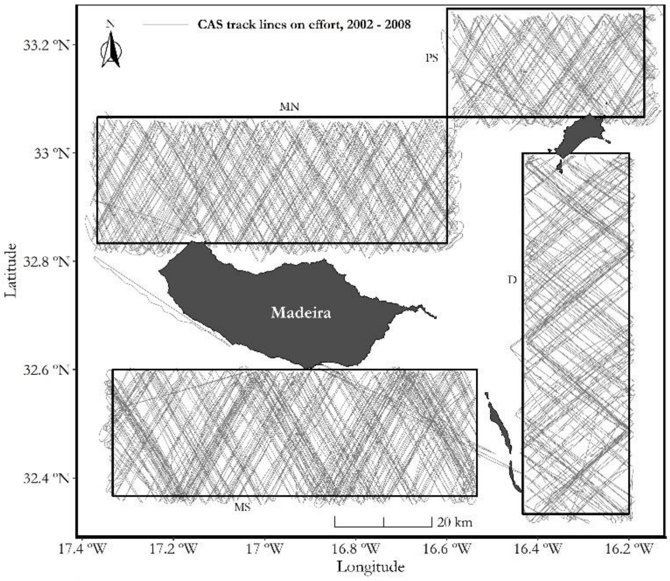
Survey	Block	Area (Km2)	Perimeter (km)
ALL SLS	Madeira north (S1)	779	155
	Madeira west (S2)	761	124
	Madeira south (S3)	889	174
	Desertas east (S4)	469	102
	Desertas west (S5)	444	110
SLS 2001 - 09	Travessa (S6)	692	120
	Porto Santo south (S7)	366	97
	Porto Santo North (S8)	419	110
SLS 2010 - 12	Travessa (S6)	462	90
	Porto Santo south (S7)	402	92
	Porto Santo North (S8)	591	118
SLS 2007 - 12	Travessa (S6)	462	90
	Porto Santo south (S7)	366	97
	Porto Santo North (S8)	419	110
SLS 2001 - 09	All sectors	4 818	722
SLS 2010 - 12	All sectors	4 797	713
SLS 2007 - 12	All sectors	4 588	722
SLS-RD 2017	MSII North	400	123
	MSII South	635	133
	All sectors	1 035	229
ALS 2002 - 08	South Madeira (MS)	1 945	202
	North Madeira (MN)	1 855	195
	Porto Santo (PS)	896	125
	Desertas (D)	1 617	192
	All sectors	6 312	714
NSS 2004 -16	Madeira southwest (MSW)	1 945	202
	Madeira south (MS)	1 855	195
	Madeira east (ME)	896	125
	Porto Santo (PS)	1 617	192
	All sectors	6 312	714
WWO 2010 - 17	South Madeira	1 512	219
FO 2010 - 12	Madeira extended area	11 923	715

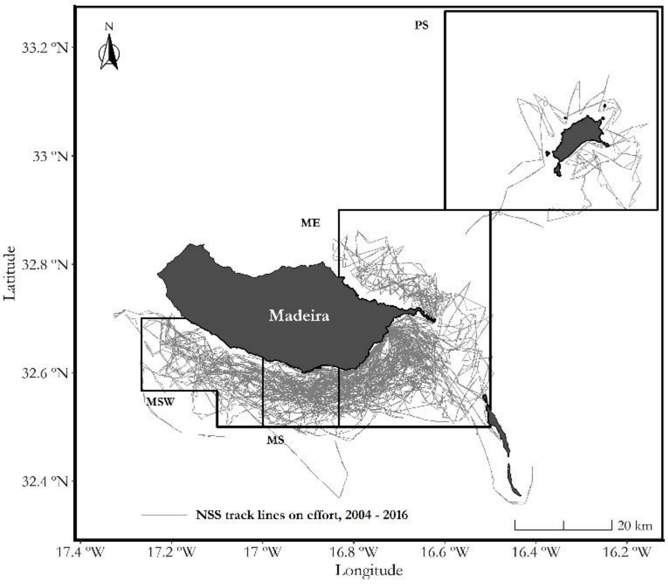
III.2 Maps of effort by type of survey, season and period

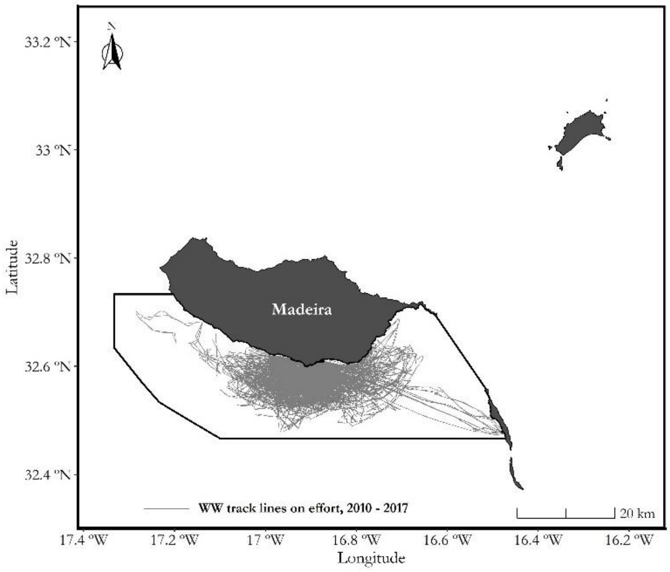
III.2.1 Effort by types of survey for the study period (2001 – 2017)

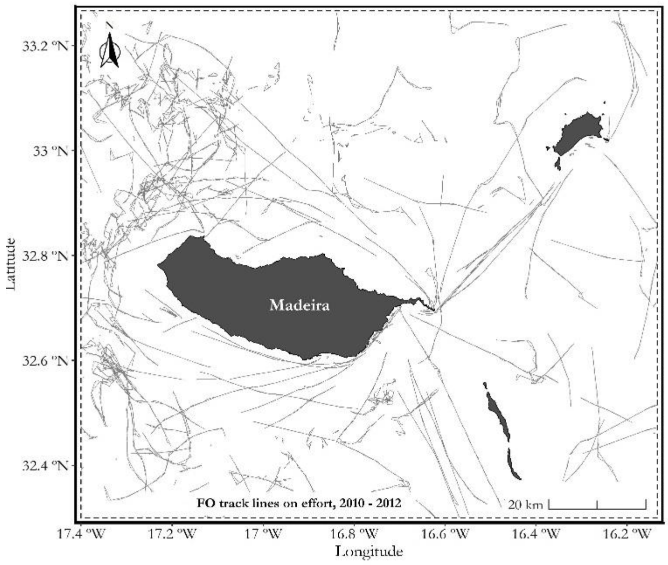




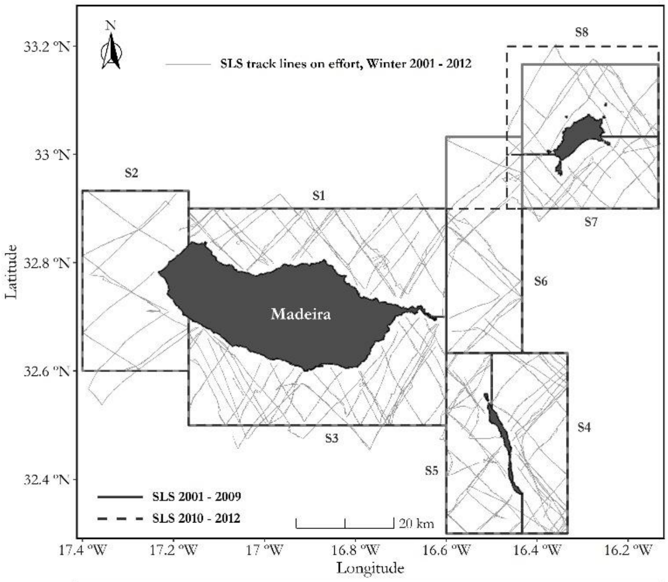


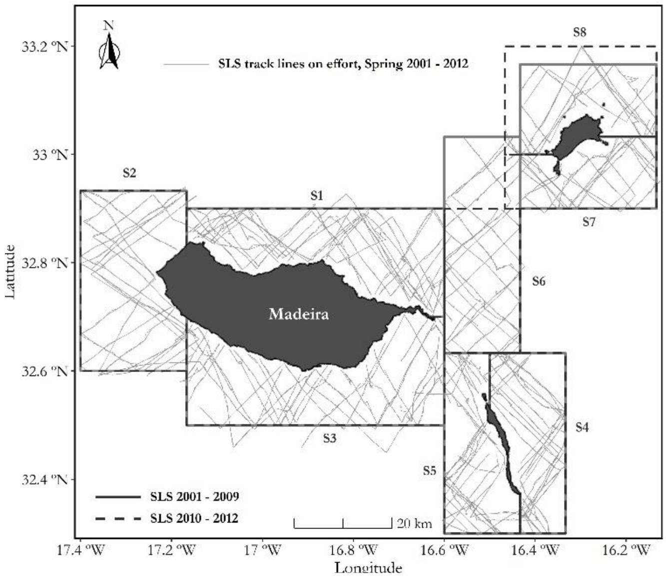


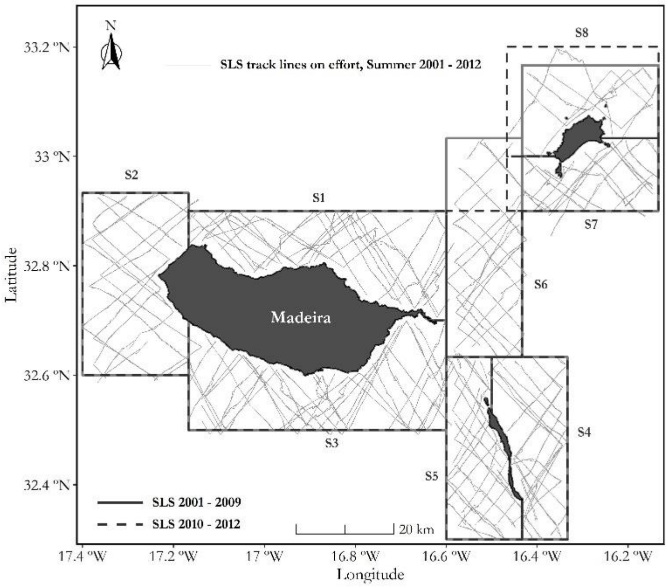


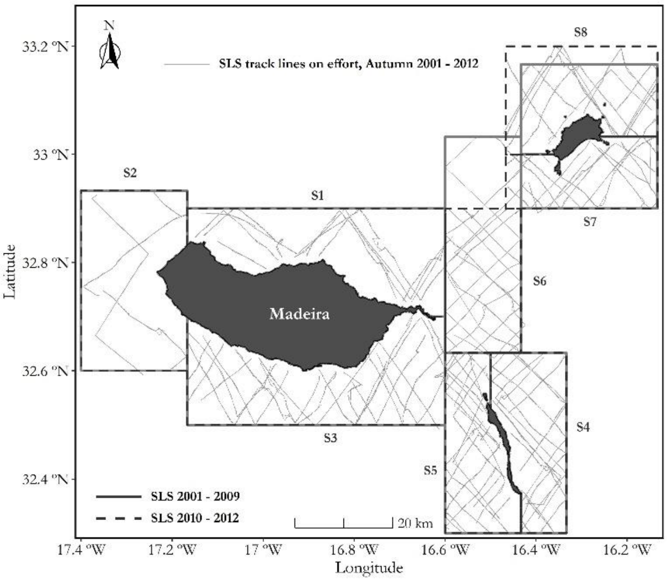


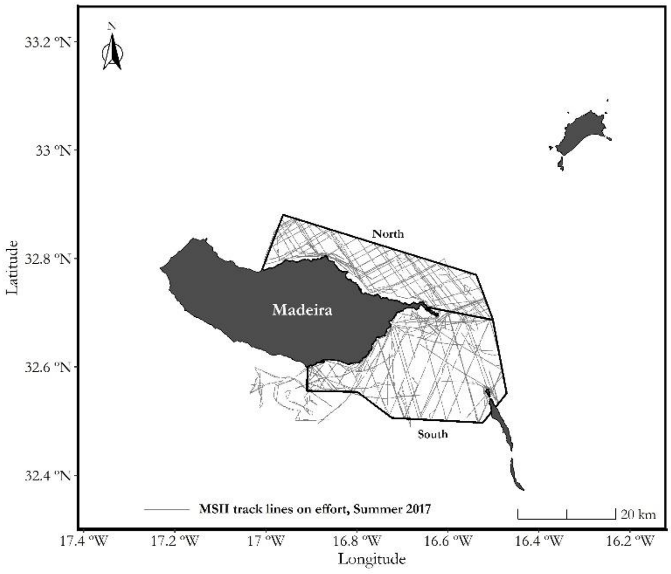
III.2.2. Effort of systematic shipboard line-transect surveys by season (Winter, Spring, Summer and Autumn) for 2001 – 2012 and 2017

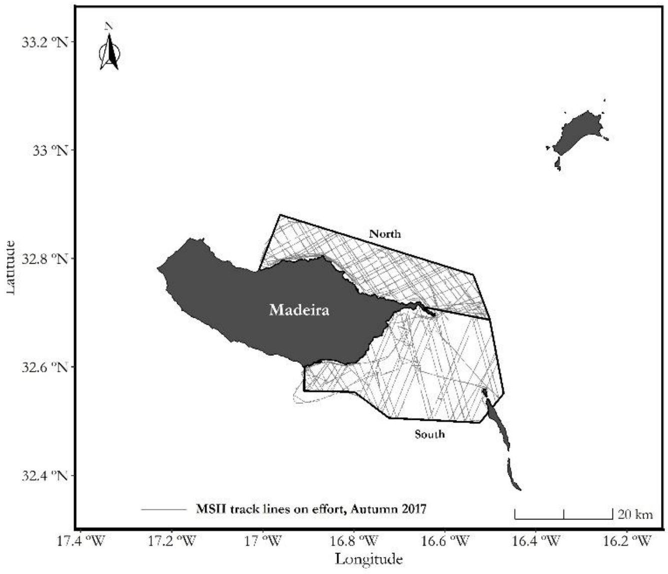




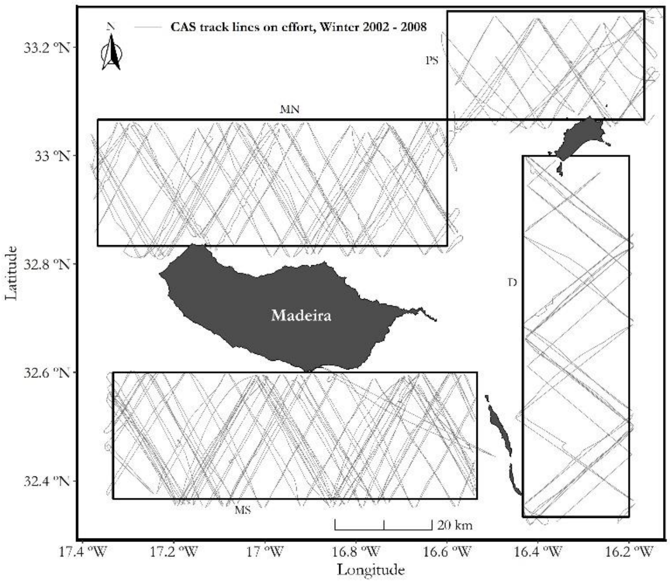


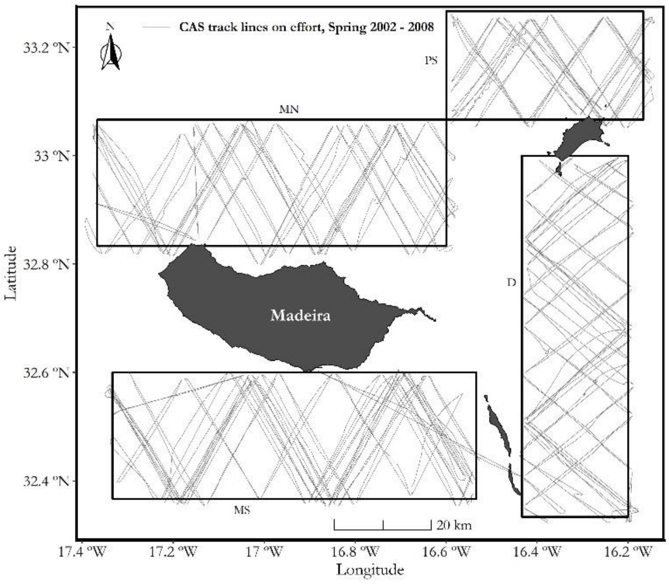


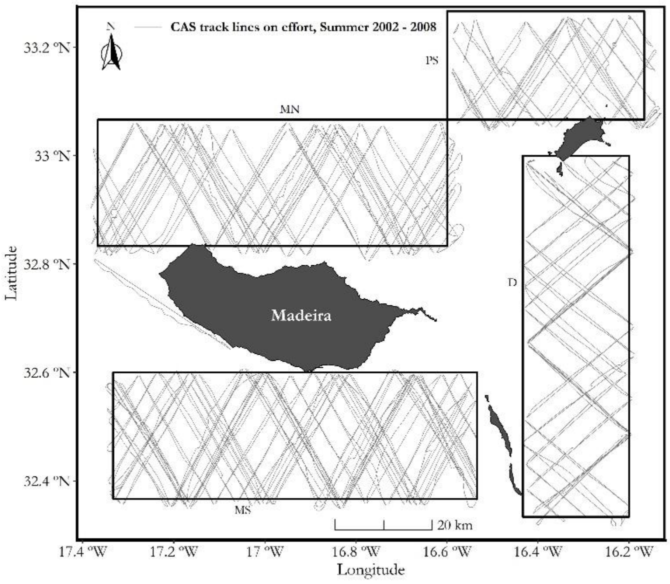


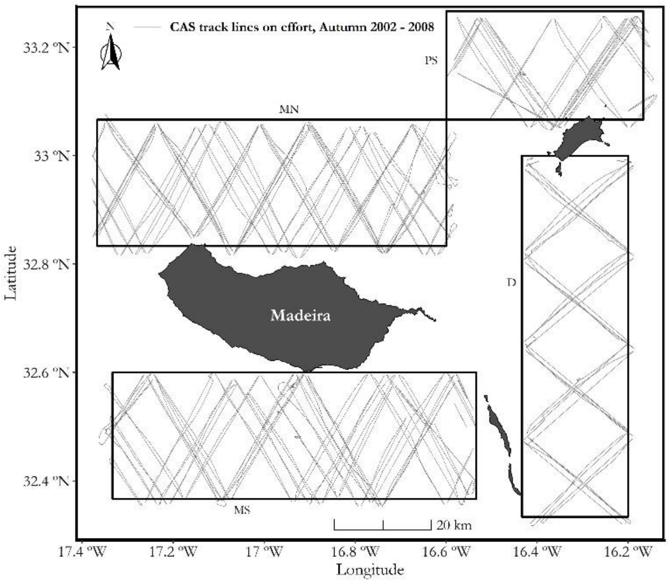


III.2.3 Effort of systematic aerial line-transect surveys by season (Winter, Spring, Summer and Autumn) for 2002 – 2018

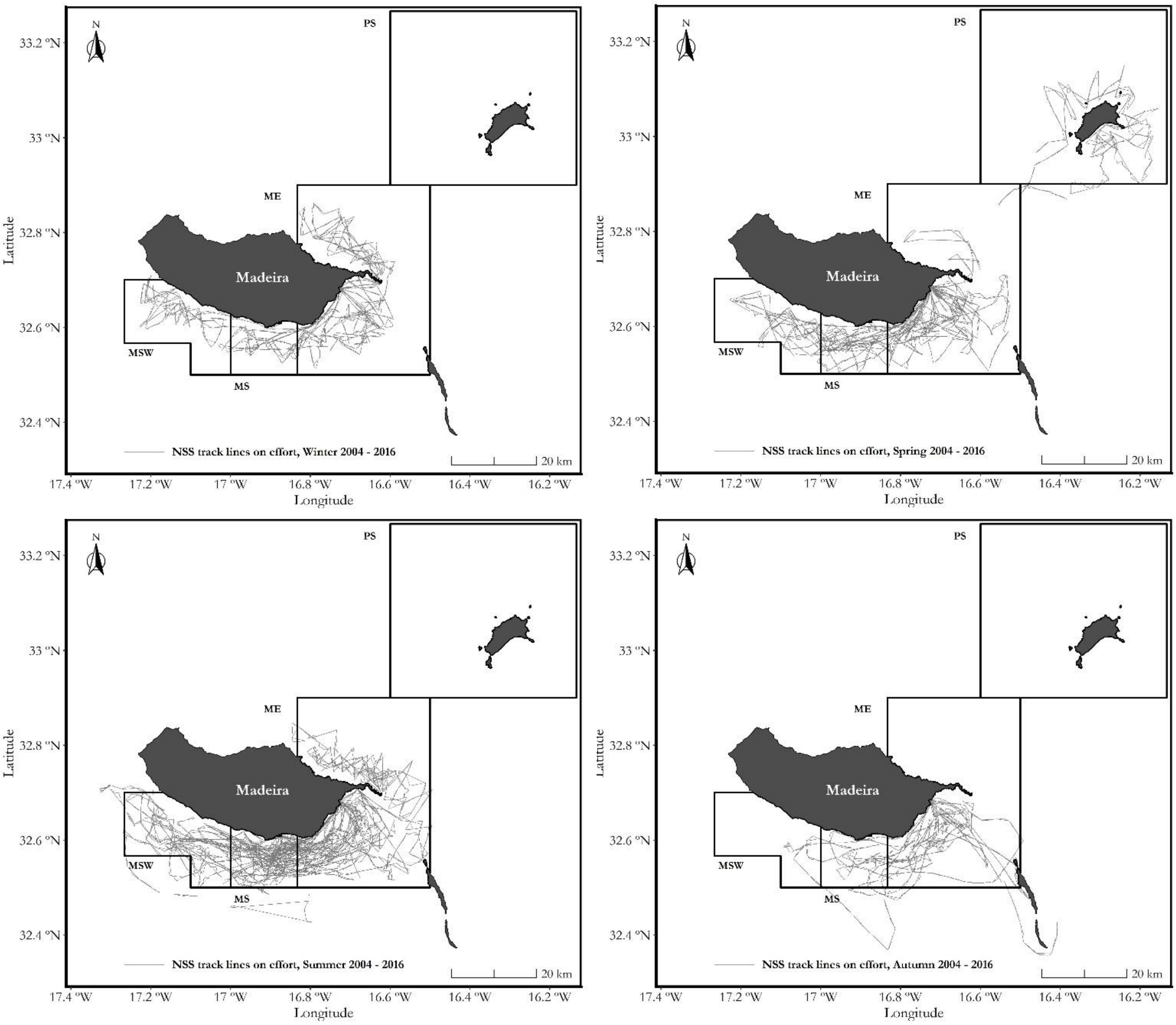




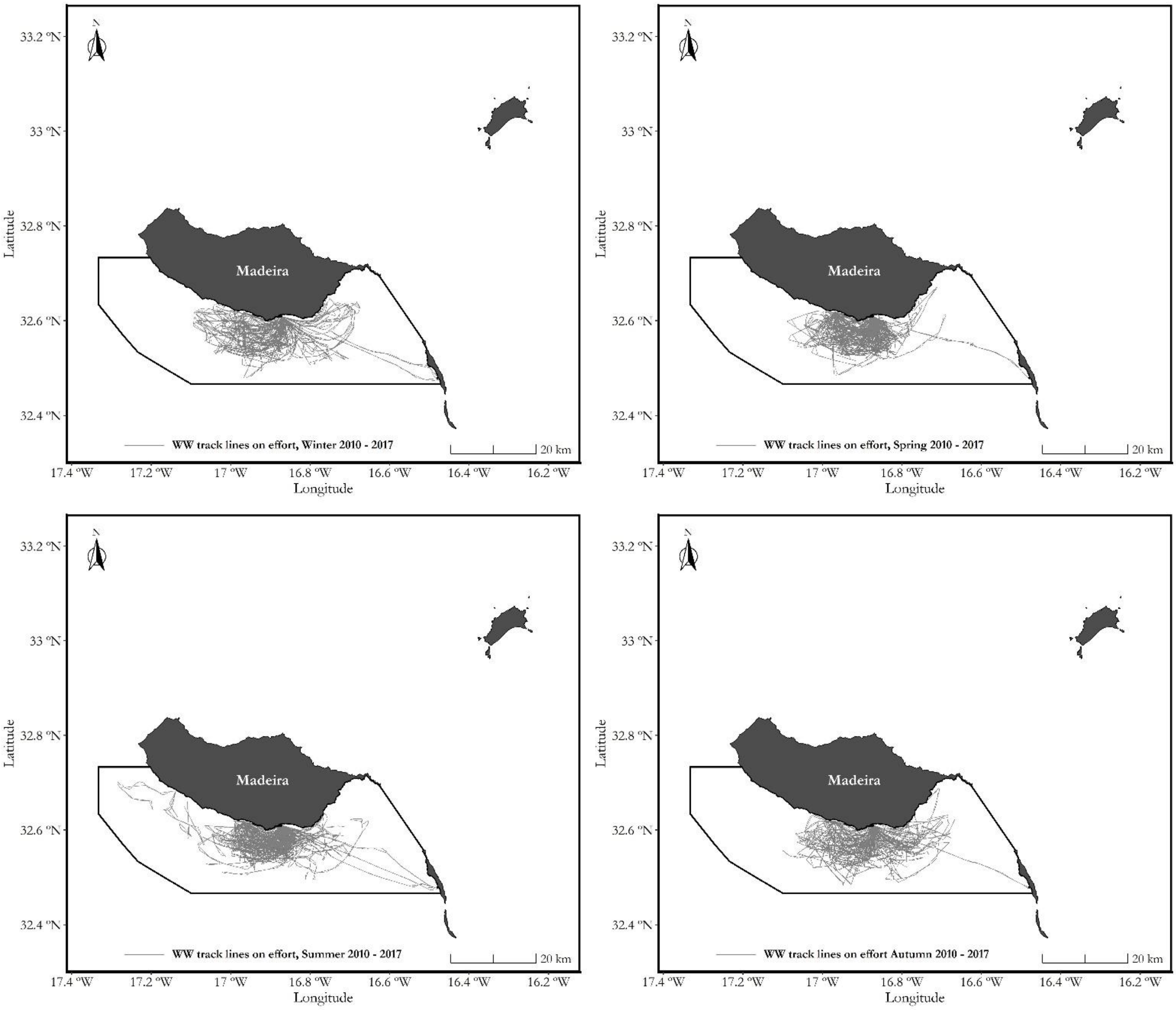




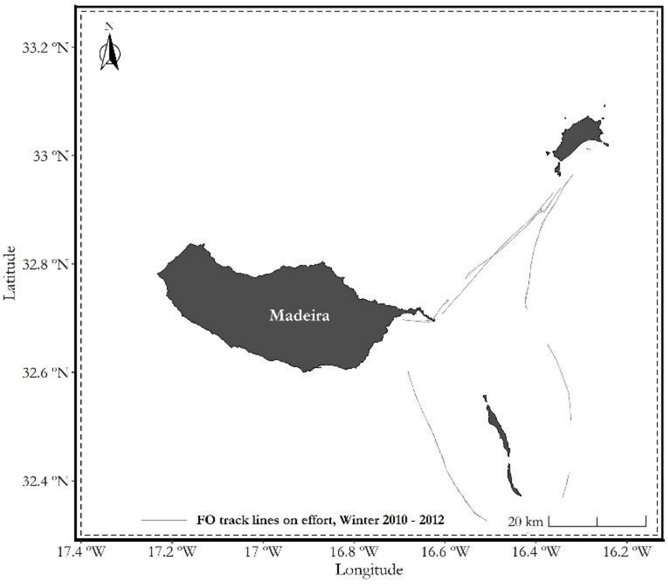
III.2.4 Effort of non-systematic shipboard surveys by season (Winter, Spring, Summer and Autumn) for 2004 – 2016

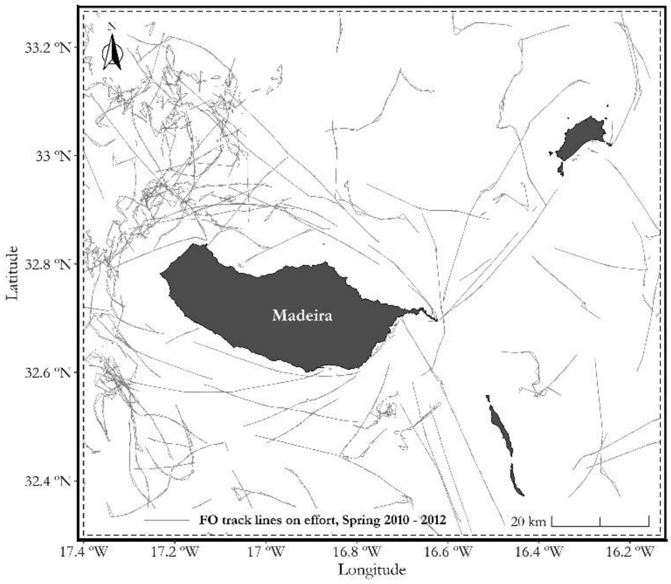


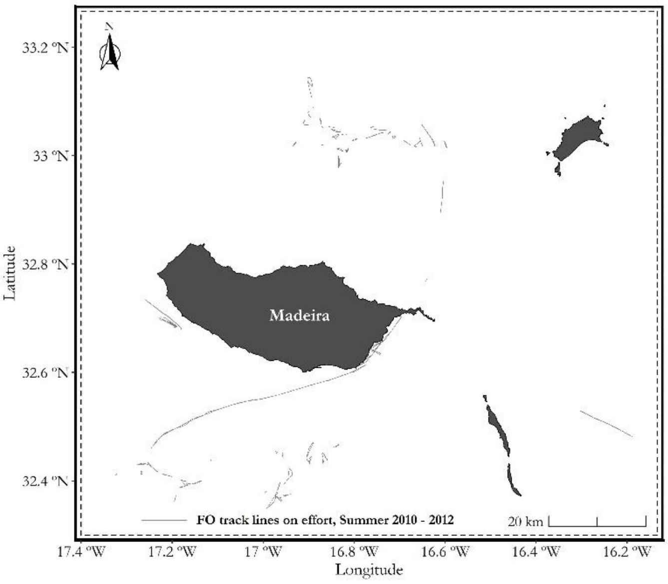
III.2.5 Effort of whale-watching observers' surveys by season (Winter, Spring, Summer and Autumn) for 2010 – 2017



III.2.6. Effort of fisheries observers' surveys by season (Winter, Spring, and Summer) for 2010 – 2012







III.3. Average covariates values in the study area and offshore waters over the study period

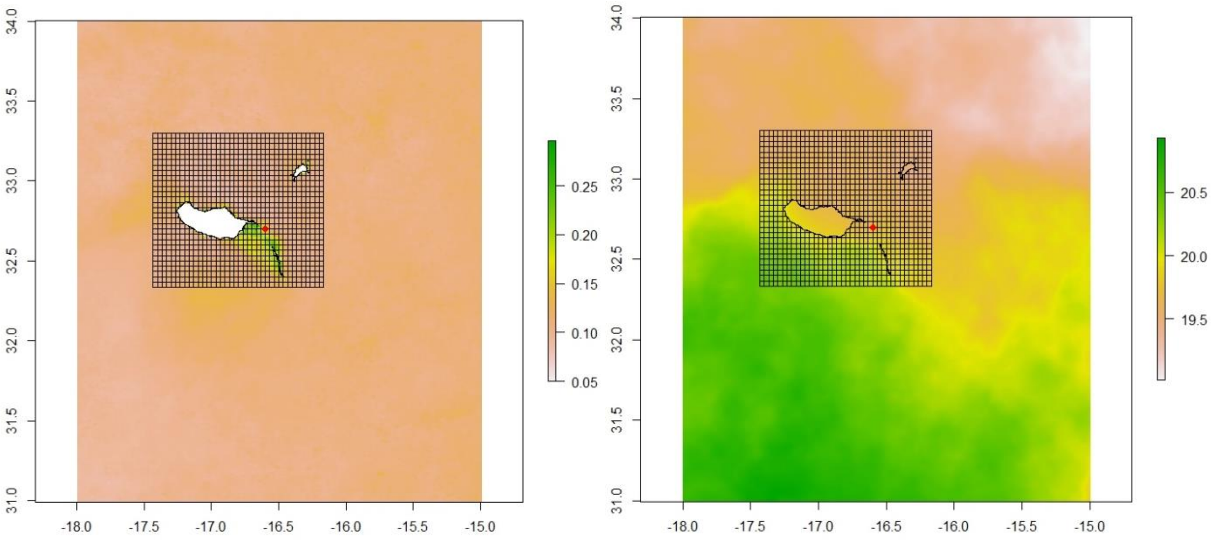


Figure III.1-1 – Example of monthly averaged satellite measurements of chlorophyll-a concentration (left) and sea surface temperature (right) used to calculate the dynamic environmental variables used in the habitat use modelling. The grid encompasses the study area. The average values of the dynamic environmental variables by year, presented Figure III.3.2 and Figure III.3.3, and by month, presented in Figure III.3.4 and Figure III.3.5, were calculated for the inshore area as the average of the values under the grid, and for offshore area as the average of the remaining values in the plots.

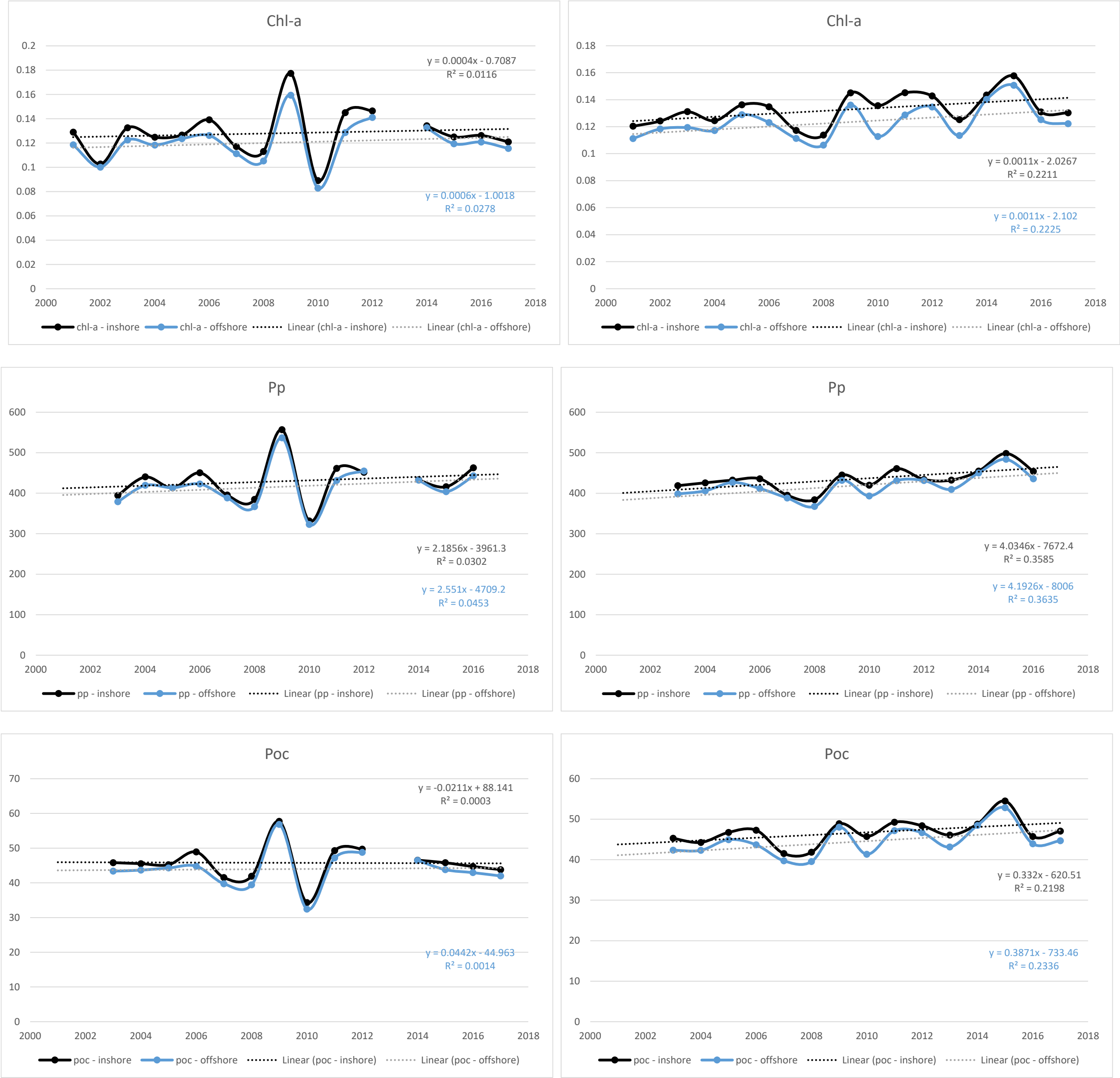


Figure III.3-2 – Yearly averaged values of the dynamic environmental variables (Chl-a: chlorophyll-a; Pp: primary productivity; Poc: particulate organic carbon) used in the habitat use modelling for the study period (2001 – 2017). The values presented on the graphs on the left were calculated as the yearly average of the months for which there was sampling effort in this study, while values presented on the graphs on the right were calculated as the yearly average of all months. The black line, identified as inshore in the graphs, represents the variables' average values in to the study area (inside the grid, in Figure III.3-1) and the blue line, identified as offshore in the graphs, represents the variables' average values in the surrounding area (outside the grid, in Figure III.3-1).

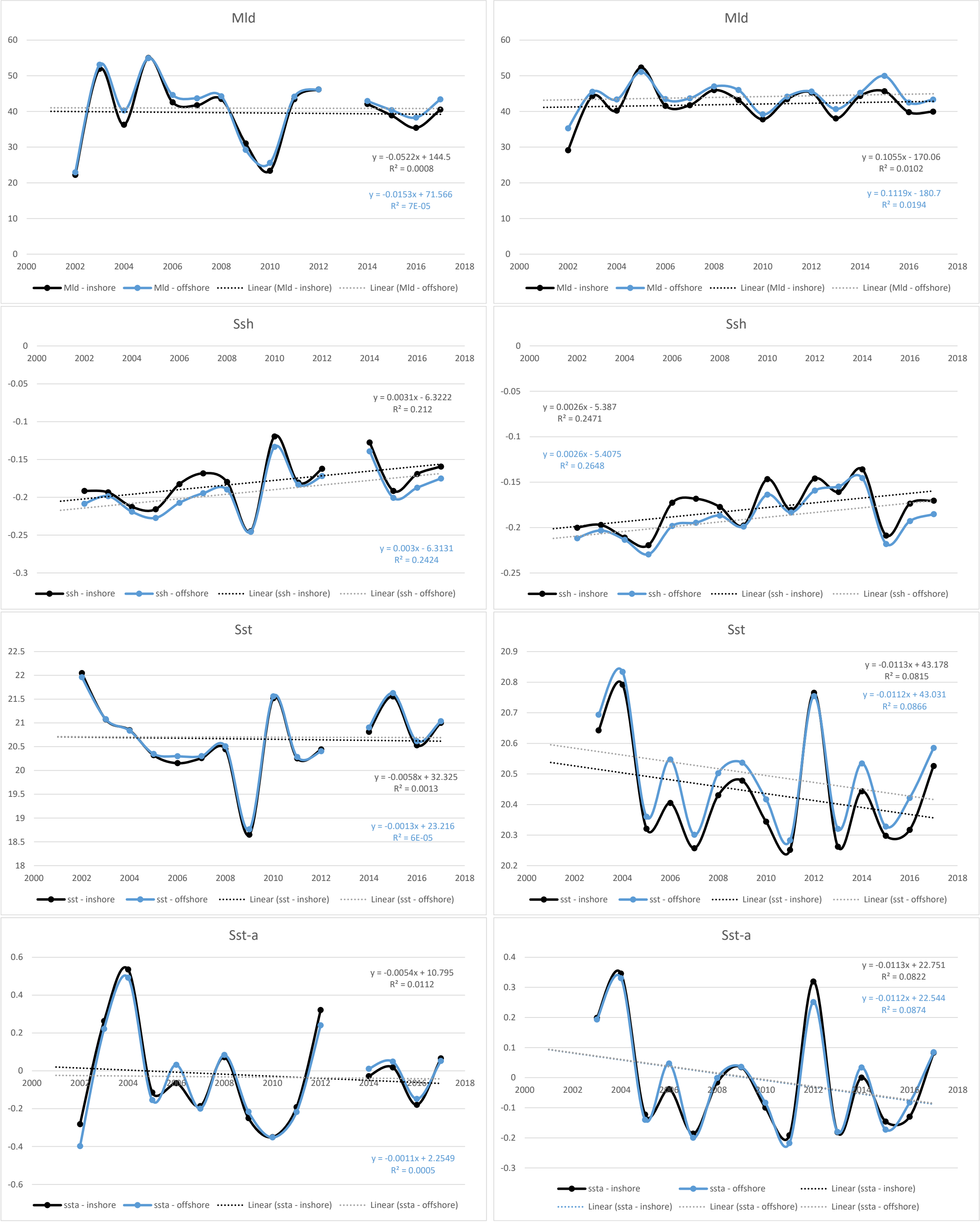


Figure III.3-3 – Yearly averaged values of the dynamic environmental variables (Mld: mixed layer depth; Ssh: sea surface height; Sst: sea surface temperature; Sst-a: sea surface temperature anomaly) used in the habitat use modelling for the study period (2001 – 2017). The values presented on the graphs on the left were calculated as the yearly average of the months for which there was sampling effort in this study, while values presented on the graphs on the right were calculated as the yearly average of all months. The black line, identified as inshore in the graphs, represents the variables' average values in to the study area (inside the grid, in Figure III.3-1) and the blue line, identified as offshore in the graphs, represents the variables' average values in the surrounding area (outside the grid, in Figure III.3-1).

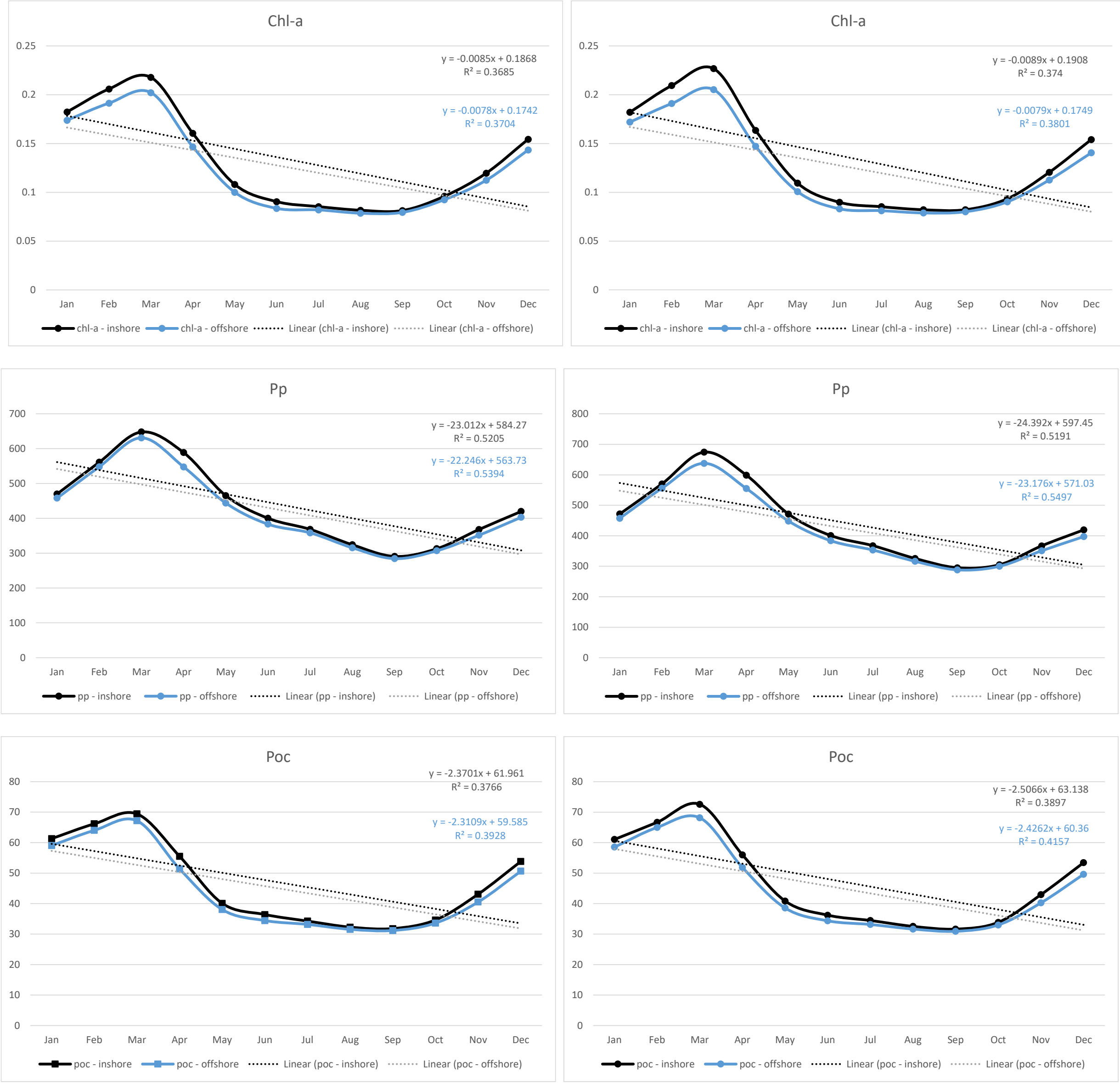


Figure III.3-4 – Monthly averaged values of the dynamic environmental variables (Chl-a: chlorophyll-a; Pp: primary productivity; Poc: particulate organic carbon) used in the habitat use modelling for the study period (2001 – 2017). The values presented on the graphs on the left were calculated as the monthly average of the months for which there was sampling effort in this study, while values presented on the graphs on the right were calculated as the monthly average of all months. The black line, identified as inshore in the graphs, represents the variables' average values in to the study area (inside the grid, in Figure III.3-1) and the blue line, identified as offshore in the graphs, represents the variables' average values in the surrounding area (outside the grid, in Figure III.3-1).

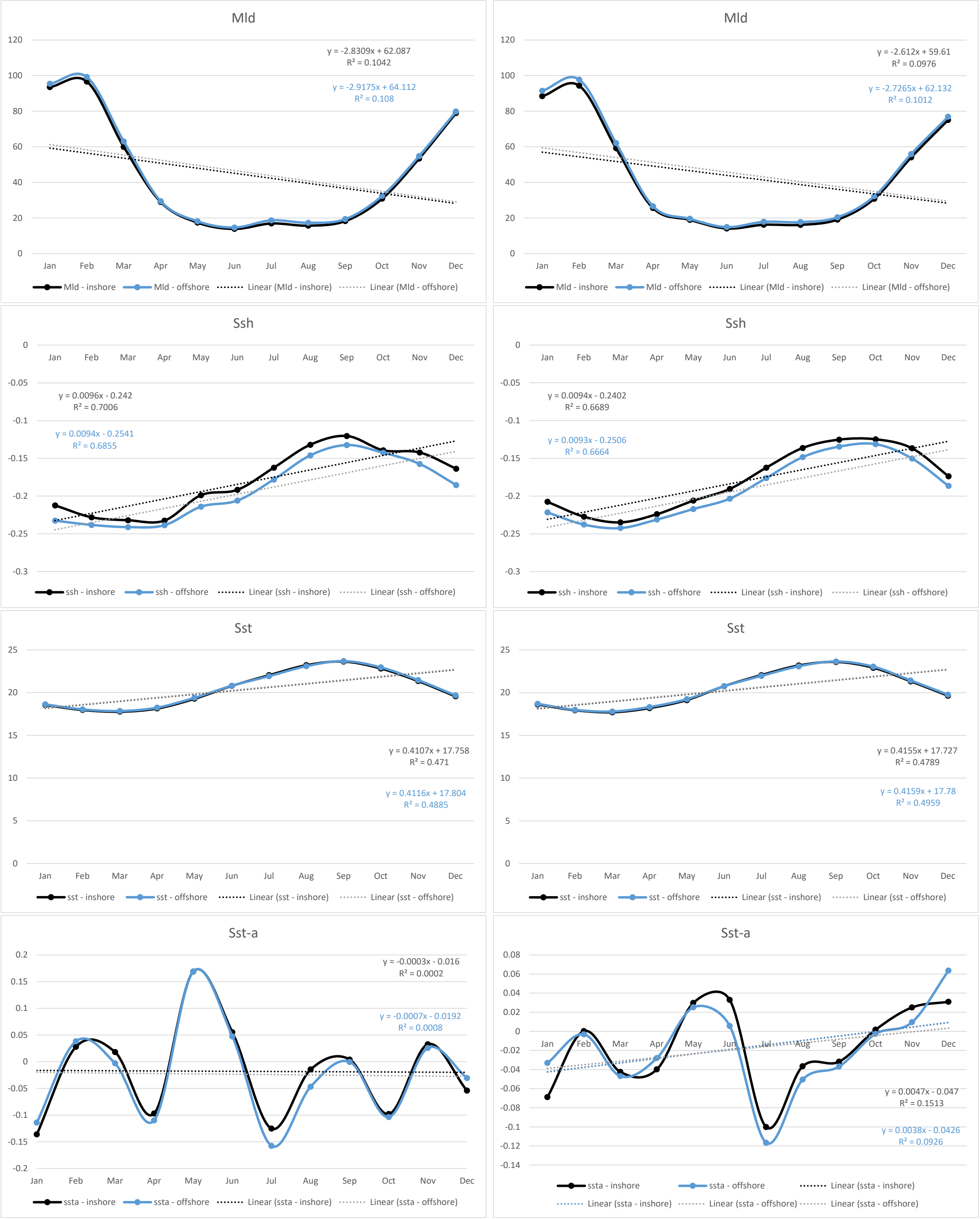


Figure III.3-5 – Monthly averaged values of the dynamic environmental variables (Mld: mixed layer depth; Ssh: sea surface height; Sst: sea surface temperature; Sst-a: sea surface temperature anomaly) used in the habitat use modelling for the study period (2001 – 2017). The values presented on the graphs on the left were calculated as the monthly average of the months for which there was sampling effort in this study, while values presented on the graphs on the right were calculated as the monthly averages of all months. The black line, identified as inshore in the graphs, represents the variables' average values in to the study area (inside the grid, in Figure III.3-1) and the blue line, identified as offshore in the graphs, represents the variables' average values in the surrounding area (outside the grid, in Figure III.3-1).

APPENDIX IV

APPENDIX IV.

IV.1. Encounter rates

IV.1.1. Group encounter rates by type of survey

Table IV.1.1-1. Summary of the number of sightings and observed encounter rates (ER) of cetacean species by type of survey for the period 2001-2017 in extended area of the Madeira inshore waters. SLS – systematic line-transect surveys, including SLS-RD – systematic line-transect surveys for photo-identification using robust design; ALS – aerial line-transect surveys; NSS – non-systematic surveys (photo-identification and biopsy sampling); WWO – observers on whale-watching vessels; FO – observers on tuna fishing vessels.

ER order	Survey type	SLS		ALS		SNS		FO		WWO		All		
	Species	Sightings	ER	Sightings	ER	Sightings	ER	Sightings	ER	Sightings	ER	Sightings	ER	%
1	*Tursiops truncatus*	116	0.652	29	0.167	99	1.177	5	0.136	146	1.635	395	0.704	20.93%
2	*Stenella frontalis*	86	0.484	26	0.150	99	1.177	5	0.136	168	1.882	384	0.684	20.35%
3	*Delphinus delphis*	118	0.664	50	0.289	57	0.678	61	1.654	71	0.795	357	0.636	18.92%
4	*Globicephala macrorhynchus*	68	0.382	13	0.075	68	0.809	3	0.081	84	0.941	236	0.420	12.51%
5	*Balanenoptera edeni*	31	0.174	10	0.058	30	0.357	2	0.054	49	0.549	122	0.217	6.47%
6	*Physeter macrocephalus*	30	0.169	13	0.075	18	0.214	2	0.054	22	0.246	85	0.151	4.50%
7	*Stenella coeruleoalba*	24	0.135	9	0.052	11	0.131	3	0.081	12	0.134	59	0.105	3.13%
8	*Balaenoptera physalus*	15	0.084	0	0.000	2	0.024	0	0.000	11	0.123	28	0.050	1.48%
9	*Ziphius cavirostris*	8	0.045	4	0.023	0	0.000	0	0.000	1	0.011	13	0.023	0.69%
10	*Grampus griseus*	4	0.022	1	0.006	2	0.024	0	0.000	4	0.045	11	0.020	0.58%
11	*Mesoplodon densirostris*	3	0.017	0	0.000	4	0.048	0	0.000	4	0.045	11	0.020	0.58%
12	*Kogia breviceps*	6	0.034	0	0.000	3	0.036	0	0.000	1	0.011	10	0.018	0.53%
13	*Steno bredanensis*	1	0.006	0	0.000	4	0.048	0	0.000	5	0.056	10	0.018	0.53%
14	*Pseudorca crassidens*	0	0.000	0	0.000	3	0.036	2	0.054	0	0.000	5	0.009	0.26%
15	*Balaenoptera borealis*	2	0.011	2	0.012	0	0.000	0	0.000	0	0.000	4	0.007	0.21%
16	*Orcinus orca*	0	0.000	0	0.000	1	0.012	1	0.027	1	0.011	3	0.005	0.16%
17	*Feresa attenuata*	0	0.000	0	0.000	1	0.012	1	0.027	0	0.000	2	0.004	0.11%
18	*Pepenocephala electra*	0	0.000	0	0.000	1	0.012	0	0.000	0	0.000	1	0.002	0.05%
19	*Mesoplodon bidens*	1	0.006	0	0.000	0	0.000	0	0.000	0	0.000	1	0.002	0.05%
20	*Balaenoptera acuturostrata*	1	0.006	0	0.000	0	0.000	0	0.000	0	0.000	1	0.002	0.05%
21	*Balaenoptera musculus*	0	0.000	0	0.000	1	0.012	0	0.000	0	0.000	1	0.002	0.05%
	total species	***514***	***2.891***	***157***	***0.906***	***404***	***4.805***	***85***	***2.304***	***579***	***6.486***	***1739***	***3.098***	**-**
	Balaenoptera sp.	35	0.197	7	0.040	24	0.285	30	0.813	5	0.136	101	0.180	5.35%
	Mesoplodon sp.	11	0.062	1	0.006	2	0.024	2	0.054	4	0.108	20	0.036	1.06%
	Kogia sp.	1	0.006	1	0.006	1	0.012	0	0.000	0	0.000	3	0.005	0.16%
	Ziphiidae	15	0.084	2	0.012	4	0.048	0	0.000	3	0.081	24	0.043	1.27%
	total	***576***	***3.240***	***168***	***0.970***	***435***	***5.174***	***117***	***3.172***	***591***	***6.811***	***1887***	***3.362***	100.00%

IV.1.2 Group encounter rates by Season

Table IV.1.2-1. Summary of the number of sightings and observed encounter rates (ER) of cetacean species by season (Winter, Spring, Summer, Autumn for the period 2001-2017 in extended area of the Madeira inshore waters.

ER order	Season	Winter		Spring		Summer		Autumn		All	
	Species	Sightings	ER	Sightings	ER	Sightings	ER	Sightings	ER	Sightings	ER
1	*Tursiops truncatus*	54	0.497	115	0.666	144	0.857	82	0.733	395	0.704
2	*Stenella frontalis*	40	0.368	119	0.689	175	1.041	50	0.447	384	0.684
3	*Delphinus delphis*	130	1.195	205	1.188	11	0.065	11	0.098	357	0.636
4	*Globicephala macrorhynchus*	36	0.331	29	0.168	78	0.464	93	0.831	236	0.420
5	*Balanenoptera edeni*	3	0.028	26	0.151	61	0.363	32	0.286	122	0.217
6	*Physeter macrocephalus*	11	0.101	25	0.145	22	0.131	27	0.241	85	0.151
7	*Stenella coeruleoalba*	12	0.110	29	0.168	13	0.077	5	0.045	59	0.105
8	*Balaenoptera physalus*	15	0.138	7	0.041	4	0.024	2	0.018	28	0.050
9	*Ziphius cavirostris*	1	0.009	2	0.012	9	0.054	1	0.009	13	0.023
10	*Grampus griseus*	0	0	4	0.023	5	0.030	2	0.018	11	0.020
11	*Mesoplodon densirostris*	0	0	4	0.023	4	0.024	3	0.027	11	0.020
12	*Kogia breviceps*	1	0.009	5	0.029	4	0.024	0	0	10	0.018
13	*Steno bredanensis*	0	0	3	0.017	5	0.030	2	0.018	10	0.018
14	*Pseudorca crassidens*	0	0	1	0.006	4	0.024	0	0	5	0.009
15	*Balaenoptera borealis*	0	0	1	0.006	2	0.012	1	0.009	4	0.007
16	*Orcinus orca*	0	0	1	0.006	2	0.012	0	0	3	0.005
17	*Feresa attenuata*	0	0	2	0.012	0	0	0	0	2	0.004
18	*Pepenocephala electra*	0	0	0	0	1	0.006	0	0	1	0.002
19	*Mesoplodon bidens*	0	0	0	0	1	0.006	0	0	1	0.002
20	*Balaenoptera acuturostrata*	0	0	0	0	1	0.006	0	0	1	0.002
21	*Balaenoptera musculus*	0	0	1	0.006	0	0	0	0	1	0.002
	total species	***303***	***2.786***	***579***	***3.354***	***546***	***3.249***	***311***	***2.780***	***1739***	***3.098***
	Balaenoptera sp.	8	0.074	32	0.185	38	0.226	23	0.206	101	0.180
	Mesoplodon sp.	2	0.018	9	0.052	4	0.024	5	0.045	20	0.036
	Kogia sp.	0	0	1	0.006	2	0.012	0	0	3	0.005
	Ziphiidae	2	0.018	7	0.041	13	0.077	2	0.018	24	0.043
	total	***315***	***2.897***	***628***	***3.638***	***603***	***3.588***	***341***	***3.048***	***1887***	***3.362***

IV.2. Group size

IV.2.1. Group size by survey type

Table IV.2.1-1. Summary of the observed group size and respective statistics (sd - standard deviation; n – observations) for each type of survey. SLS – systematic line-transect surveys; ALS – aerial line-transect surveys; SLS-RD – systematic line-transect surveys for photo-identification using robust design; NSS – non-systematic surveys (photo-identification and biopsy sampling); WWO – observers on whale-watching vessels; FO – observers on tuna fishing vessels.

	ALL (Except FO)						SLS						SAS					
	mean	**median**	**sd**	**n**	**min**	**max**	**mean**	**median**	**sd**	**n**	**min**	**max**	**mean**	**median**	**sd**	**n**	**min**	**max**
Tursiops truncatus	**16.0**	**12**	15	390	1	90	16.9	11	17	116	1	90	23.2	16	20	29	2	90
Stenella frontalis	**36.6**	**25**	45	378	1	500	32.7	12	72	86	1	500	68.3	60	50	25	11	200
Delphinus delphis	**21.5**	**12**	26	294	1	170	14.0	8	22	117	1	170	38.9	33	34	50	1	150
Globicephala macrorhynchus	**14.7**	**12**	12	233	1	60	12.2	10	10	68	1	55	13.5	14	8	13	1	30
Balaenoptera edeni	**1.7**	**1**	1	120	1	5	1.7	2	1	31	1	5	1.7	2	1	10	1	3
Physeter macrocephalus	**3.0**	**2**	3	85	1	15	2.6	1	3	30	1	13	2.2	1	2	13	1	7
Stenella coeruleoalba	**21.4**	**16**	18	56	1	70	14.0	12	11	24	1	35	34.0	25	22	9	4	70
Balaenoptera physalus	**2.1**	**2**	2	28	1	10	2.1	1	2	15	1	10	0.0	0	0	0	0	0
Mesoplodon sp.	**2.9**	**2**	2	19	1	8	2.4	2	2	11	1	6	5.0	5	-	1	5	5
Kogia sp.	**1.2**	**1**	0	14	1	2	1.3	1	0	7	1	2	2.0	2	-	1	2	2
Ziphius cavirostris	**2.1**	**2**	1	14	1	4	2.3	2	1	8	1	4	2.0	2	1	5	1	3
Mesoplodon densirostris	**3.8**	**4**	2	17	1	8	3.3	4	2	4	1	5	3.0	3	-	1	3	3
Grampus griseus	**12.6**	**8**	8	16	1	30	10.2	7	12	5	1	30	11.5	12	5	2	8	15
Steno bredanensis	**17.8**	**12**	12	12	4	60	6.7	6	3	3	4	10	0.0	0	-	0	0	0
Balaenoptera borealis	**1.6**	**1**	1	12	1	5	1.5	1	1	4	1	3	2.7	2	2	3	1	5
Orcinus orca	**4.0**	**4**	3	2	2	6	0	0	-	0	0	0	0	0	-	0	0	0
Pseudorca crassidens	**31.7**	**25**	16	3	20	50	0	0	-	0	0	0	0	0	-	0	0	0
Balaenoptera acuturostrata	**1**	**1**	-	1	1	1	0	0	-	0	0	0	0	0	-	0	0	0
Balaenopteridae	**1.3**	**1**	1	64	1	3	1.2	1	0	28	1	2	1.3	1	0	7	1	2
Ziphiidae	**1.6**	**1**	1	24	1	4	1.5	1	1	15	1	3	2.0	2	1	2	1	3

	NSS						WWO						FO					
	mean	**median**	**sd**	**n**	**min**	**max**	**mean**	**median**	**sd**	**n**	**min**	**max**	**mean**	**median**	**sd**	**n**	**min**	**max**
Tursiops truncatus	**16.2**	**13**	14	99	1	85	13.9	10	12	146	1	50	7.2	8.0	3.7	5	1	10
Stenella frontalis	**27.7**	**20**	23	99	1	150	39.2	30	31	168	1	200	19.2	15.0	15.4	5	3	40
Delphinus delphis	**17.3**	**12**	19	57	1	100	25.2	14	25	70	1	100	15.4	13.0	13.5	60	1	80
Globicephala	**19.0**	**18**	13	68	1	60	13.4	10	13	84	1	60	19.0	20.0	16.5	3	2	35
Balaenoptera edeni	**1.8**	**2**	1	30	1	5	1.7	1	1	49	1	5	2.0	2.0	0.0	2	2	2
Physeter macrocephalus	**3**	**2**	4	18	1	15	4.2	3	3	22	1	12	1	1	0	2	1	1
Stenella coeruleoalba	**22.6**	**15**	16	11	8	50	25.3	18	12	12	70	70	7	5	4	3	4	12
Balaenoptera physalus	**2.0**	**2**	0	2	2	2	2.3	2	1	11	1	4	0.0	0.0	-	0	0	0
Mesoplodon sp.	**1.5**	**2**	1	2	1	2	4.2	3	3	5	1	8	2.0	2.0	1.4	2	1	3
Kogia sp.	**1.0**	**1**	0	4	1	1	1.0	1	0	2	1	1	0.0	0.0	0.0	0	0	0
Ziphius cavirostris	**0**	**0**	-	0	0	0	1.0	1	-	1	1	1	0.0	0.0	-	0	0	0
Mesoplodon densirostris	**3.8**	**3**	1	5	3	5	4.1	4	2	7	1	8	0.0	0.0	-	0	0	0
Grampus griseus	**16.3**	**18**	9	4	5	25	12.6	12	5	5	7	20	0.0	0.0	-	0	0	0
Steno bredanensis	**15.3**	**17**	5	4	8	20	26.6	13	23	5	10	60	0.0	0.0	-	0	0	0
Balaenoptera borealis	**1.0**	**1**	-	1	1	1	1.0	1	0	4	1	1	0.0	0.0	-	0	0	0
Orcinus orca	**2.0**	**2**	-	1	2	2	6.0	6	-	1	6	6	6.0	6.0	-	1	6	6
Pseudorca crassidens	**31.7**	**25**	16	3	20	50	0	0	-	0	0	0	9.0	9.0	8.5	2	3	15
acuturostrata	**0**	**0**	-	0	0	0	0	0	-	0	0	0	0	0	-	0	0	0
Balaenopteridae	**1.5**	**1**	1	24	1	3	1.0	1	0	5	1	1	1.7	1.0	1.3	30	1	5
Ziphiidae	**2.0**	**2**	1	4	1	4	1.3	1	1	3	1	2	0.0	0.0	0.0	0	0	0

IV.2.2. Group size by season (include data from all surveys except FO)

Table IV.2.2-1. Summary of the observed group size and respective statistics (sd - standard deviation; n – observations) by season for the period 2001-2017.

	Winter						Spring						Summer						Autumn					
	mean	**median**	**sd**	**n**	**min**	**max**	**mean**	**median**	**sd**	**n**	**min**	**max**	**mean**	**median**	**sd**	**n**	**min**	**max**	**mean**	**median**	**sd**	**n**	**min**	**max**
Tursiops truncatus	**14.1**	**10**	14	54	2	60	**13.2**	**10**	12	112	1	60	**19.0**	**15**	15	142	1	85	**16.0**	**11**	18	82	1	90
Stenella frontalis	**36.8**	**20**	43	40	1	200	**26.6**	**25**	20	113	1	100	**38.1**	**25**	42	177	0	370	**52.2**	**35**	79	50	1	500
Delphinus delphis	**20.4**	**12**	26	130	1	150	**19.4**	**12**	21	145	0	100	**58.0**	**50**	50	11	8	170	**22.6**	**13**	36	10	0	120
Globicephala macrorhynchus	**14.8**	**12**	12	36	1	55	**18.5**	**17**	13	26	1	50	**17.8**	**14**	14	78	1	60	**10.9**	**9**	9	93	1	50
Balaenoptera edeni	**2.0**	**2**	0	3	2	2	**1.5**	**1**	1	25	1	4	**1.8**	**1**	1	60	1	5	**1.8**	**2**	1	32	1	5
Physeter macrocephalus	**3.4**	**3**	2	11	1	7	**3.3**	**2**	4	23	1	15	**2.1**	**1**	2	22	1	10	**3.6**	**2**	3	27	1	12
Stenella coeruleoalba	**20.3**	**13**	17	12	1	60	**19.8**	**17**	15	26	4	60	**26.4**	**15**	24	13	2	70	**19.0**	**20**	10	5	8	30
Balaenoptera physalus	**1.9**	**1**	1	15	1	4	**3.4**	**2**	3	7	1	10	**1.3**	**1**	1	4	1	2	**1.5**	**2**	1	2	1	2
Mesoplodon sp.	**2.0**	**2**	1	2	1	3	**2.9**	**2**	2	7	1	6	**4.2**	**5**	3	5	1	8	**2.0**	**2**	1	5	1	3
Kogia sp.	**1.0**	**1**	-	1	1	1	**1.3**	**1**	0	7	1	2	**1.2**	**1**	0	6	1	2	**0.0**	**0**	-	1	0	0
Ziphius cavirostris	**1.0**	**1**	-	1	1	1	**2.0**	**2**	0	2	2	2	**2.1**	**2**	1	10	1	4	**3.0**	**3**	-	1	3	3
Mesoplodon densirostris	**0.0**	**0**	-	0	0	0	**3.3**	**3**	0	7	3	4	**5.0**	**5**	2	7	3	8	**2.0**	**1**	2	3	1	4
Grampus griseus	**0.0**	**0**	-	0	0	0	**13.2**	**12**	5	5	7	20	**13.5**	**11**	12	6	1	30	**11.6**	**10**	6	5	5	20
Steno bredanensis	**0.0**	**0**	-	0	0	0	**12.3**	**15**	7	3	4	18	**21.3**	**10**	21	7	6	60	**14.0**	**14**	8	2	8	20
Balaenoptera borealis	**0.0**	**0**	-	0	0	0	**1.0**	**1**	0	2	1	1	**1.8**	**1**	1	8	1	5	**1.5**	**2**	1	2	1	2
Orcinus orca	**0.0**	**0**	-	0	0	0	**6.0**	**6**	-	1	6	6	**4.0**	**4**	3	2	2	6	**0.0**	**0**	-	0	0	0
Pseudorca crassidens	**0.0**	**0**	-	0	0	0	**3.0**	**3**	-	1	3	3	**31.7**	**25**	16	3	20	50	**0.0**	**0**	-	0	0	0
Balaenoptera acuturostrata	**0.0**	**0**	-	0	0	0	**0.0**	**0**	-	0	0	0	**1.0**	**1**	-	1	1	1	**0.0**	**0**	-	0	0	0
Balaenopteridae	**1.3**	**1**	1	4	1	2	**1.3**	**1**	0	7	1	2	**1.4**	**1**	1	34	1	3	**1.1**	**1**	0	19	1	2
Ziphiidae	**1.0**	**1**	0	2	1	1	**2.1**	**1**	1	7	1	4	**1.3**	**1**	1	13	1	3	**2.0**	**2**	0	2	2	2

IV.3. Degree of seasonality

Table IV.3.1-1. Classification of species degree of seasonality by comparing the difference between the average of the three months with lower ER (excluding months with no sightings) and the three months with higher ER.

Species	Three months		ratio
	lower	upper	
Delphinus delphis	0.03	1.63	**63**
Balaenoptera edeni	0.04	0.40	**10**
Balaenoptera physalus	0.02	0.16	6
Stenella frontalis	0.24	1.46	6
Globicephala macrorhynchus	0.15	0.86	6
Physeter macrocephalus	0.05	0.24	5
Stenella coeruleoalba	0.05	0.18	4
Mesoplodon sp.	0.03	0.07	3
Grampus griseus	0.02	0.05	2
Mesoplodon densirostris	0.02	0.04	2
Tursiops truncatus	0.43	0.91	2
Steno bredanensis	0.03	0.06	2
Kogia sp.	0.02	0.05	2
Ziphius cavirostris	0.02	0.05	2
Orcinus orca	0.01	0.02	2
Balaenoptera borealis	0.02	0.02	1
Pseudorca crassidens	0.01	0.01	1
Balaenoptera acuturostrata	0.02	0.02	1

APPENDIX V

APPENDIX V.

V.1. Spatial Modelling – habitat use (2001 – 2017)

V.1.1. Diagnostic and Uncertainty plots

V.1.1.1. Tursiops truncatus

Model of encounter rates of groups

Table V.1.1.1-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-3.9064	0.1138	-34.317	<0.001*
Survey type SLS-RD	-0.7728	0.2753	-2.807	0.005*
Survey type ALS	-0.8636	0.229	-3.771	<0.001*
Survey type NSS	0.3127	0.1583	1.975	0.048*
Survey type WWO	0.3362	0.1759	1.911	0.056
Survey type FO	-1.3705	0.4696	-2.918	0.004*
*Significant at α = 0.05				

Table V.1.1.1-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Distance to coast	0.8922	9	0.795	0.004*
Beaufort	0.9314	5	2.527	<0.001*
Effort	7.944	9	23.074	<0.001*
Year	0.9394	15	1.013	<0.001*
*Significant at α = 0.05				

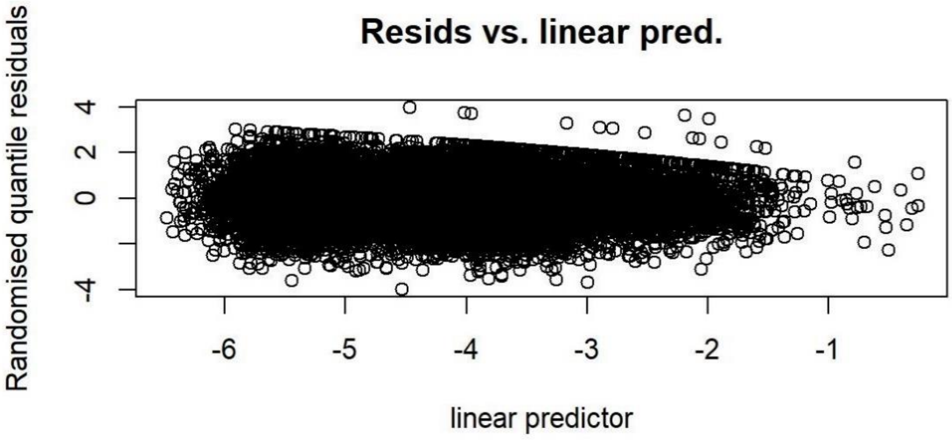


Figure V.1.1.1-1. Randomised quantile residuals plot of the selected generalised additive model of the encounter rate of bottlenose dolphin groups to check heteroskedasticity.

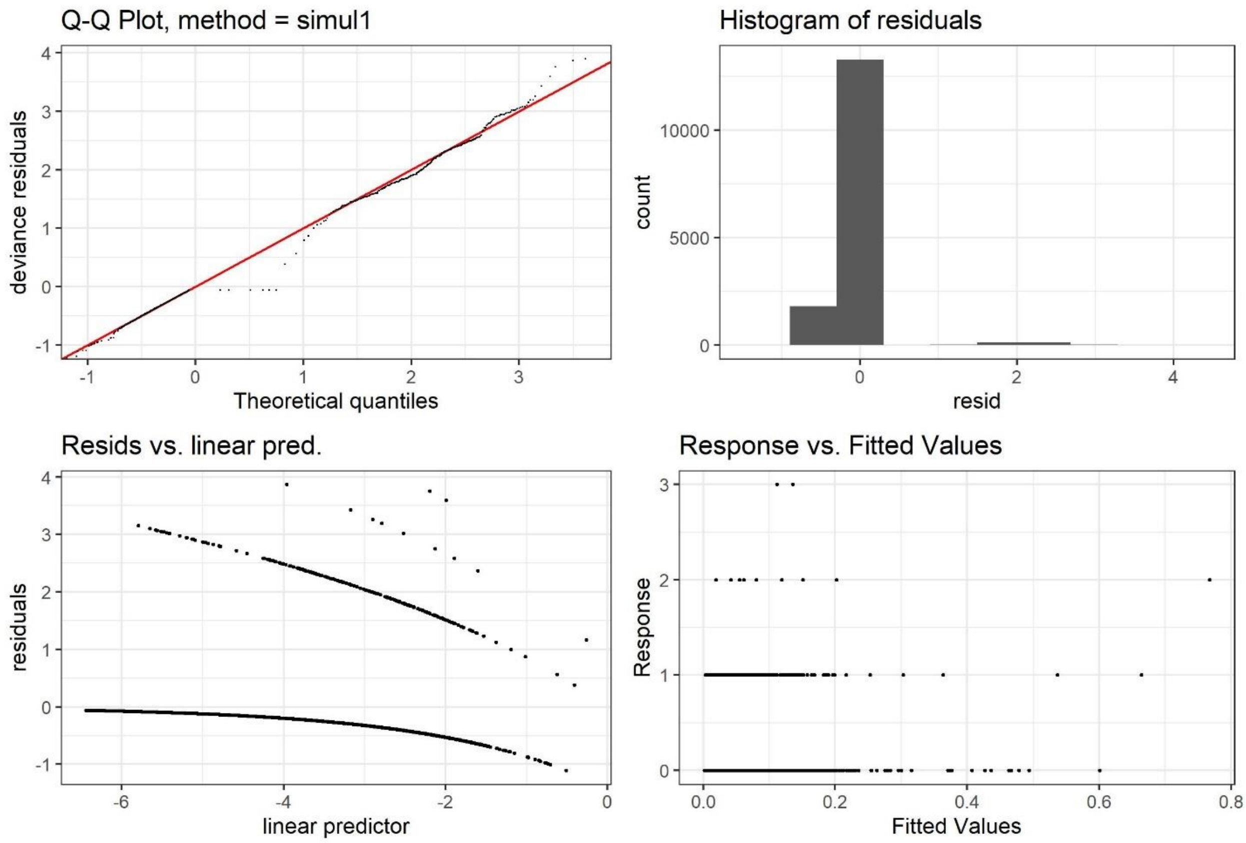


Figure V.1.1.1-2. Diagnostic plots of the selected generalised additive model of the encounter rate of bottlenose dolphin groups.

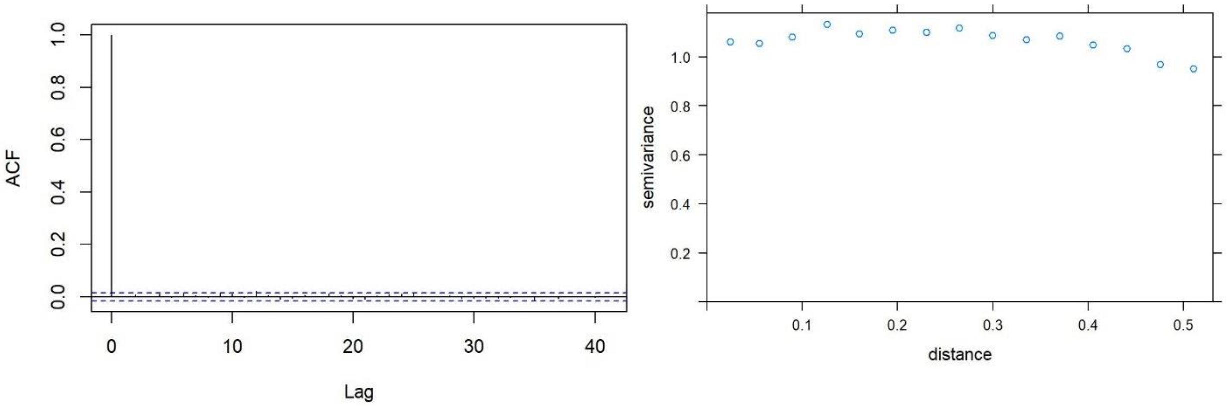


Figure V.1.1.1-3. Temporal auto-correlation regression plot from “acf” function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of bottlenose dolphin groups for the period 2001-2017.

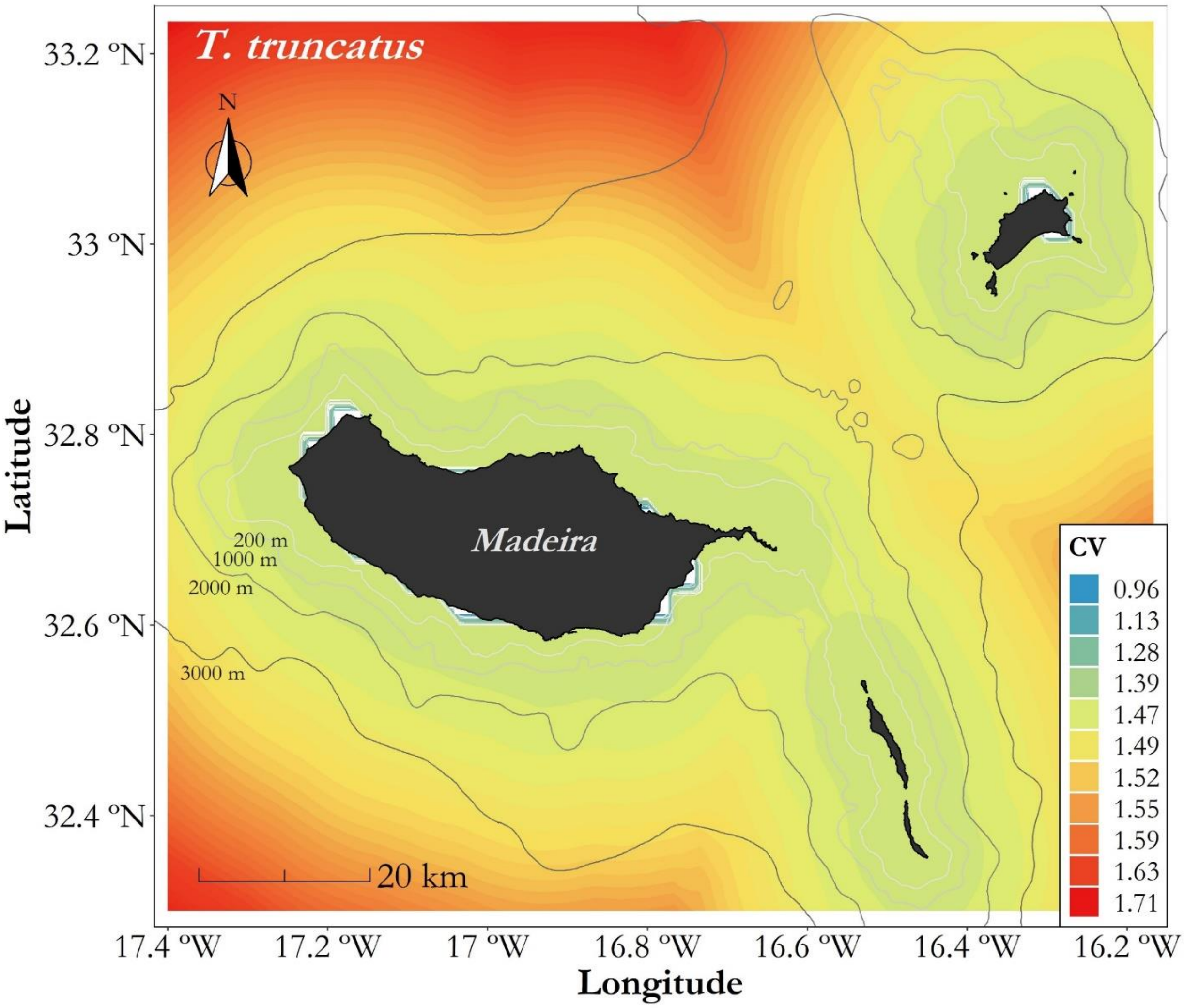


Figure V.1.1.1-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of bottlenose dolphins in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.1.1.2. *Stenella frontalis*

Model of encounter rates of groups

Table V.1.1.2-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-4.1995	0.1472	-28.523	<0.001*
Survey type SLS-RD	-0.5181	0.3906	-1.326	0.18471
Survey type ALS	-1.3912	0.2557	-5.441	<0.001*
Survey type NSS	0.1567	0.1964	0.798	0.42486
Survey type WWO	0.7831	0.2185	3.583	<0.001*
Survey type FO	-0.7784	0.4914	-1.584	0.1132
*Significant at α = 0.05				

Table V.1.1.2-2. Smooth terms in the encounter rate of groups estimation model (Poc 200-17- Mean particulate organic carbon for the period 2001 – 2017; Ssh 2001-17 – Mean sea surface height for the period 2001 – 2017; Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Slope area	1.0611	9	3.9160	<0.001*
Distance to escarpment	0.8007	9	0.3870	0.036*
Poc 2001-17	0.7756	9	0.3630	0.038*
Ssh 2001-17	0.8892	9	0.6890	0.007*
Aspect std dev	0.2221	9	0.0320	0.25312
Contour index	0.0791	5	0.0100	0.28016
Beaufort	0.8376	5	1.0100	0.013*
Month	5.5320	10	8.1620	<0.001*
Year	4.2209	14	1.0410	0.003*
Effort	6.6004	9	11.9840	<0.001*
*Significant at α = 0.05				

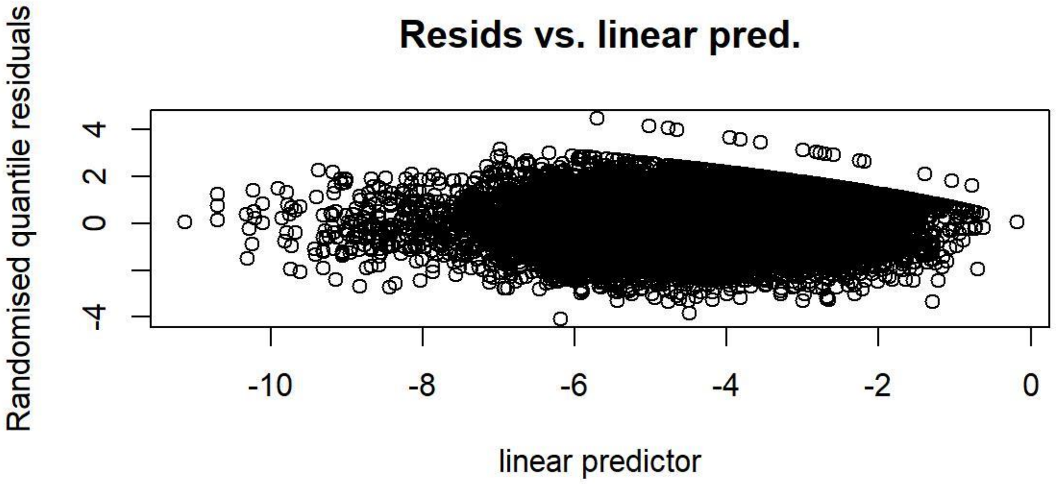


Figure V.1.1.2-1. Randomised quantile residuals plot of the selected generalised additive model of the encounter rate of spotted dolphin groups to check heteroskedasticity.

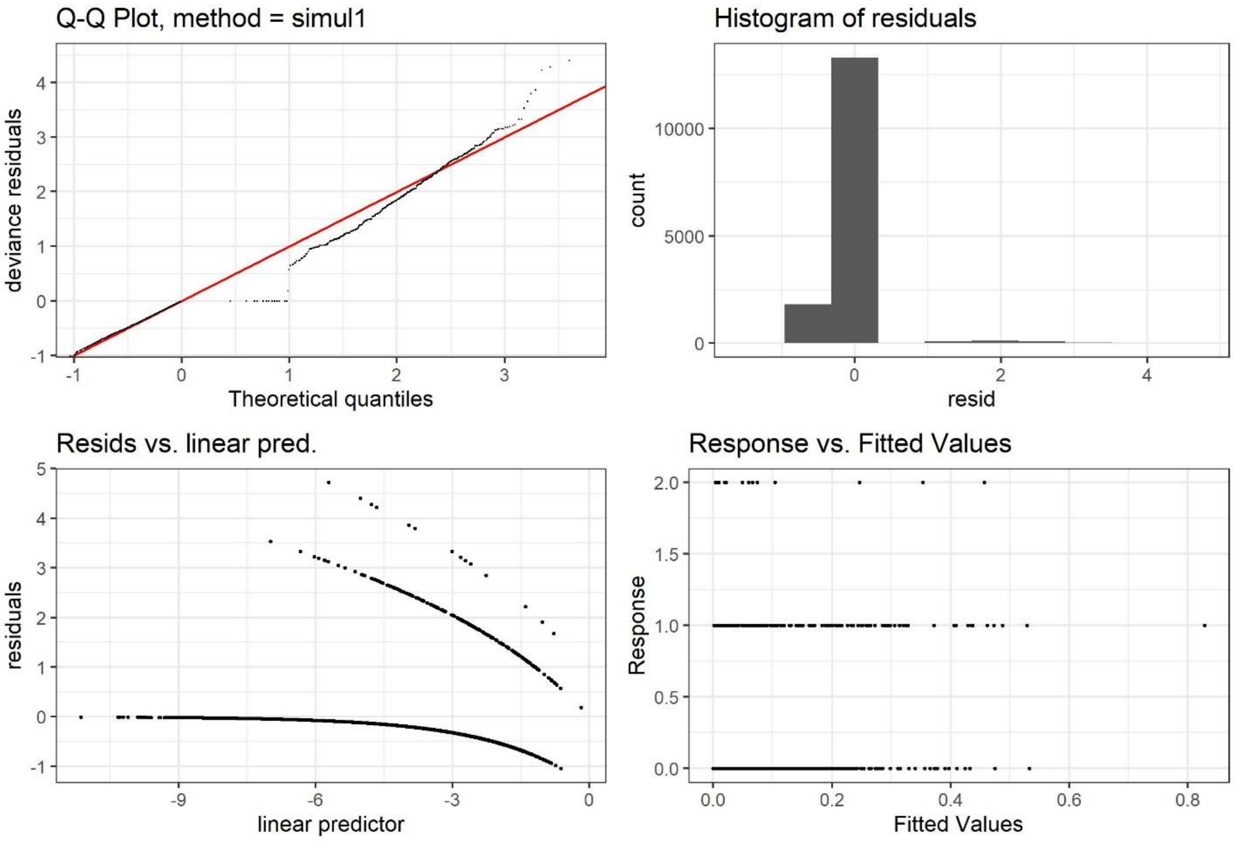


Figure V.1.1.2-2. Diagnostic plots of the selected generalised additive model of the encounter rate of spotted dolphin groups.

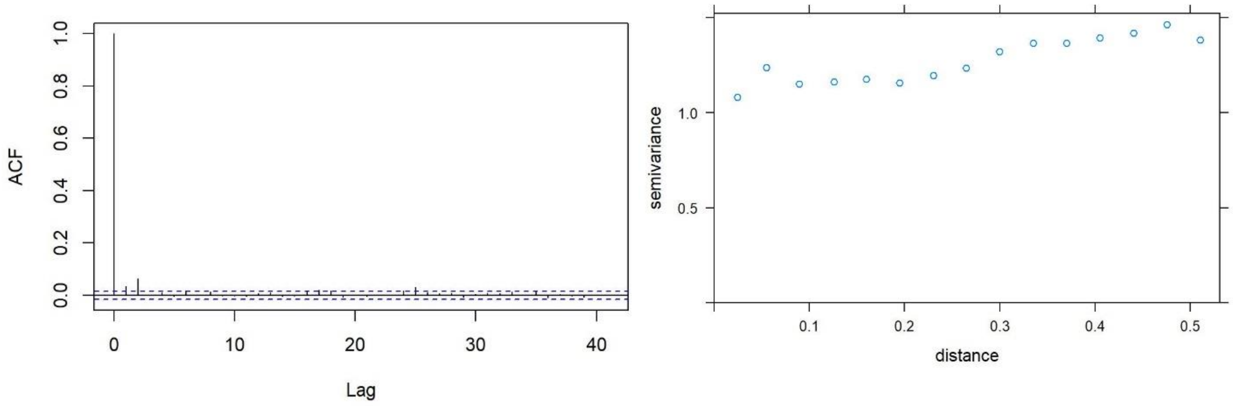


Figure V.1.1.2-3. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of spotted dolphin groups for the period 2001-2017.

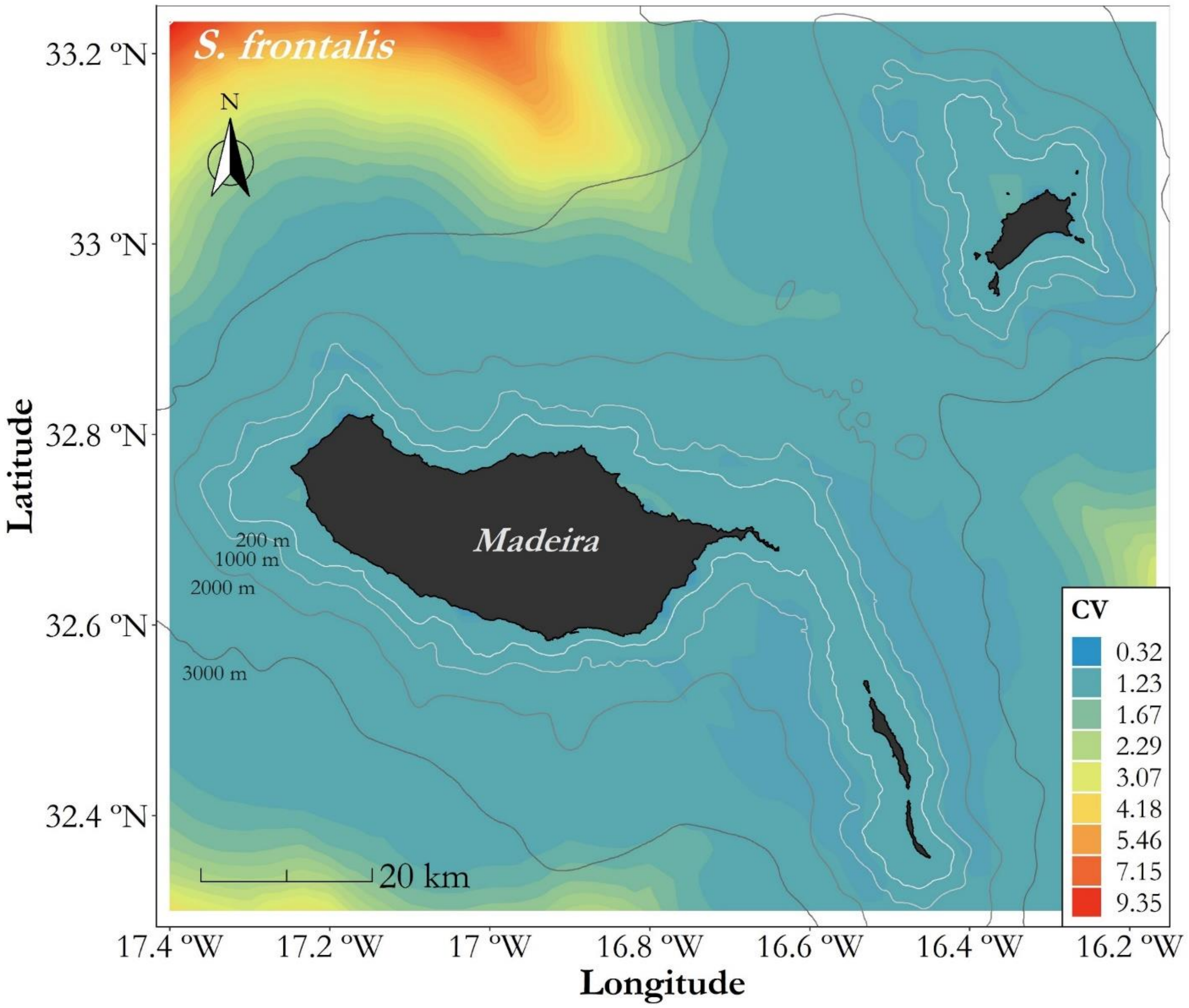


Figure V.1.1.2-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of spotted dolphins in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.1.3. Delphinus delphis

Model of encounter rates of groups

Table V.1.1.3-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-3.4107	0.1083	-31.495	<0.001*
Survey type SLS-RD	-	-	-	-
Survey type ALS	-0.8133	0.1787	-4.552	<0.001*
Survey type NSS	0.1674	0.1738	0.964	0.335
Survey type WWO	0.2177	0.176	1.237	0.216
Survey type FO	0.2124	0.1885	1.127	0.26
*Significant at α = 0.05				

Table V.1.1.3-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Slope area	0.835	9	0.503	0.015*
Average slope	0.8303	9	0.481	0.019*
Chl-a 200-17	0.8523	9	0.617	0.008*
Sst-a 2001-7	0.9297	9	1.028	0.001*
Month	3.9855	5	19.878	<0.001*
Beaufort	0.9519	5	3.526	<0.001*
Effort	5.1357	9	6.386	<0.001*
*Significant at α = 0.05				

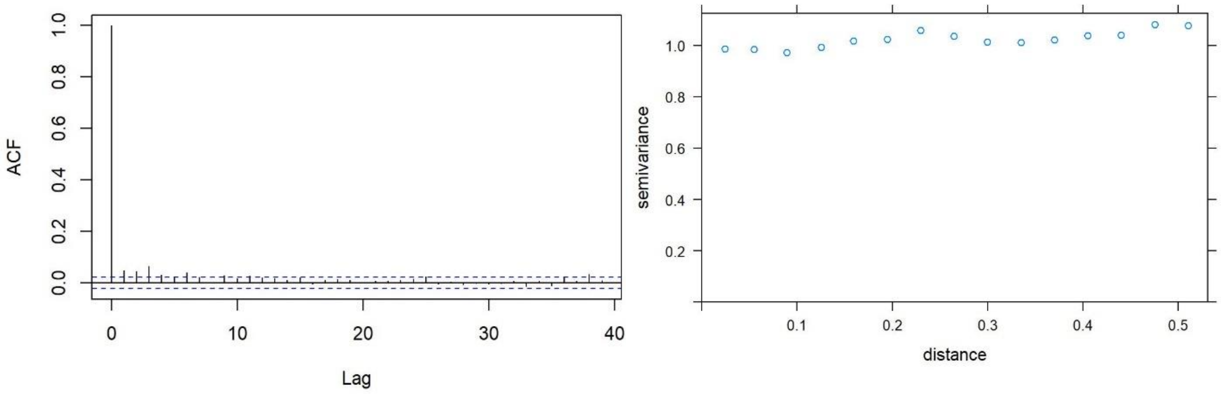


Figure V.1.1.3-1. Temporal auto-correlation regression plot from “acf” function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of common dolphins’ group for the period 2001-2017.

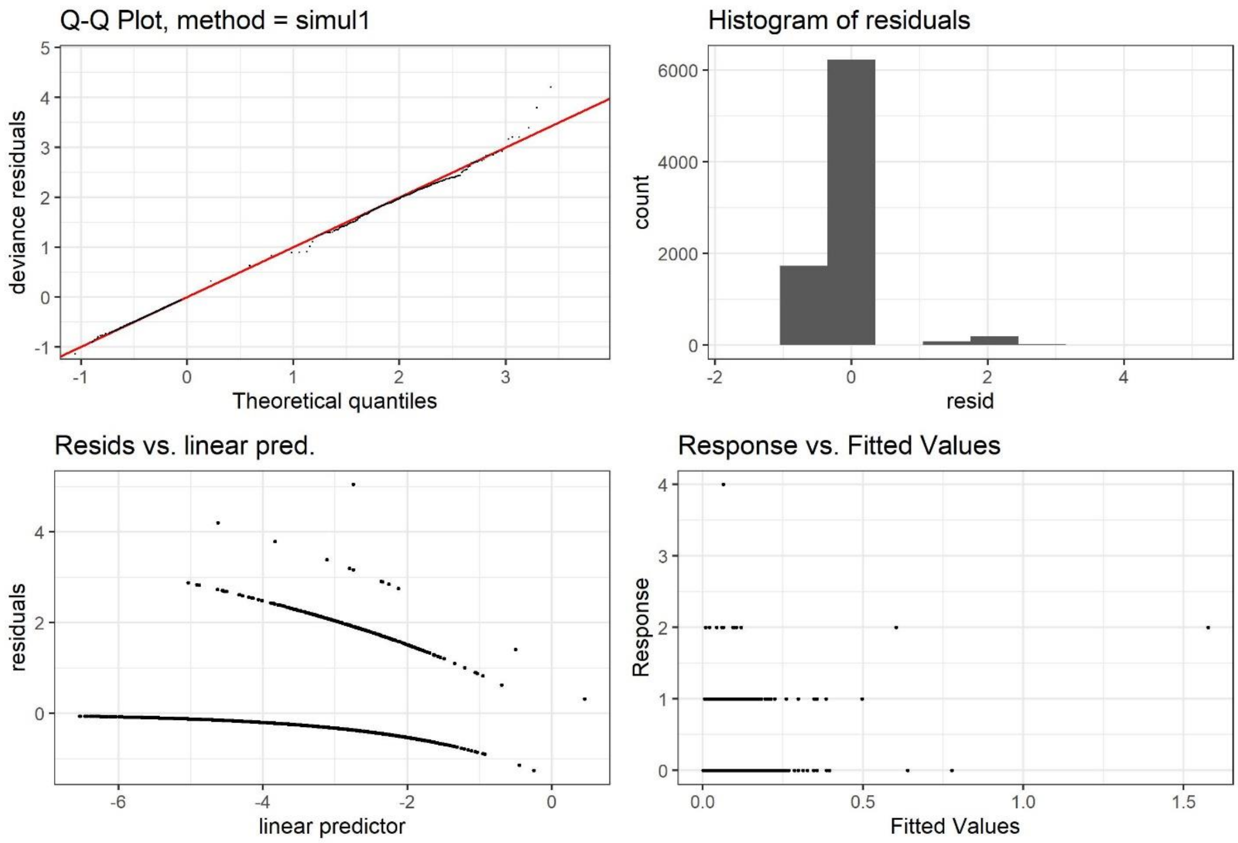


Figure V.1.1.3-2. Diagnostic plots of the selected generalised additive model of the encounter rate of common dolphins' groups.

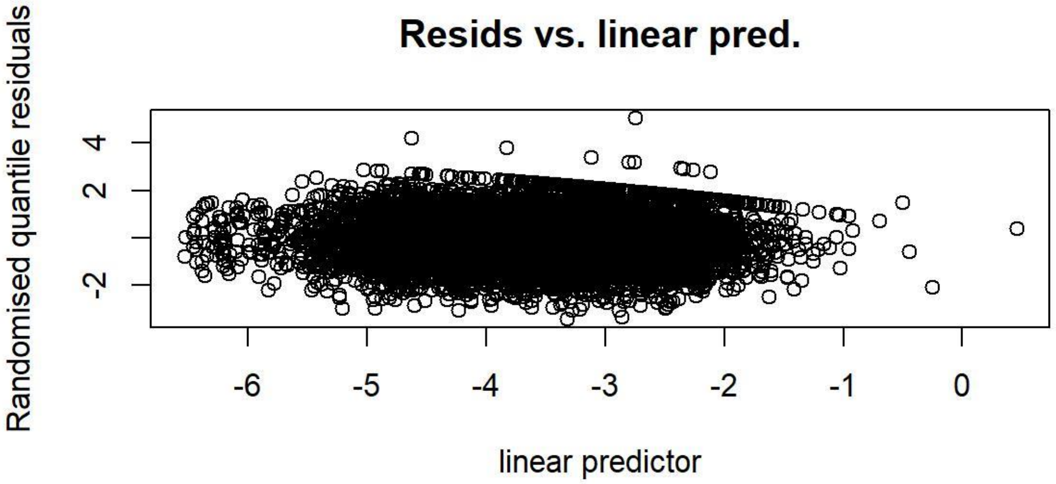


Figure V.1.1.3-3. Randomised quantile residuals plot of the selected generalised additive model of the encounter rate of the common dolphins' groups to check heteroskedasticity.

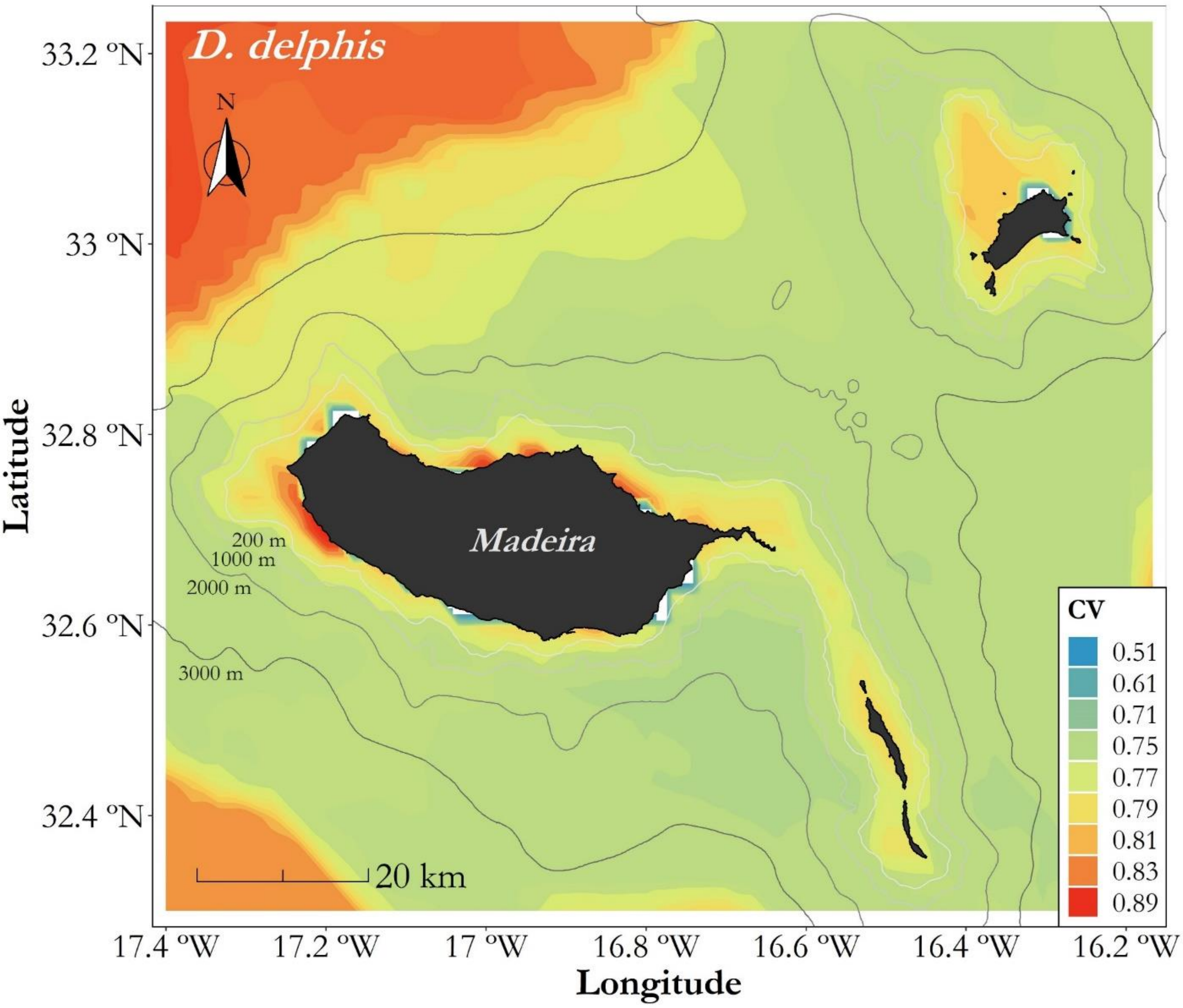


Figure V.1.1.3-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of common dolphins in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.1.1.4. Stenella coeruleoalba

Model of encounter rates of groups

Table V.1.1.4-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-5.7028	0.26190	-21.777	<0.001*
Survey type SLS-RD	-0.376	1.05800	-0.355	0.7223
Survey type ALS	-1.8644	0.43450	-4.290	<0.001*
Survey type NSS	0.5723	0.41550	1.377	0.1685
Survey type WWO	0.9906	0.46470	2.132	0.033*
Survey type FO	-1.6319	0.67750	-2.409	0.016*
*Significant at α = 0.05				

Table V.1.1.4-2. Smooth terms in the encounter rate of groups estimation model (Sst 2001-17 = Sea surface temperature for the period 2001 – 2017; Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Average depth	0.9785	9	1.036	0.001*
Sst 2001-17	0.8944	9	0.72	0.006*
Chl-a 2001-17	0.8083	9	0.424	0.025*
Beaufort	0.9289	4	2.153	0.002*
Effort	0.8783	9	0.745	0.005*
Month	3.0181	9	1.349	0.003*
*Significant at α = 0.05				

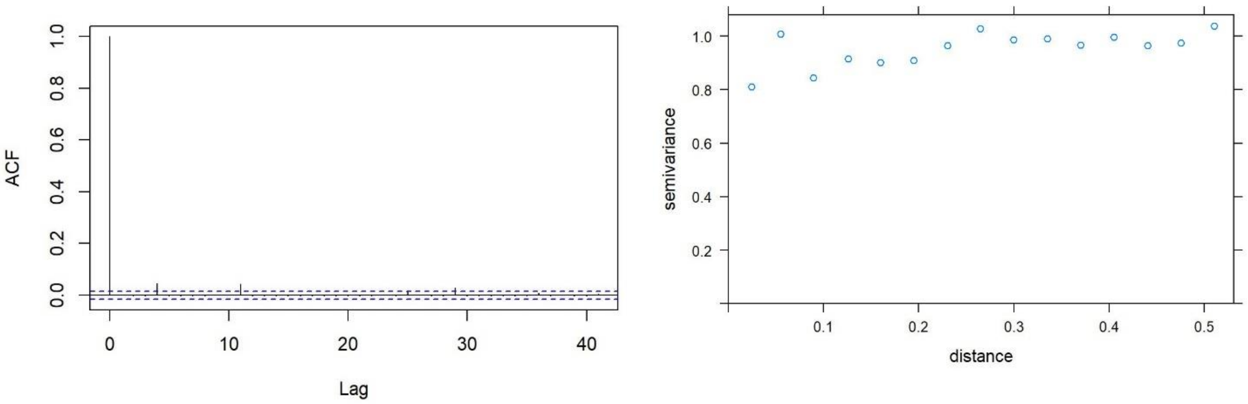


Figure V.1.1.4-1. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of striped dolphins' group for the period 2001-2017.

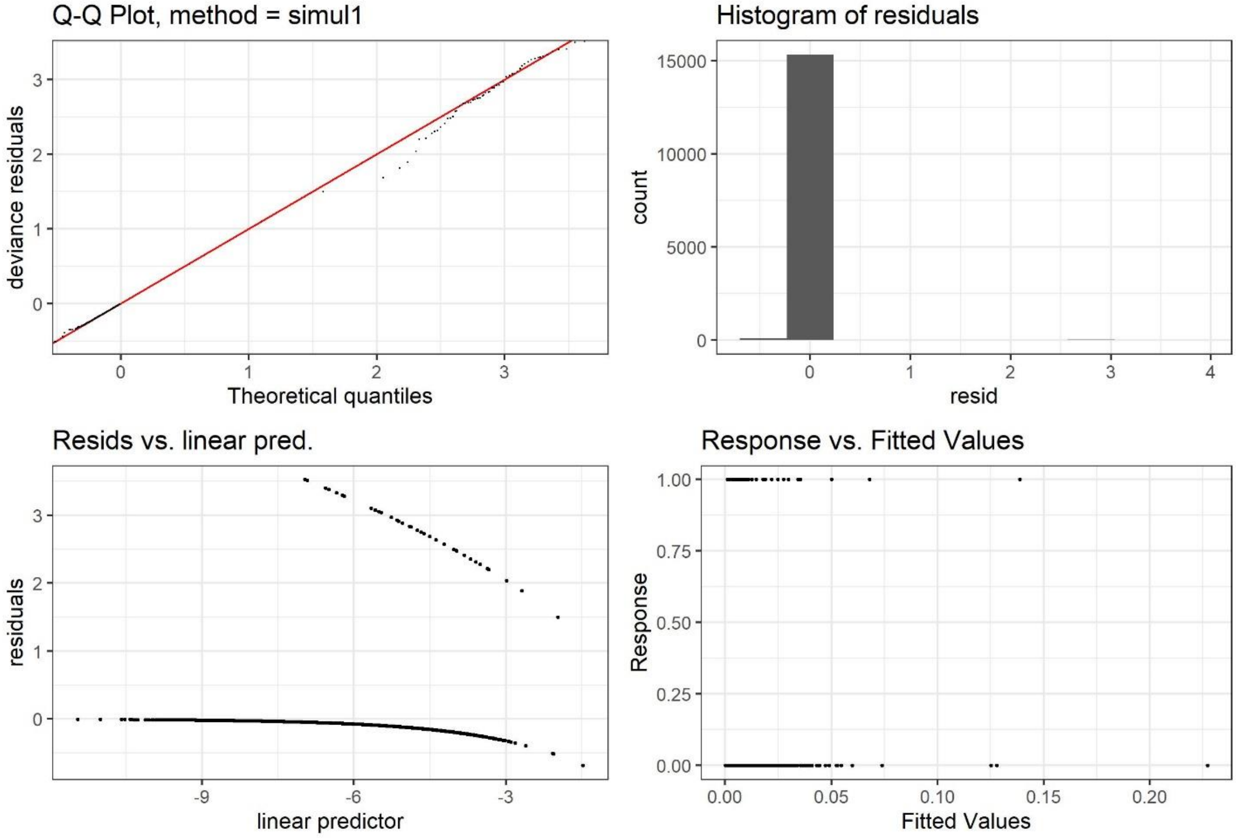


Figure V.1.1.4-2. Diagnostic plots of the selected generalised additive model of the encounter rate of the striped dolphins' groups.

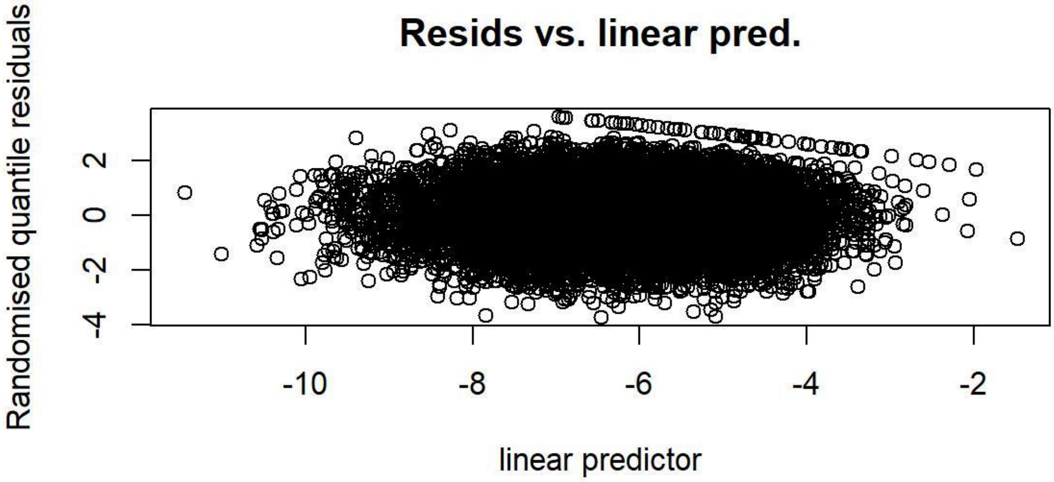


Figure V.1.1.4-3. Randomised quantile residuals plot of the selected generalised additive model of the encounter rate of striped dolphins' groups to check heteroskedasticity.

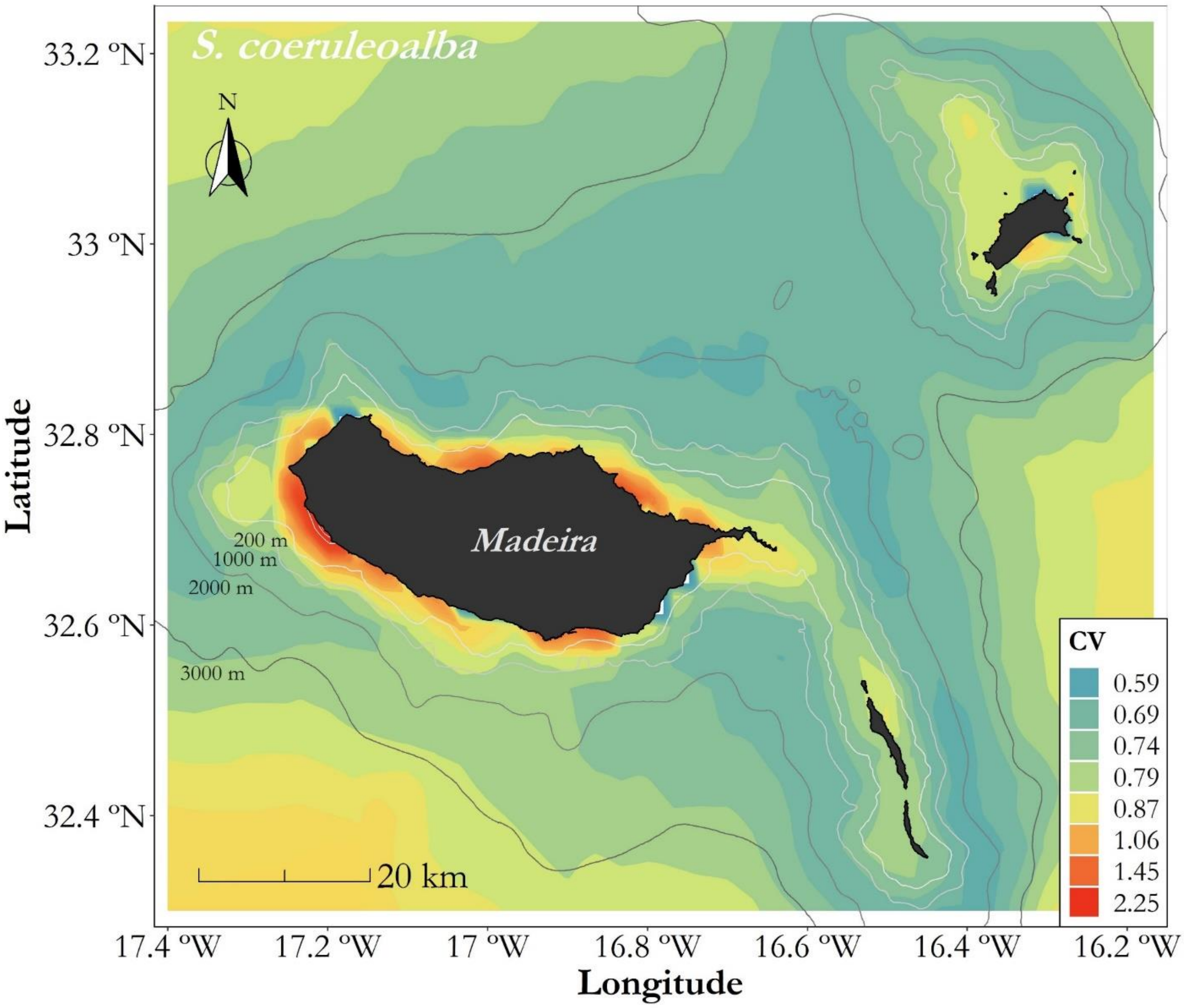


Figure V.1.1.4-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of striped dolphins in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.1.1.5. Globicephala macrorhynchus

Model of encounter rates of groups

Table V.1.1.5-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-5.3767	0.1926	-27.92	<0.001*
Survey type SLS-RD	-0.3365	0.3497	-0.962	0.3358
Survey type ALS	-0.7753	0.3283	-2.362	<0.018*
Survey type NSS	0.3543	0.2303	1.538	0.124
Survey type WWO	0.4811	0.2612	1.842	0.0655
Survey type FO	-0.3101	0.6274	-0.494	0.6211
*Significant at α = 0.05				

Table V.1.1.5-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Distance to 1500m isobath	0.9895	9	3.368	<0.001*
Maximum aspect	3.8053	8	2.420	<0.001*
Contour index	1.2018	9	9.572	<0.001*
Poc 2001-17	1.0126	9	3.669	<0.001*
Mld 2001-17	0.9223	9	0.725	0.006*
Beaufort	0.9093	4	1.703	0.005*
Effort	7.4725	9	15.843	<0.001*
Month	4.0531	10	6.624	<0.001*
Year	0.8976	14	0.411	0.009*
*Significant at α = 0.05				

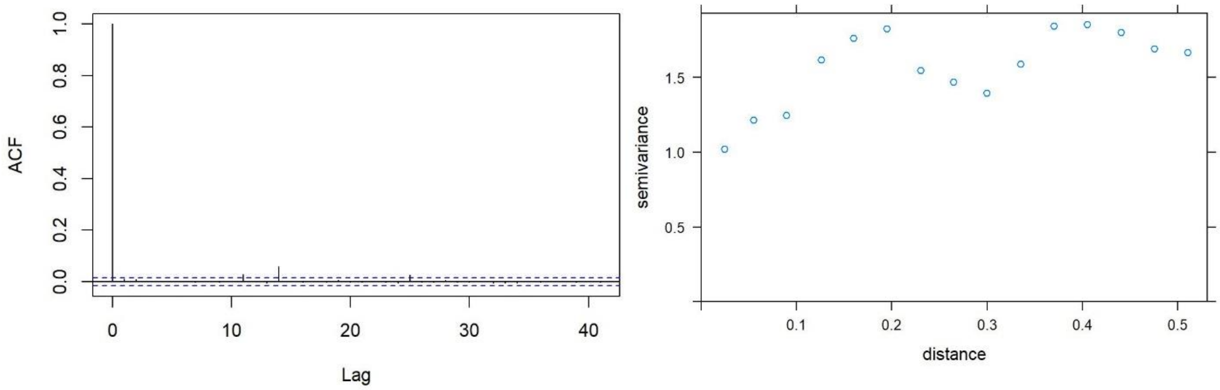


Figure V.1.1.5-1. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of short-finned pilot whale groups for the period 2001-2017.

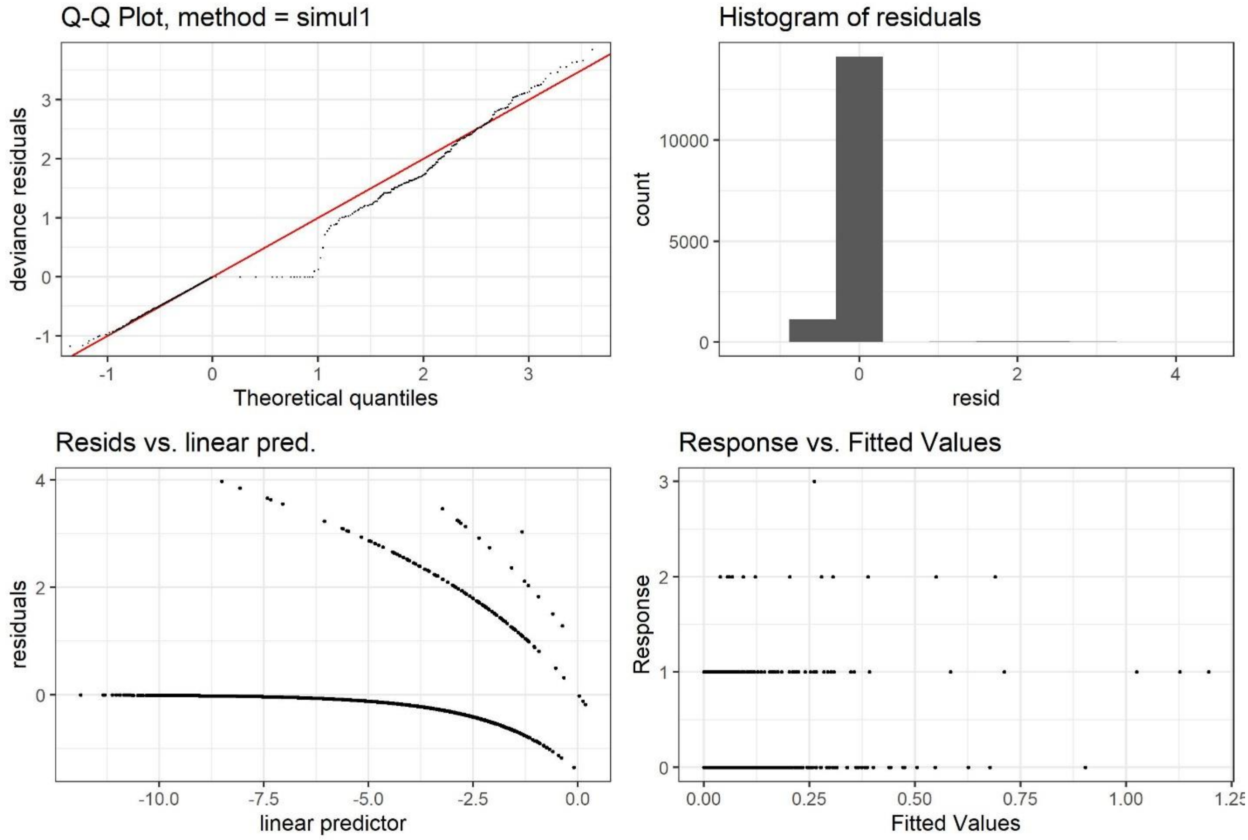


Figure V.1.1.5-2. Diagnostic plots of the selected generalised additive model of the encounter rate of short-finned pilot whale groups.

Model of group size

Table V.1.1.5-3. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	2.76696	0.12755	21.694	<0.001*
Survey type SLS-RD	-0.5227	0.19783	-2.642	0.009*
Survey type ALS	0.03226	0.25529	0.126	0.899
Survey type NSS	0.10289	0.15748	0.653	0.51419
Survey type WWO	-0.33937	0.16524	-2.054	0.0412*
Survey type FO	-0.02757	0.4621	-0.06	0.95247
*Significant at α = 0.05				

Table V.1.1.5-4. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Chl-a 2001-17	0.7863	9	0.335	0.032*
Distance to 2000 isobath	0.8627	9	0.664	0.007*
Poc 2001-17	1.0109	9	0.881	0.001*
Maximum slope	0.5633	9	0.139	0.125
Sst 2001-17	0.9751	9	1.144	<0.001*
Month	2.3214	10	1.150	0.002*
*Significant at α = 0.05				

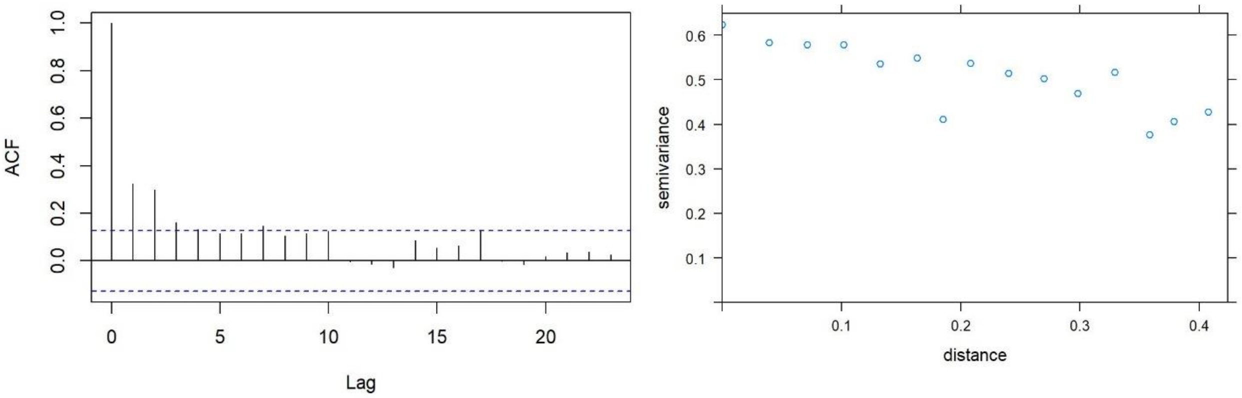


Figure V.1.1.5-3. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of short-finned pilot whale group size for the period 2001-2017.

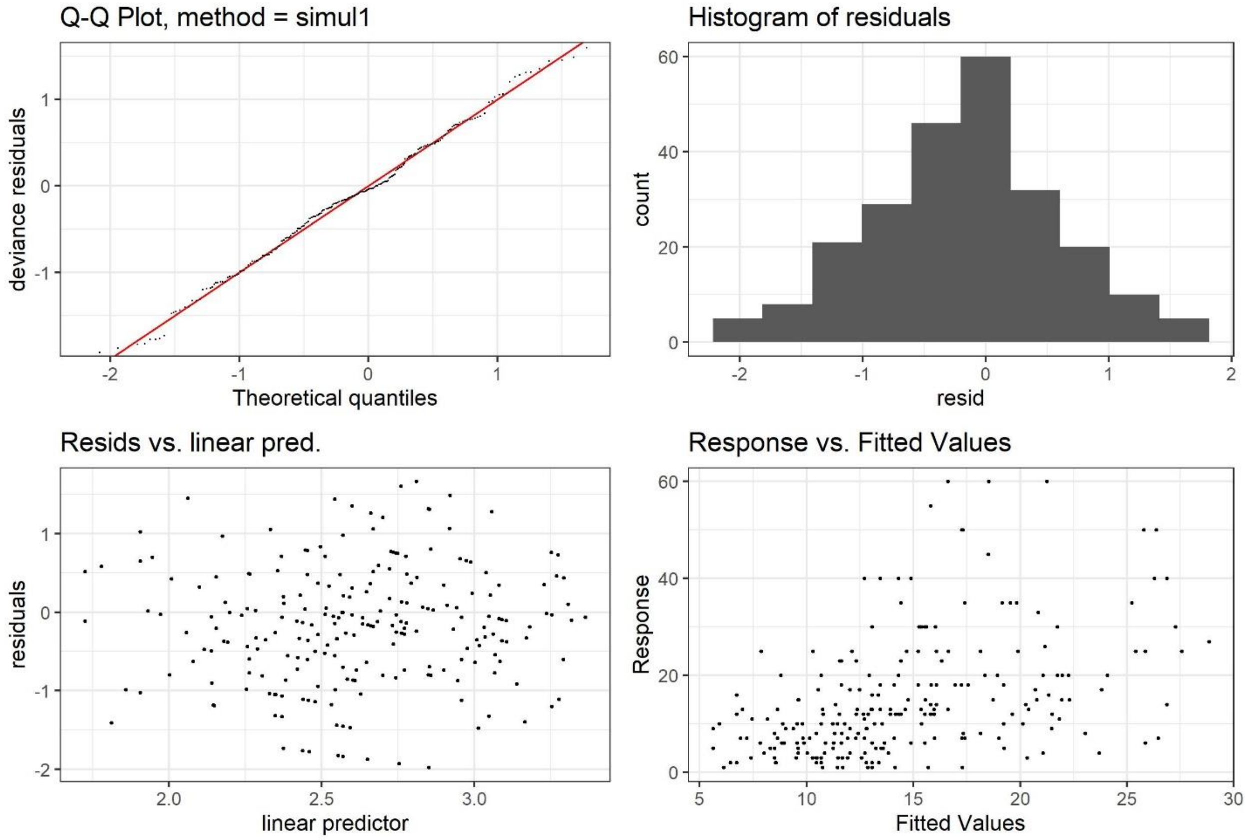


Figure V.1.1.5-4. Diagnostic plots of the selected generalised additive model of short-finned pilot whale group size for the period 2001-2017.

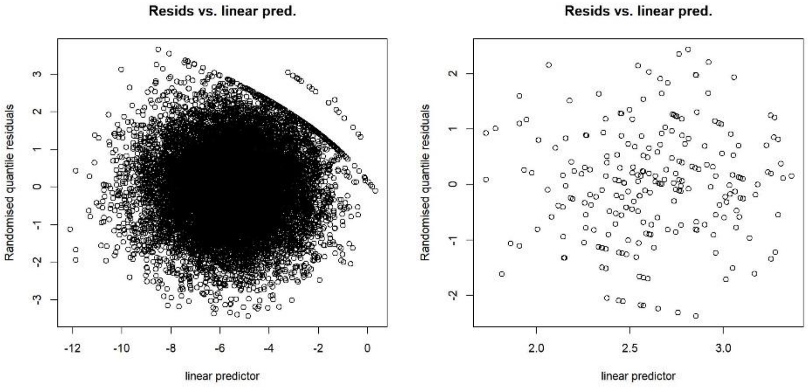


Figure V.1.1.5-5. Randomised quantile residual plots of the selected generalised additive models of the encounter rate of short-finned pilot whale groups (left) and group size (right), to check heteroskedasticity.

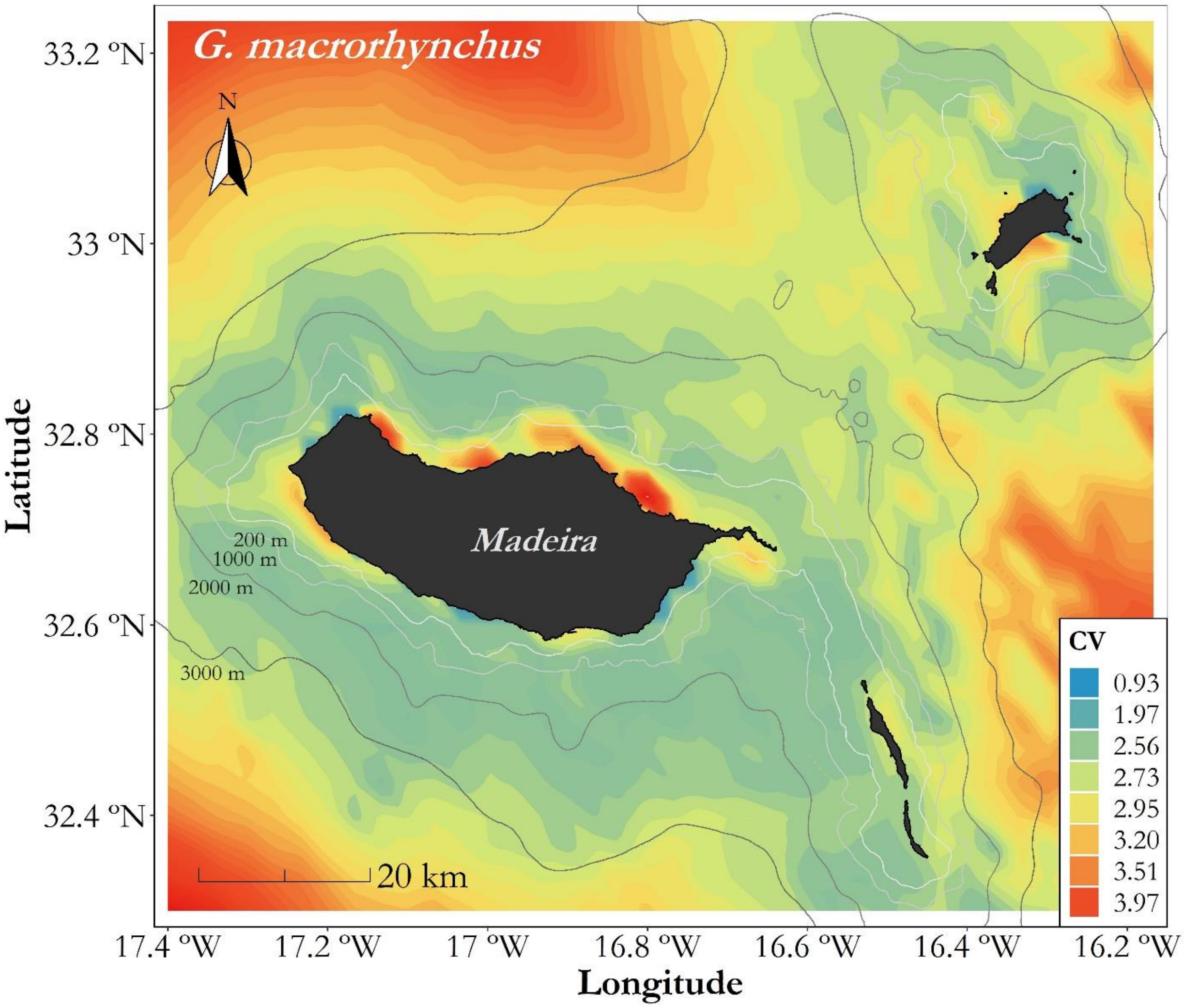


Figure V.1.1.5-6. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of short-finned pilot whale groups in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.1.1.6. *Physeter macrocephalus*

Model of encounter rates of groups

Table V.1.1.6-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-5.7747	0.2849	-20.266	<0.001*
Survey type SLS-RD	0.4753	0.4298	1.106	0.269
Survey type ALS	-0.7129	0.354	-2.014	0.044*
Survey type NSS	0.3612	0.3694	0.978	0.328
Survey type WWO	0.5753	0.3864	1.489	0.137
Survey type FO	-1.0023	0.7414	-1.352	0.176
*Significant at α = 0.05				

Table V.1.1.6-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Slope area	0.9698	9	1.421	0.001*
Average aspect	2.5894	8	1.887	<0.001*
Effort	4.3586	9	8.080	<0.001*
Sst 2001-17	0.8378	9	0.467	0.019*
*Significant at α = 0.05				

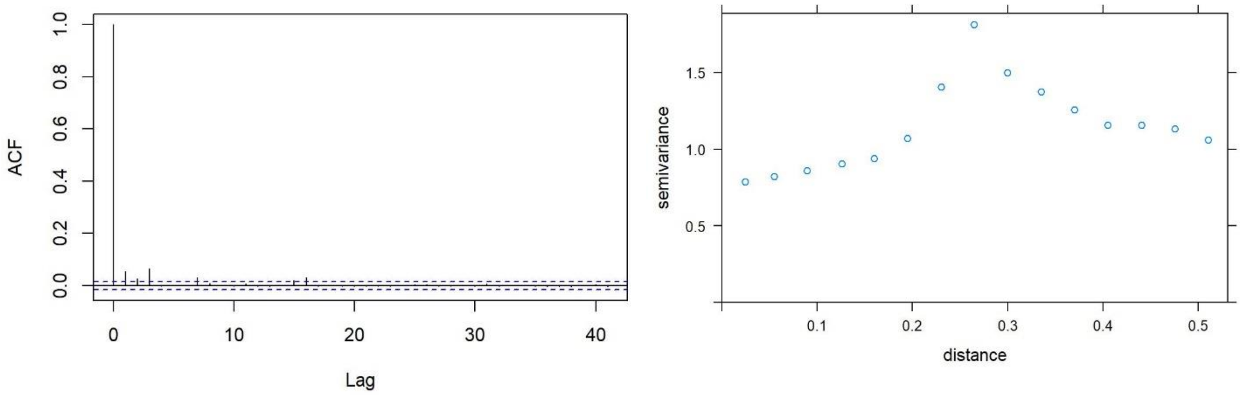


Figure V.1.1.6-1. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of sperm whale groups for the period 2001-2017.

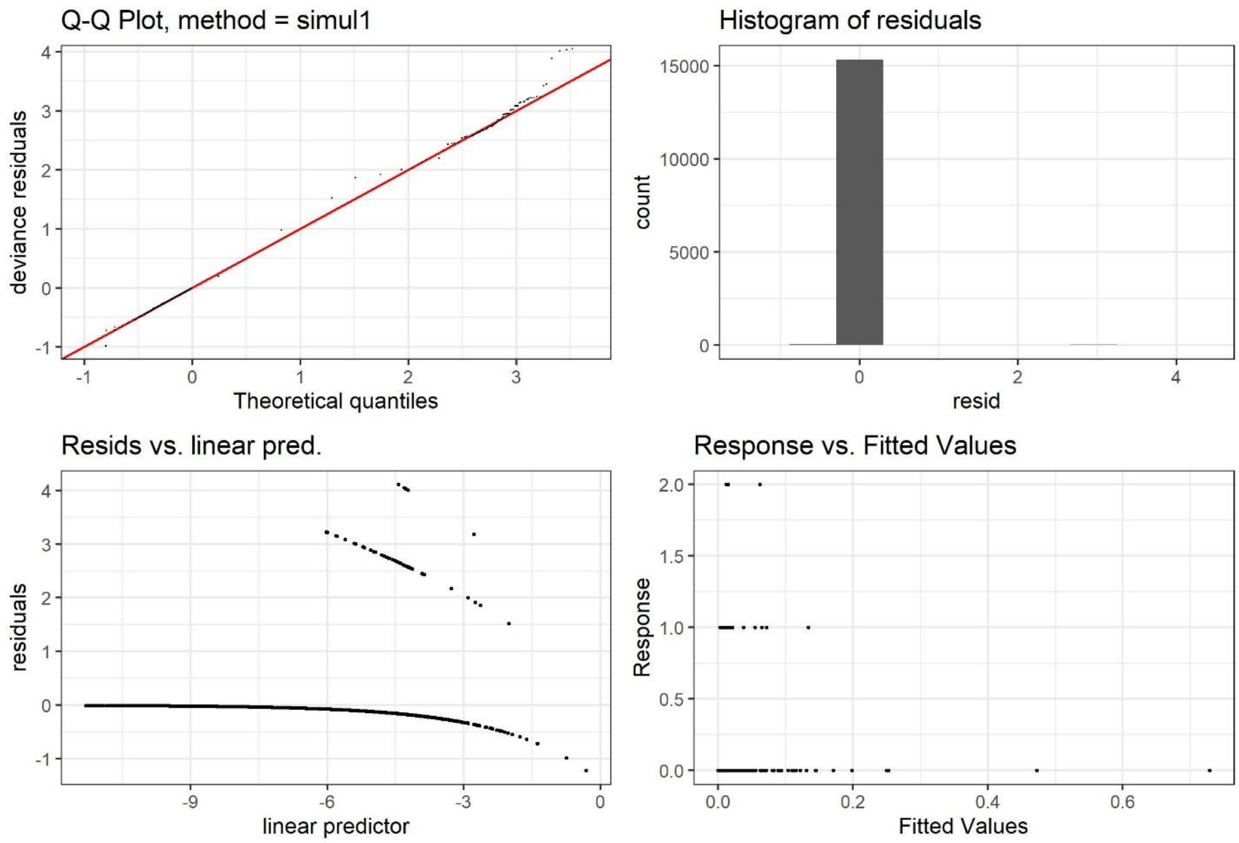


Figure V.1.1.6-2. Diagnostic plots of the selected generalised additive model of the encounter rate of sperm whale groups for the period 2001-2017.

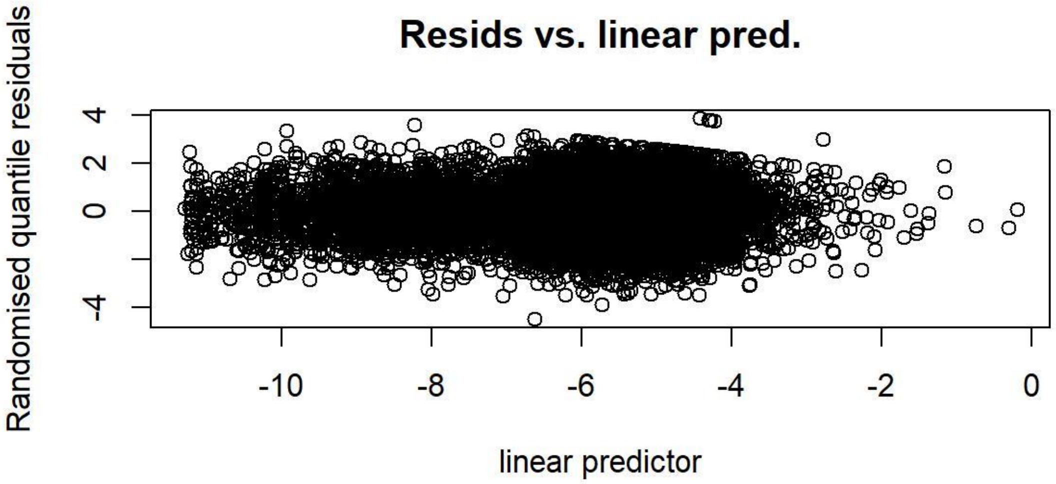


Figure V.1.1.6-3. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of sperm whale groups to check heteroskedasticity.

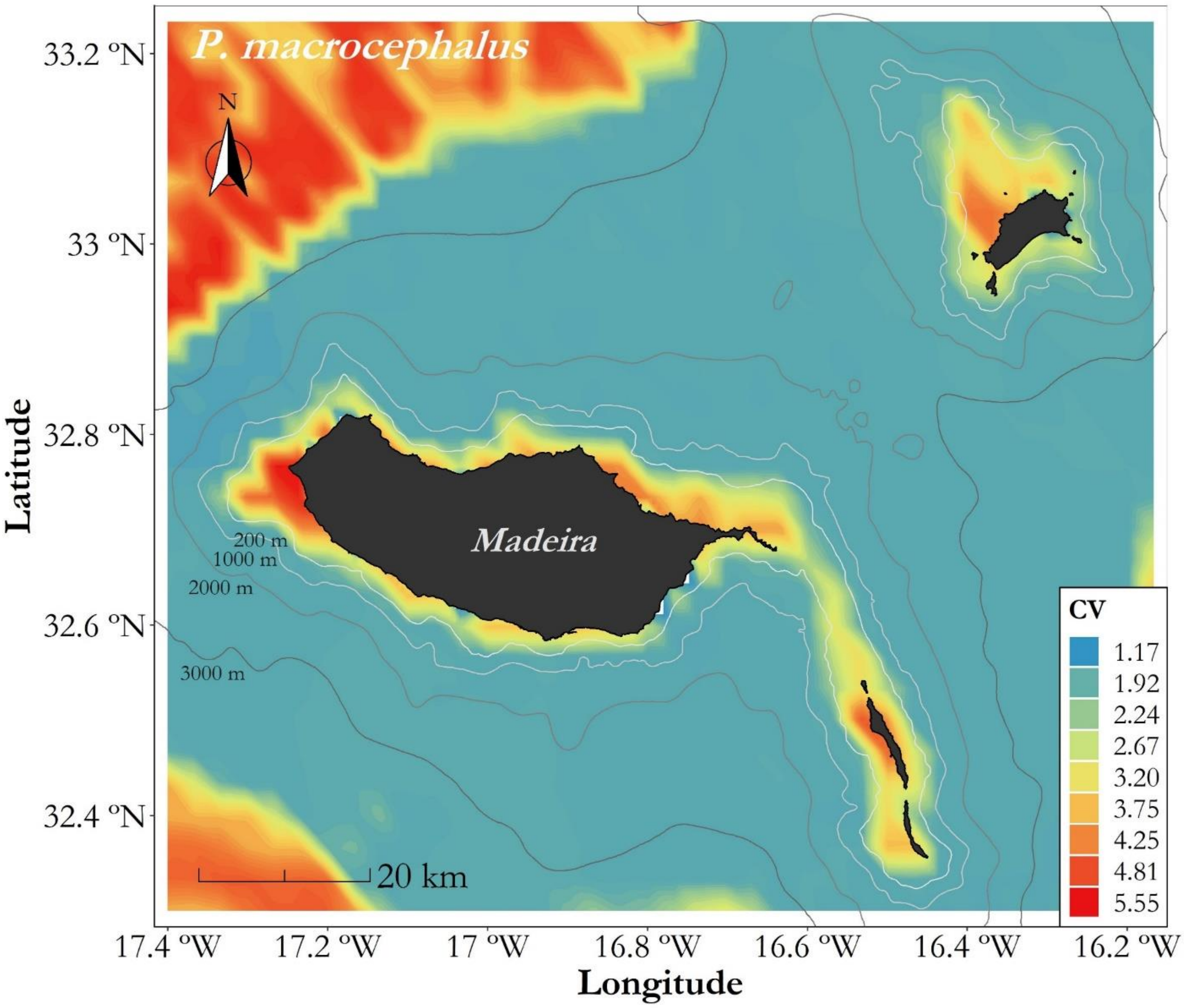


Figure V.1.1.6-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of sperm whale groups in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.1.1.7. Mesoplodon sp.

Model of encounter rates of groups

Table V.1.1.7-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-7.0270	0.3008	-23.36	<0.001*
Survey type SLS-RD	-446.3	1854000	0	0.9998
Survey type ALS	-2.6440	1.0470	-2.526	0.0116*
Survey type NSS	-0.2828	0.5344	-0.529	0.5966
Survey type WWO	-0.2538	0.6097	-0.416	0.6772
Survey type FO	-1.2140	0.7880	-1.541	0.1233
*Significant at α = 0.05				

Table V.1.1.7-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Aspect std dev	0.7984	9	0.350	0.045*
Mld 2001-17	0.8639	9	0.522	0.017*
Year	0.8806	12	0.425	0.014*
*Significant at α = 0.05				

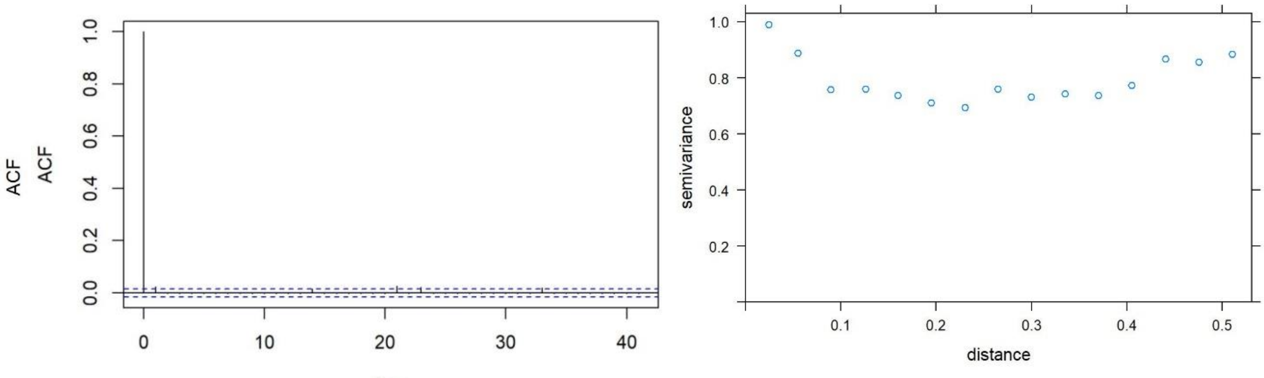


Figure V.1.1.7-1. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of individuals of *Mesoplodon sp.* whale groups for the period 2001-2017.

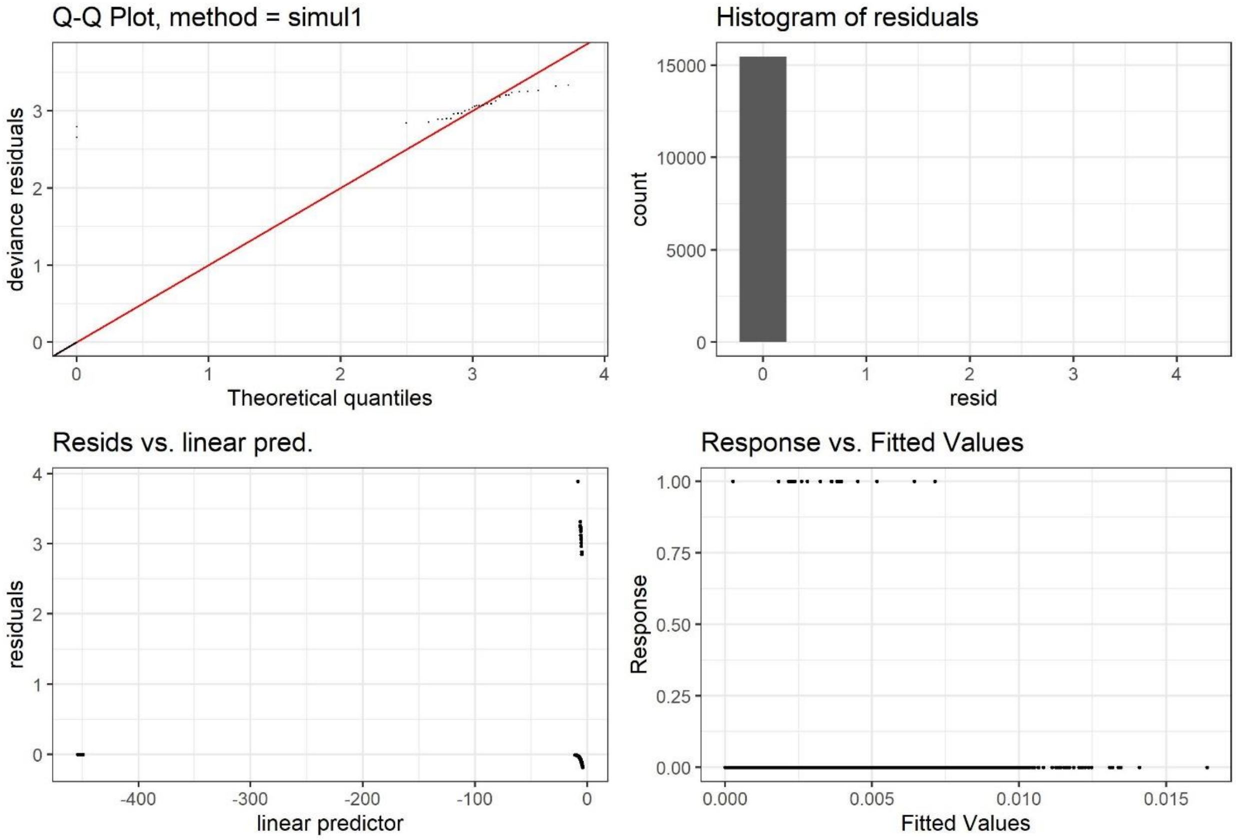


Figure V.1.1.7-2. Diagnostic plots of the selected generalised additive model of the encounter rate of of *Mesoplodon sp.* whale groups for the period 2001-2017.

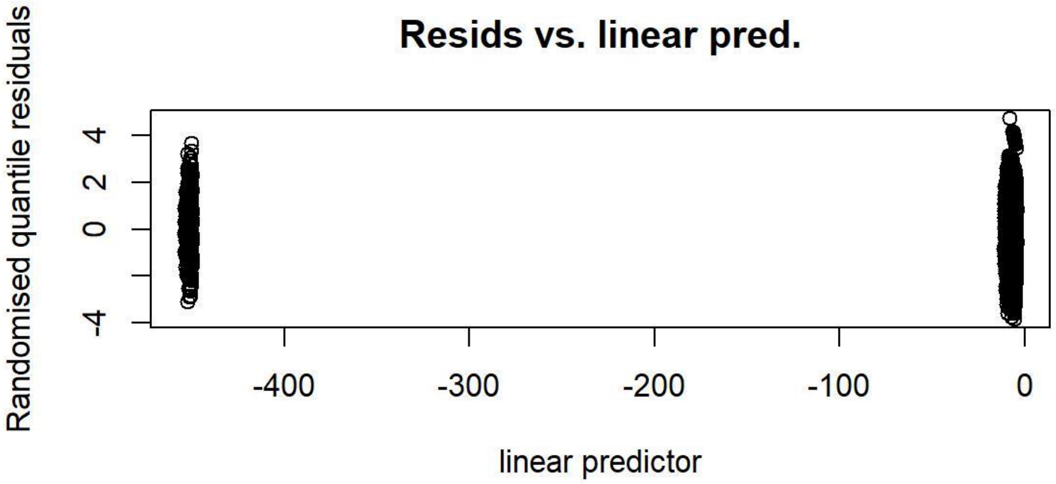


Figure V.1.1.7-3. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of *Mesoplodon sp.* whale groups to check heteroskedasticity.

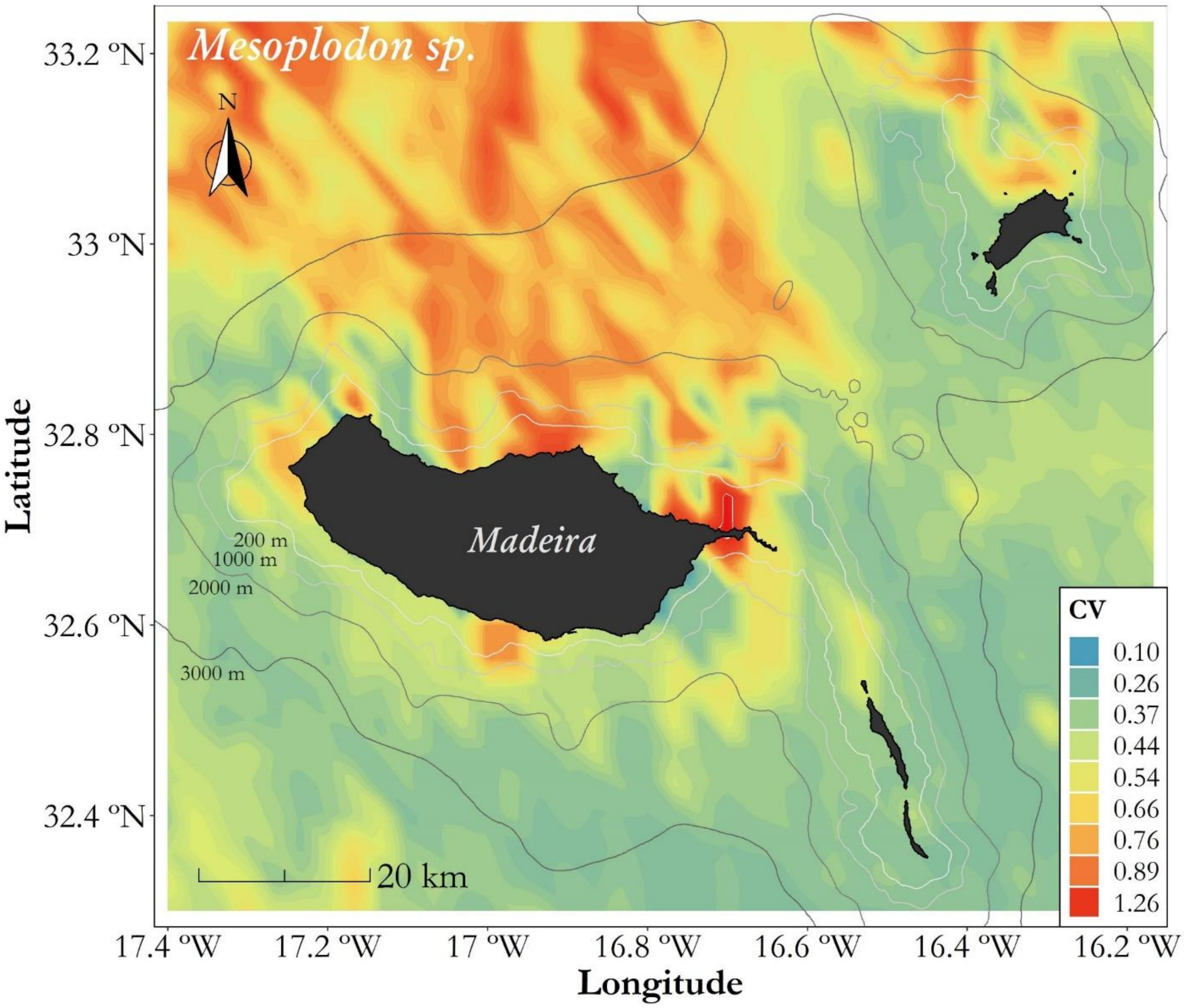


Figure V.1.1.7-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of *Mesoplodon sp.* whales in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.1.1.8. Ziphiidae

Model of encounter rates of groups

Table V.1.1.8-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-6.1560	0.2016	-30.529	<0.001*
Survey type SLS-RD	-443.70	1847000	0	0.998
Survey type ALS	-1.9800	0.4529	-4.3720	<0.001*
Survey type NSS	-0.7500	0.3960	-1.8940	0.058
Survey type WWO	-0.5182	0.4471	-1.1590	0.2464
Survey type FO	-1.7470	0.7576	-2.3060	0.021*
*Significant at α = 0.05				

Table V.1.1.8-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Aspect std dev	0.8998	9	0.744	0.006*
Mld 2001-17	0.9616	9	1.044	0.001*
Month	2.3311	9	1.251	0.002*
Year	0.7865	14	0.235	0.037*
*Significant at α = 0.05				

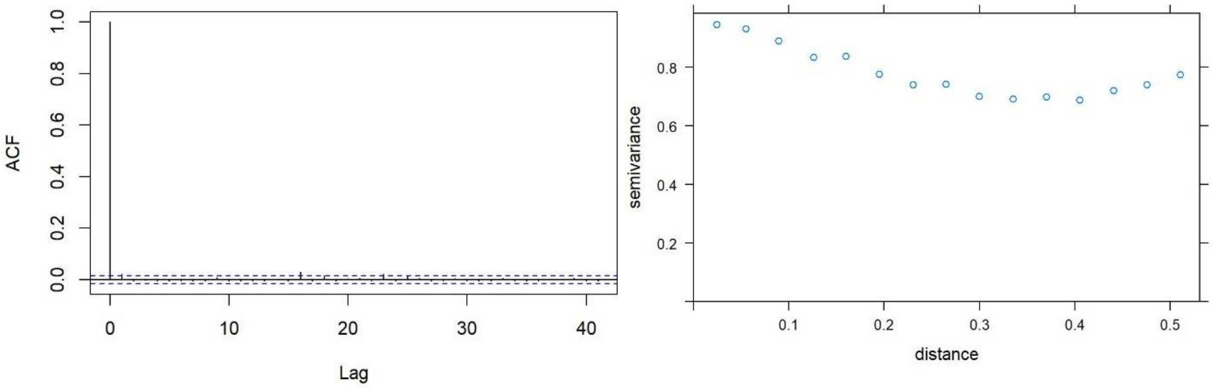


Figure V.1.1.8-1. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of beaked whale groups for the period 2001-2017.

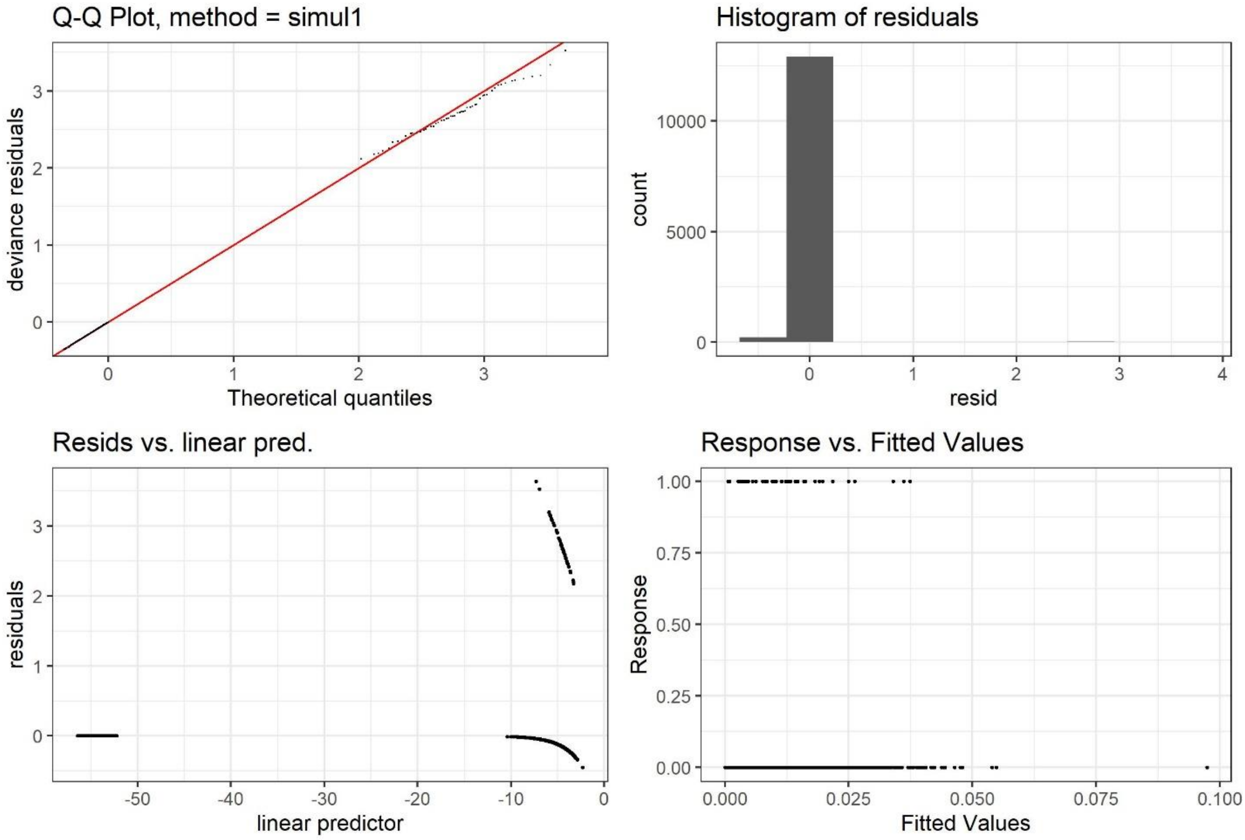


Figure V.1.1.8-2. Diagnostic plots of the selected generalised additive model of the encounter rate of beaked whales for the period 2001-2017.

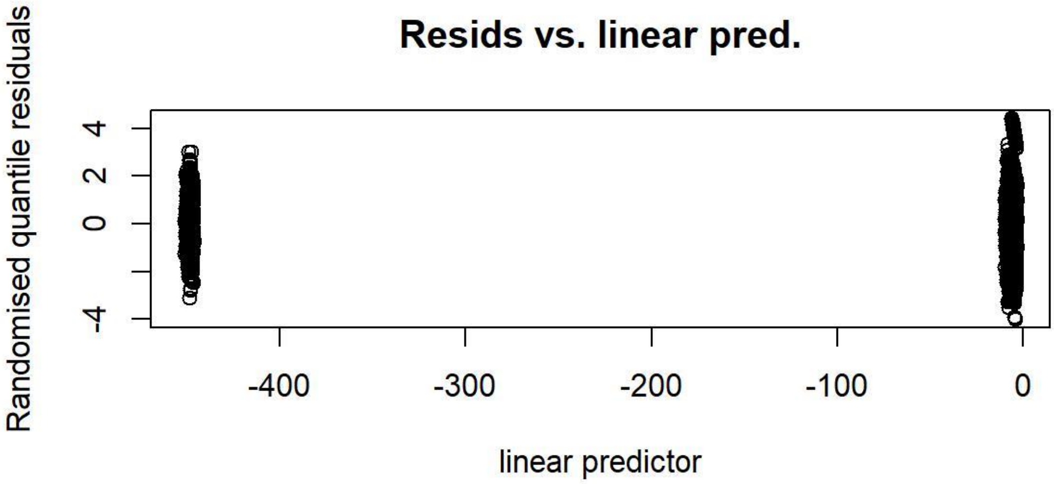


Figure V.1.1.8-3. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of beaked whales to check heteroskedasticity.

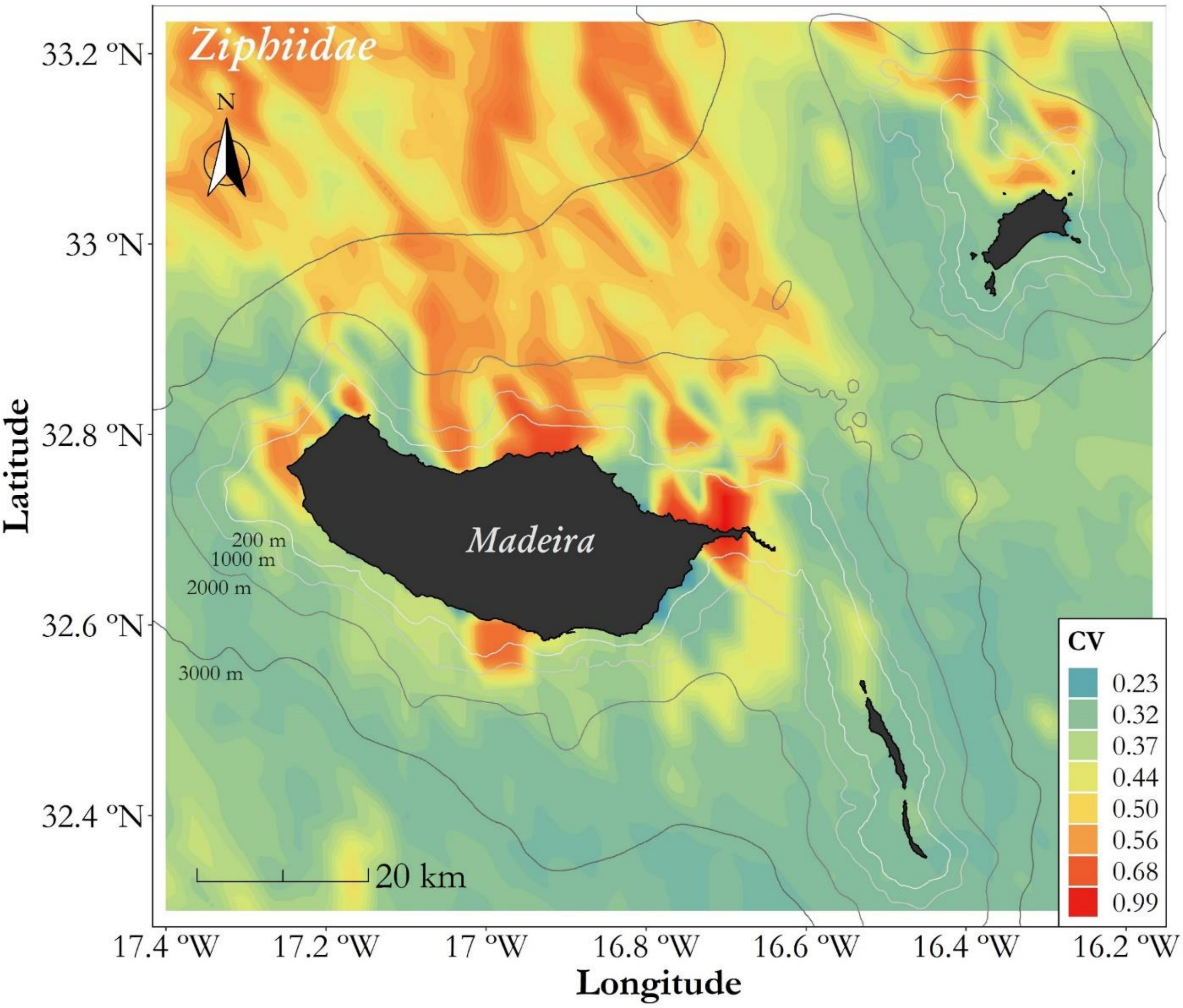


Figure V.1.1.8-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of beaked whales in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.1.1.9. Balaenoptera edeni

Model of encounter rates of groups

Table V.1.1.9-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-6.4209	0.5325	-12.06	<0.001*
Survey type SLS-RD	3.3759	1.363	2.477	0.0133*
Survey type ALS	-0.4074	0.5261	-0.774	0.4387
Survey type NSS	0.619	0.4869	1.271	0.2037
Survey type WWO	1.5514	0.6107	2.54	0.0111*
Survey type FO	1.2351	1.0258	1.204	0.2286
*Significant at α = 0.05				

Table V.1.1.9-2. Smooth terms in the encounter rate of groups estimation model (Sst 2001-17 = Sea surface temperature for the period 2001 – 2017; Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Area escarpment	0.8775	9	0.503	0.038*
Maximum depth	0.8658	9	0.593	0.01*
Distance to escarpment	0.9159	9	1.108	<0.001*
Effort	5.2324	9	10.082	<0.001*
Year	7.0893	11	7.171	<0.001*
*Significant at α = 0.05				

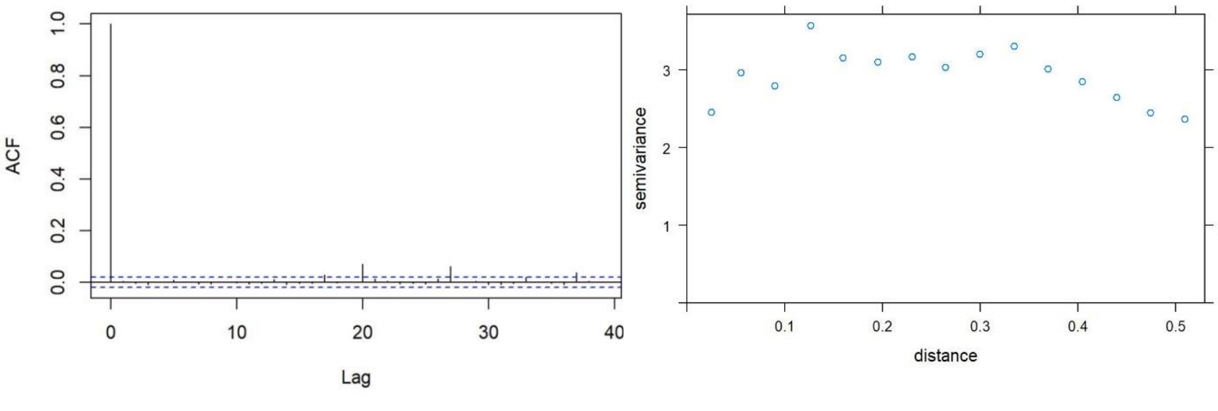


Figure V.1.1.9-1. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of Bryde's whales for the period 2004-2017.

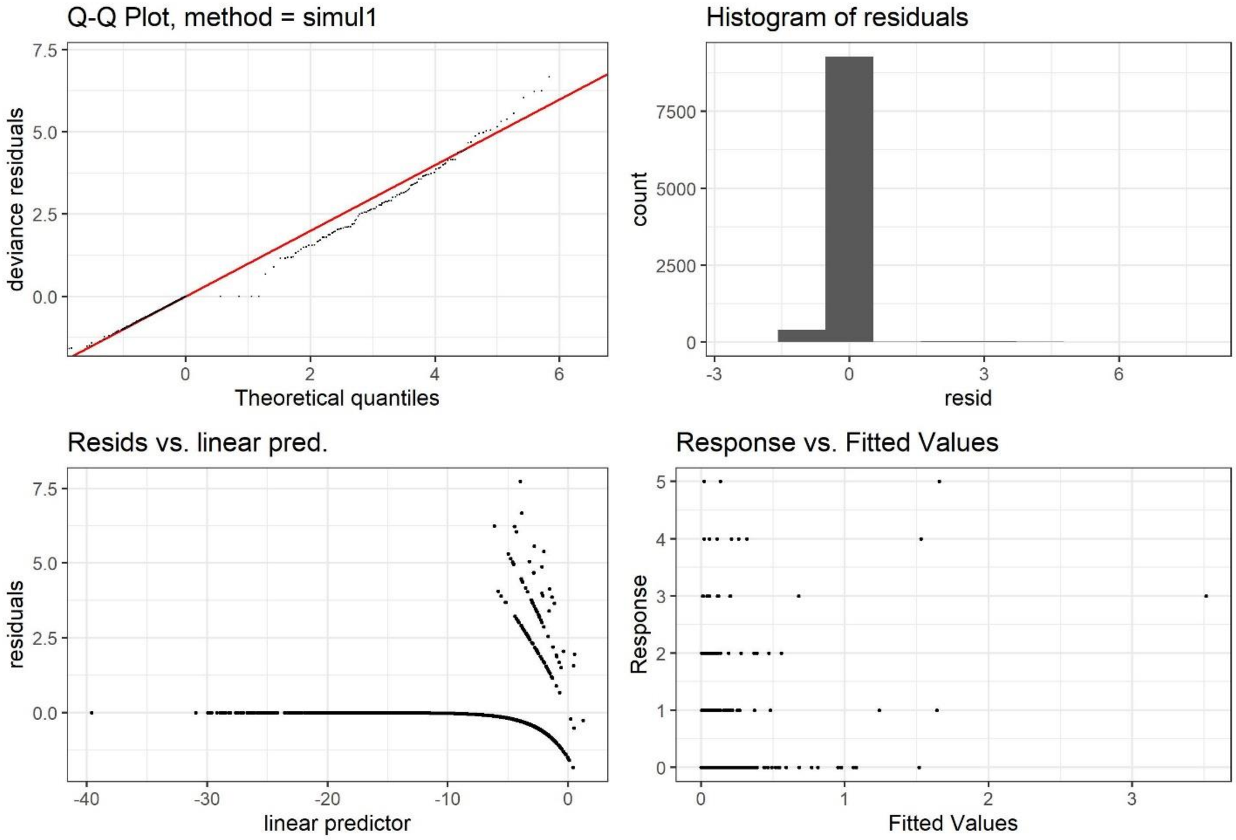


Figure V.1.1.9-2. Diagnostic plots of the selected generalised additive model of the encounter rate of the Bryde's whales.

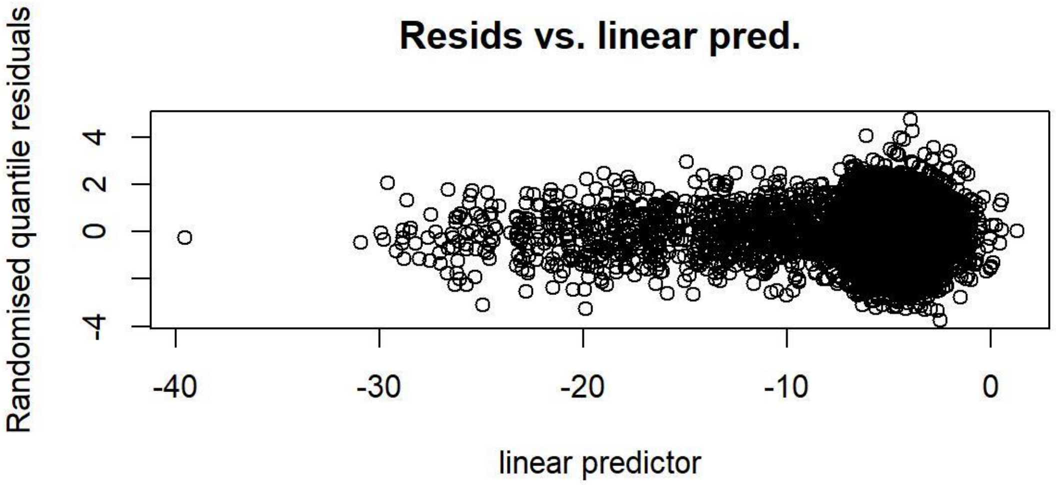


Figure V.1.1.9-3. Randomised quantile residuals plot of the selected generalised additive model of the encounter rate of Bryde's whales to check heteroskedasticity.

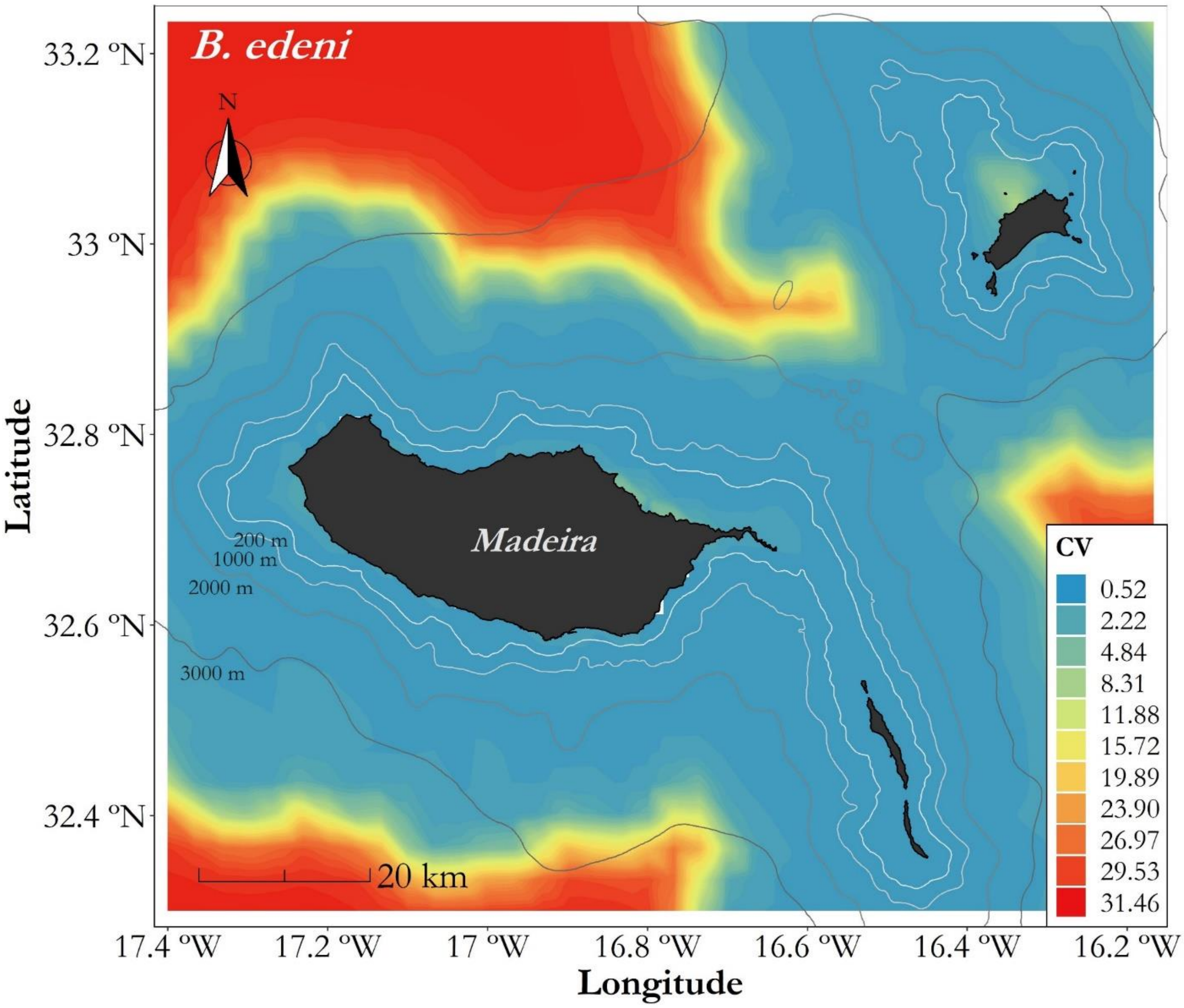


Figure V.1.1.9-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of Bryde's whales in the Madeira inshore waters for the period 2004 – 2017, based on encounter rate (animals per km of transect line).

V.1.1.10. Balaenoptera physalus

Model of encounter rates of groups

Table V.1.1.10-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-8.8790	0.5640	-15.742	<0.001*
Survey type SLS-RD	-445.7	1844000	0	1
Survey type ALS	-447.0	833700	0	1
Survey type NSS	-0.7931	0.7618	-1.041	0.298
Survey type WWO	0.6219	0.4155	1.497	0.134
Survey type FO	-448.0	1810000	0.0	1
*Significant at α = 0.05				

Table V.1.1.10-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Distance to 2000m isobath	0.9587	9	2.188	<0.001*
Month	3.7536	6	4.679	<0.001*
*Significant at α = 0.05				

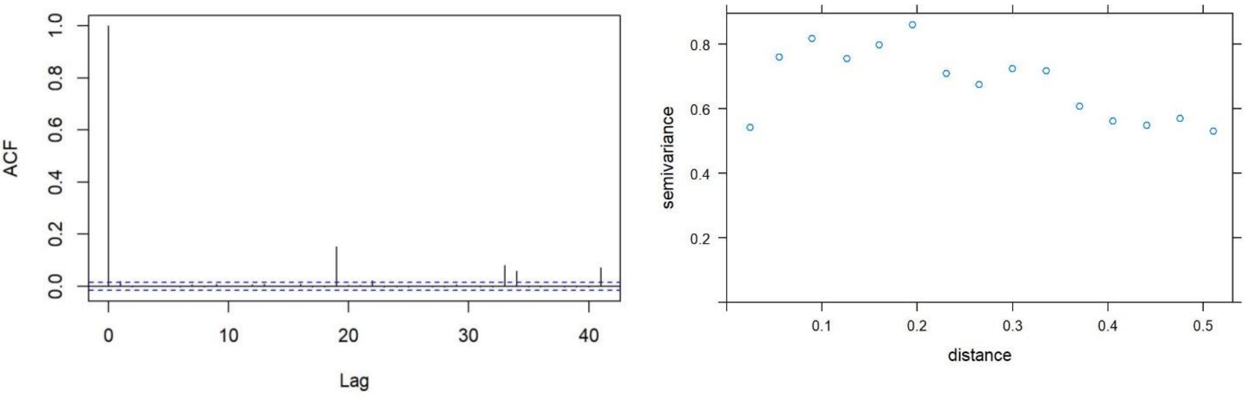


Figure V.1.1.10-1. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of fin whale groups for the period 2001-2017.

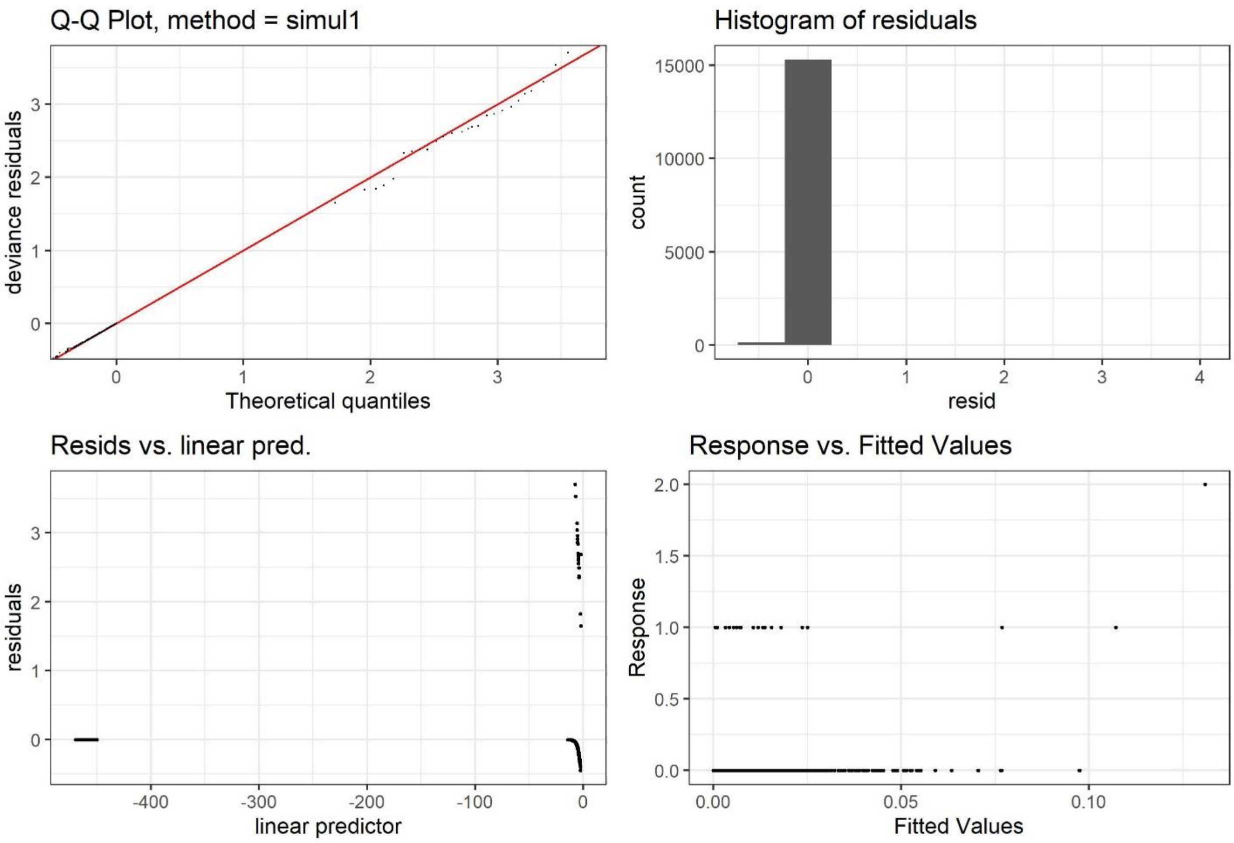


Figure V.1.1.10-2. Diagnostic plots of the selected generalised additive model of the encounter rate of fin whale groups.

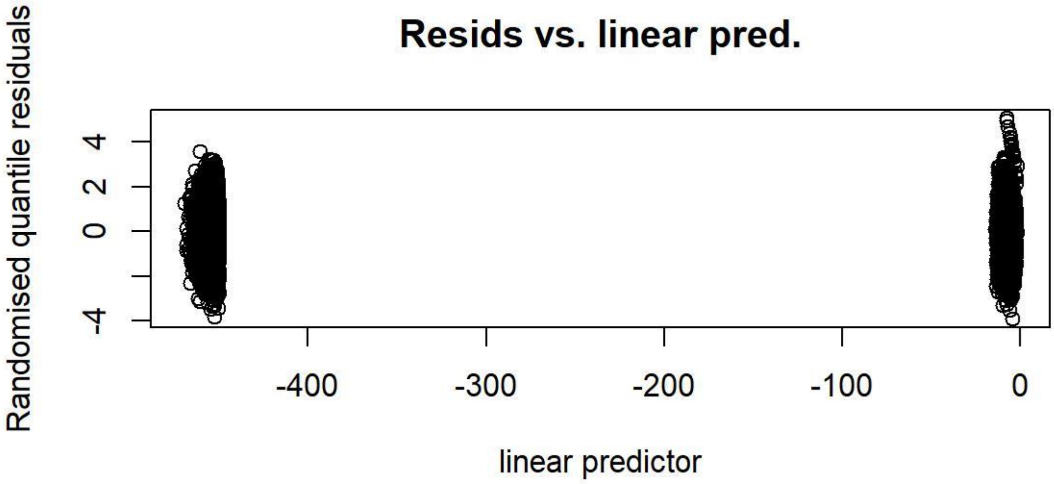


Figure V.1.1.10-3. Randomised quantile residuals plot of the selected generalised additive model of the encounter rate of fin whale groups to check heteroskedasticity.

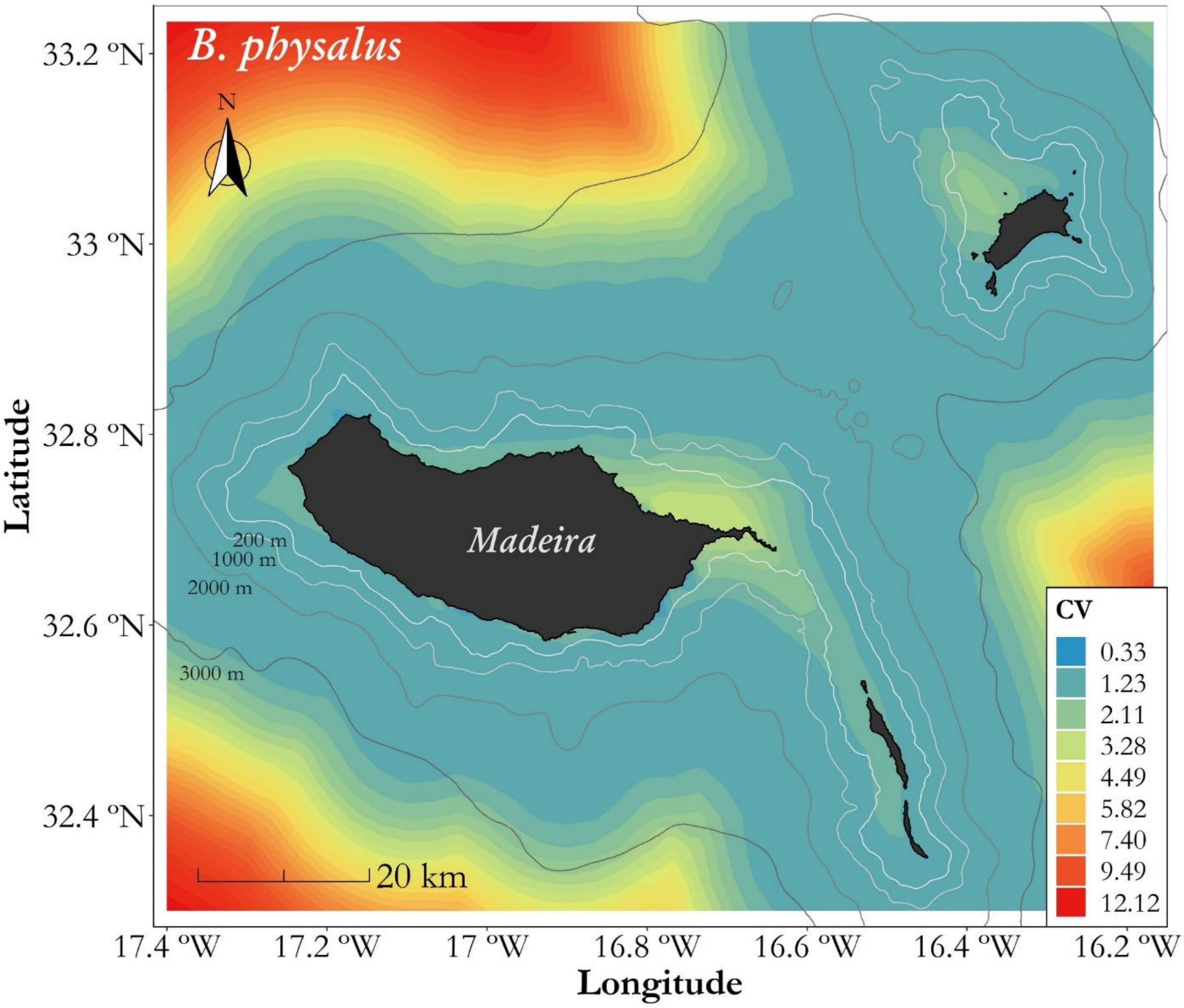


Figure V.1.1.10-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of fin whale groups in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2. Spatial Modelling – Seasonal spatial use of habitat

V.2.1. Diagnostic and Uncertainty plots

V.2.1.1 Tursiops truncatus - Winter

Model of encounter rates of groups

Table V.2.1.1-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-4.9250	0.3584	-13.74	<0.001*
Survey type SLS-RD	-	-	-	-
Survey type ALS	-0.1620	0.6495	-0.2490	0.8031
Survey type NSS	0.2714	0.4170	0.6510	0.5152
Survey type WWO	0.9544	0.4851	1.9670	0.0492*
Survey type FO	-88.5300	7937000	0	1
*Significant at $\alpha = 0.05$				

Table V.2.1.1-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Maximum depth	0.9361	9	0.916	0.00209*
Distance to slope	0.9016	9	0.846	0.00282*
Effort	5.5174	9	4.881	<0.001*
Year	3.154	11	1.325	0.00123*
*Significant at $\alpha = 0.05$				

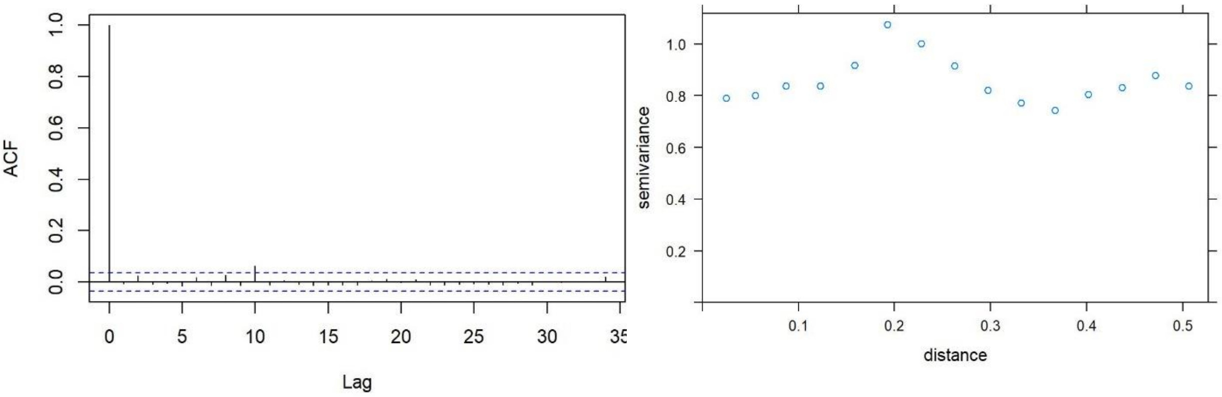


Figure V.2.1.1-1. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of bottlenose dolphin groups in Winter for the period 2001-2017.

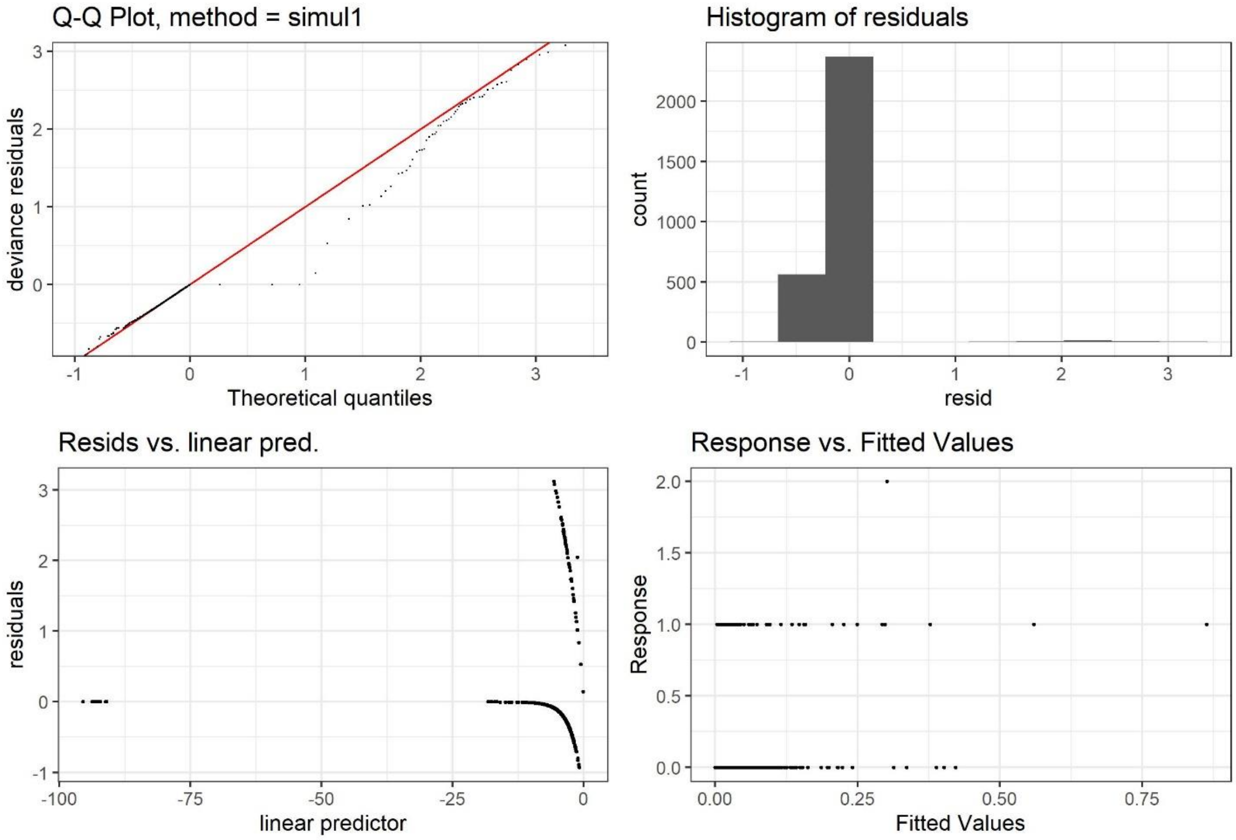


Figure V.2.1.1-2. Diagnostic plots of the selected generalised additive model of the encounter rate of bottlenose dolphin groups in Winter for the period 2001-2017.

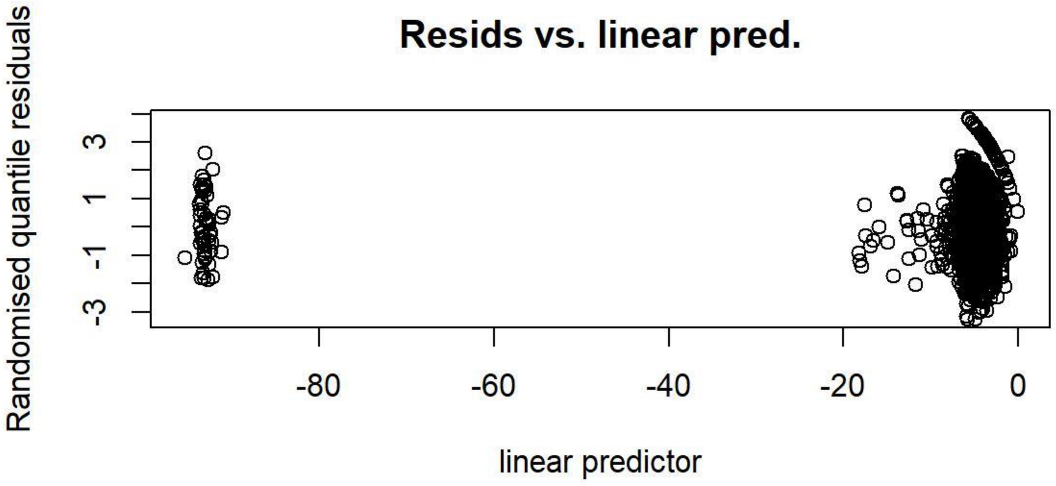


Figure V.2.1.1-3. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of bottlenose dolphin groups in Winter to check heteroskedasticity.

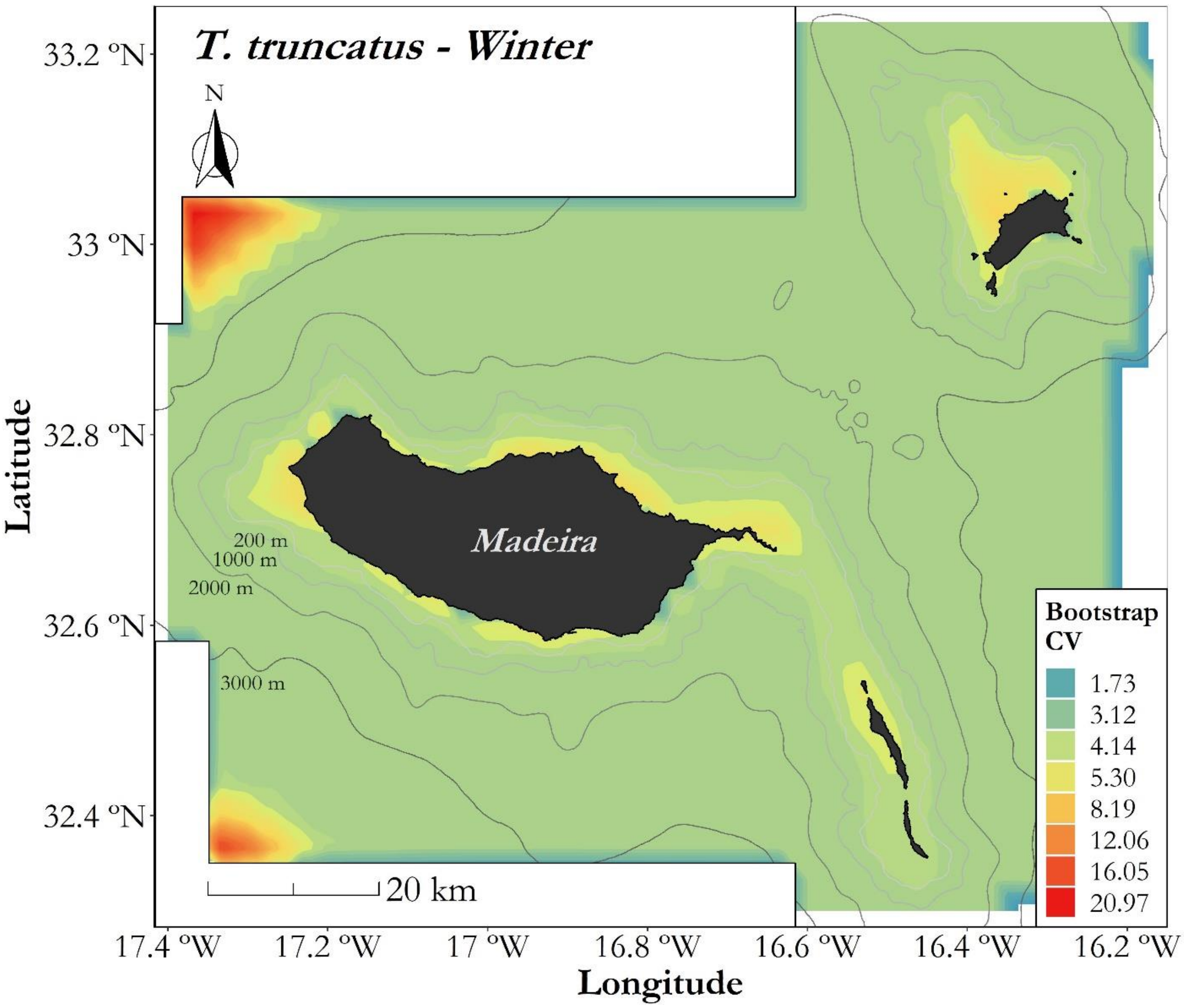


Figure V.2.1.1-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of bottlenose dolphins in Winter in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.2. *Tursiops truncatus - Spring*

Model of encounter rates of groups

Table V.2.1.2-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-3.926	0.2016	-19.471	<0.001*
Survey type SLS-RD	-	-	-	-
Survey type ALS	-0.9634	0.4473	-2.154	0.03*
Survey type NSS	-0.3530	0.2694	-1.310	0.190
Survey type WWO	-0.3804	0.3115	-1.221	0.222
Survey type FO	-2.0748	0.6079	-3.413	<0.001*
*Significant at α = 0.05				

Table V.2.1.2-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Distance to 2500m isobath	0.8909	9	0.85	0.003*
Effort	5.0054	4	3.649	<0.001*
Mld 2001-17	0.976	9	1.536	<0.001*
Pp 2001-17	2.7997	9	1.619	<0.001*
Maximum slope	0.9398	9	1.064	0.001*
Year	1.0388	11	1.179	<0.001*
*Significant at α = 0.05				

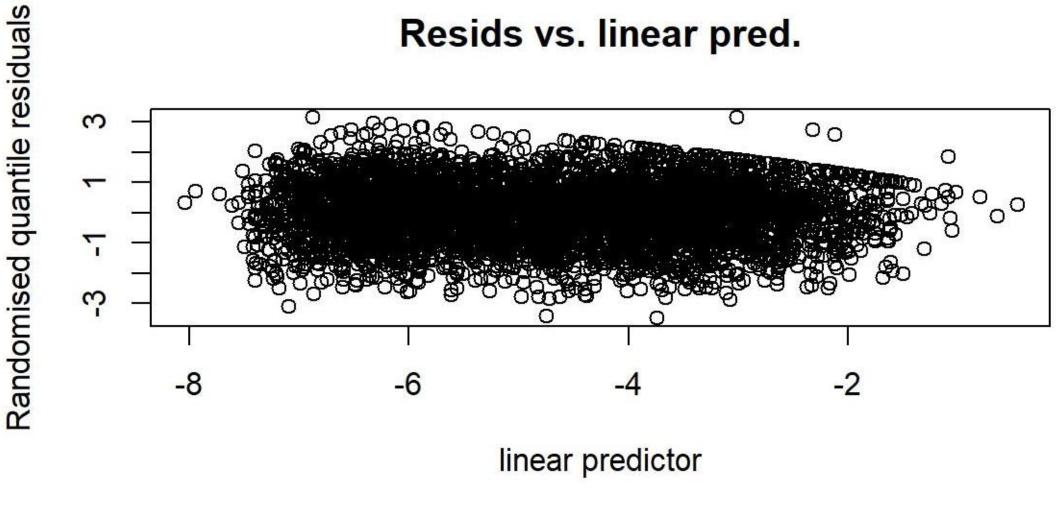


Figure V.2.1.2-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of bottlenose dolphins in Spring to check heteroskedasticity.

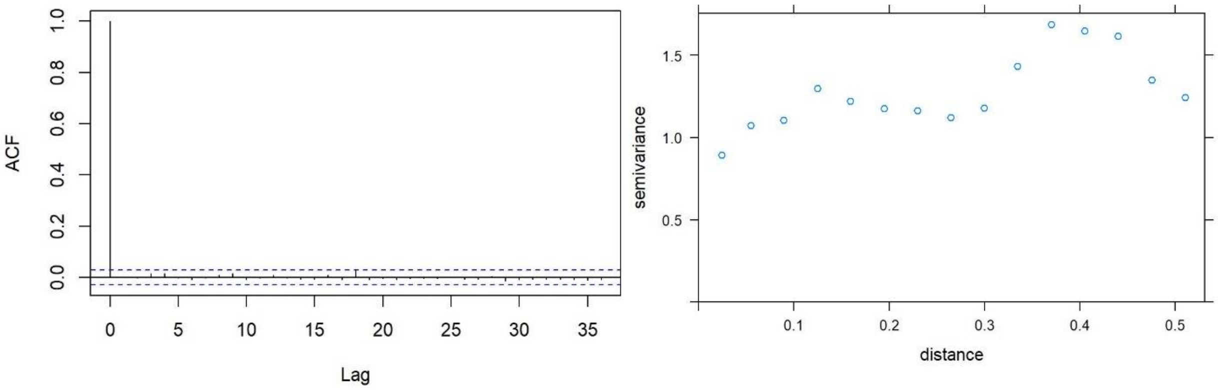


Figure V.2.1.2-2. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of bottlenose dolphin groups in Spring for the period 2001-2017.

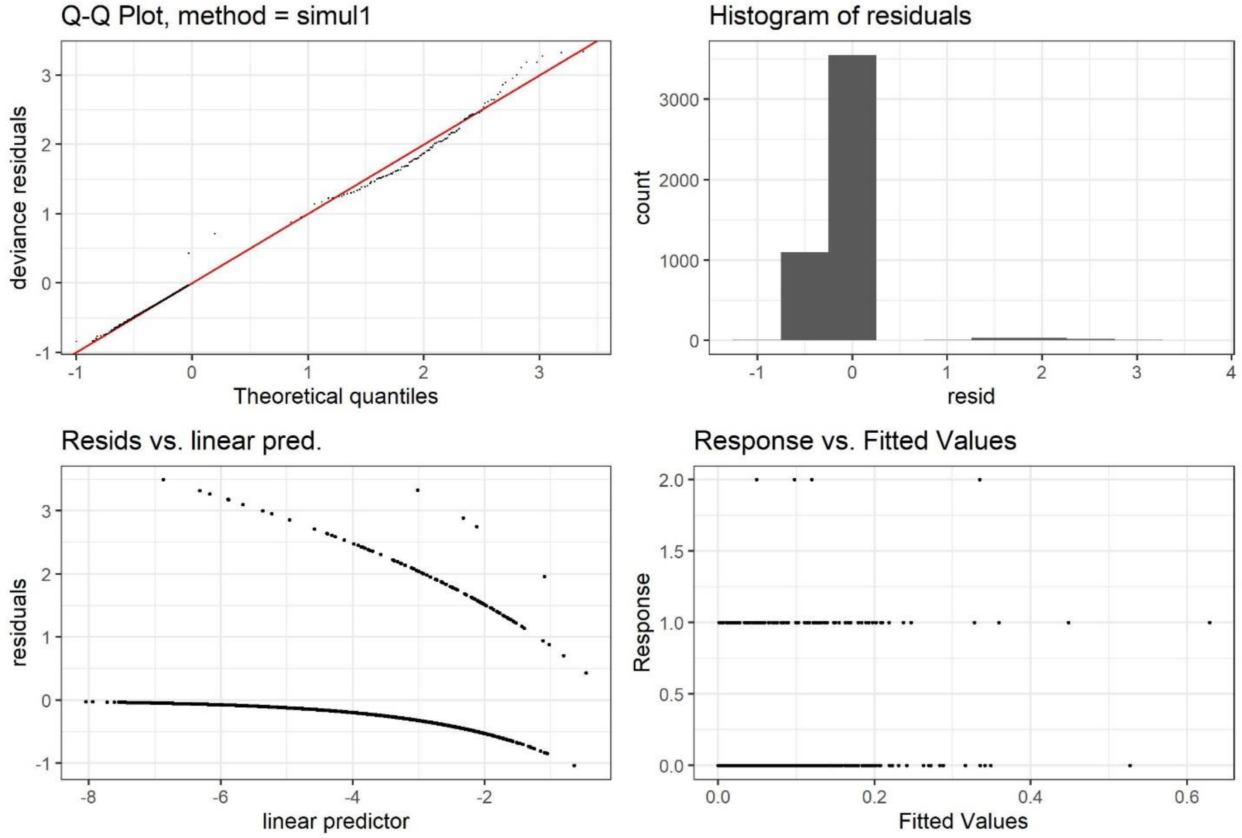


Figure V.2.1.2-3. Diagnostic plots of the selected generalised additive model of the encounter rate of bottlenose dolphin groups in Spring for the period 2001-2017.

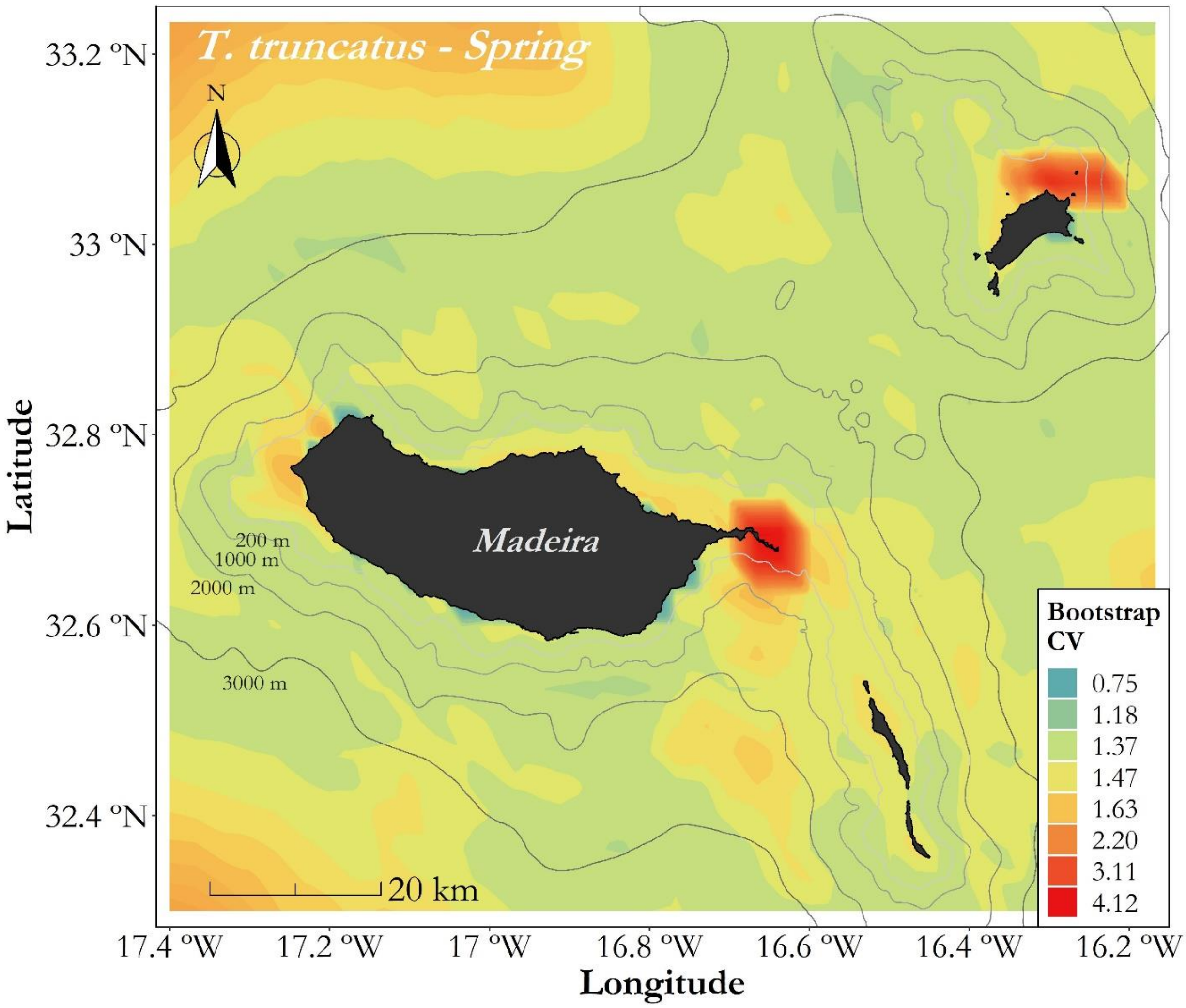


Figure V.2.1.2-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of bottlenose dolphins in Spring in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.3. Tursiops truncatus - Summer

Model of encounter rates of groups

Table V.2.1.3-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-4.4715	0.2755	-16.233	<0.001*
Survey type SLS-RD	-0.7543	0.4748	-1.489	0.1366
Survey type ALS	-0.3473	0.4591	-0.756	0.4494
Survey type NSS	0.829	0.3075	2.695	0.007*
Survey type WWO	1.1267	0.3129	3.601	<0.001*
Survey type FO	0.9169	0.758	1.21	0.2265
*Significant at α = 0.05				

Table V.2.1.3-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Distance to 500m isobath	1.9618	9	2.543	<0.001*
Mld 2001-17 Summer	0.6031	9	0.173	0.003*
Sst-a 2001-17 Summer	0.9172	9	0.858	0.014*
Beaufort	0.8351	9	1.005	0.014*
Month	0.9304	2	2.659	0.013*
Year	0.4123	13	0.055	0.18787
Effort	7.4308	9	11.834	<0.001*
*Significant at α = 0.05				

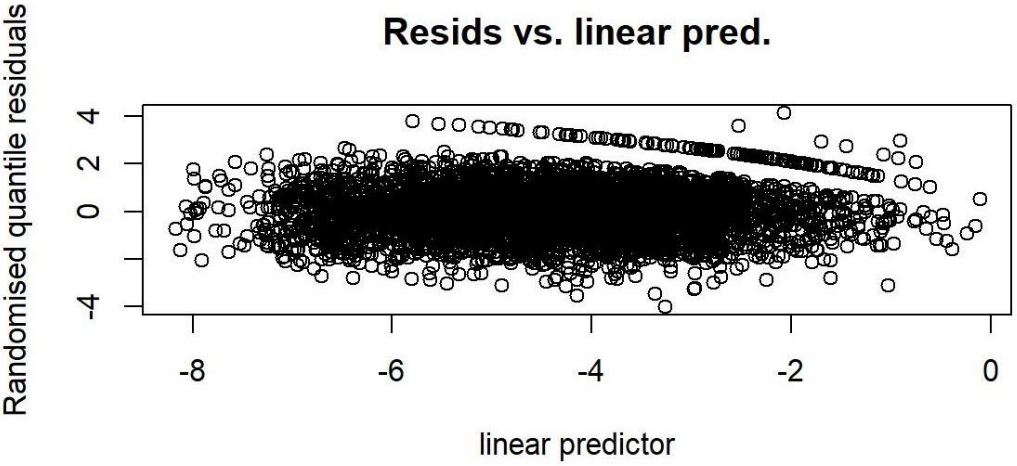


Figure V.2.1.3-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of bottlenose dolphins in Summer to check heteroskedasticity.

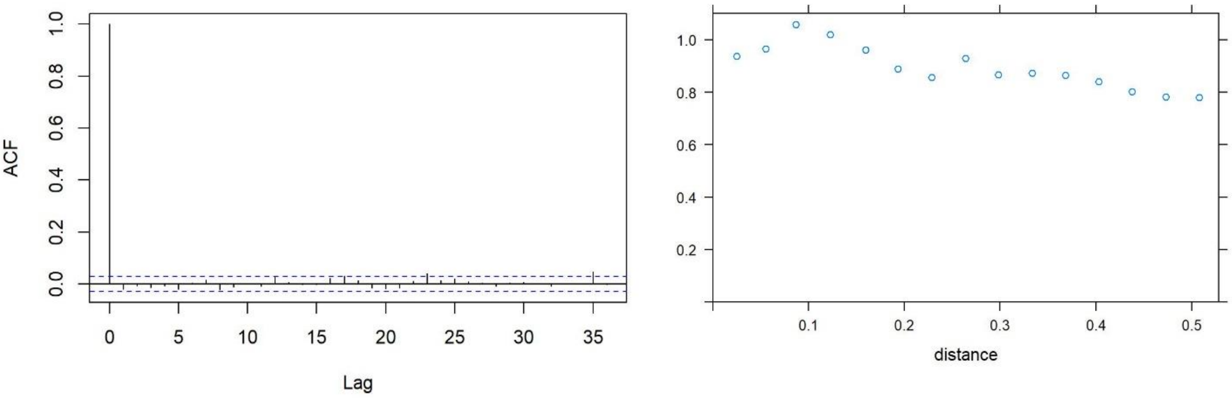


Figure V.2.1.3-2. Temporal auto-correlation regression plot from “acf” function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of bottlenose dolphin groups in Summer for the period 2001-2017.

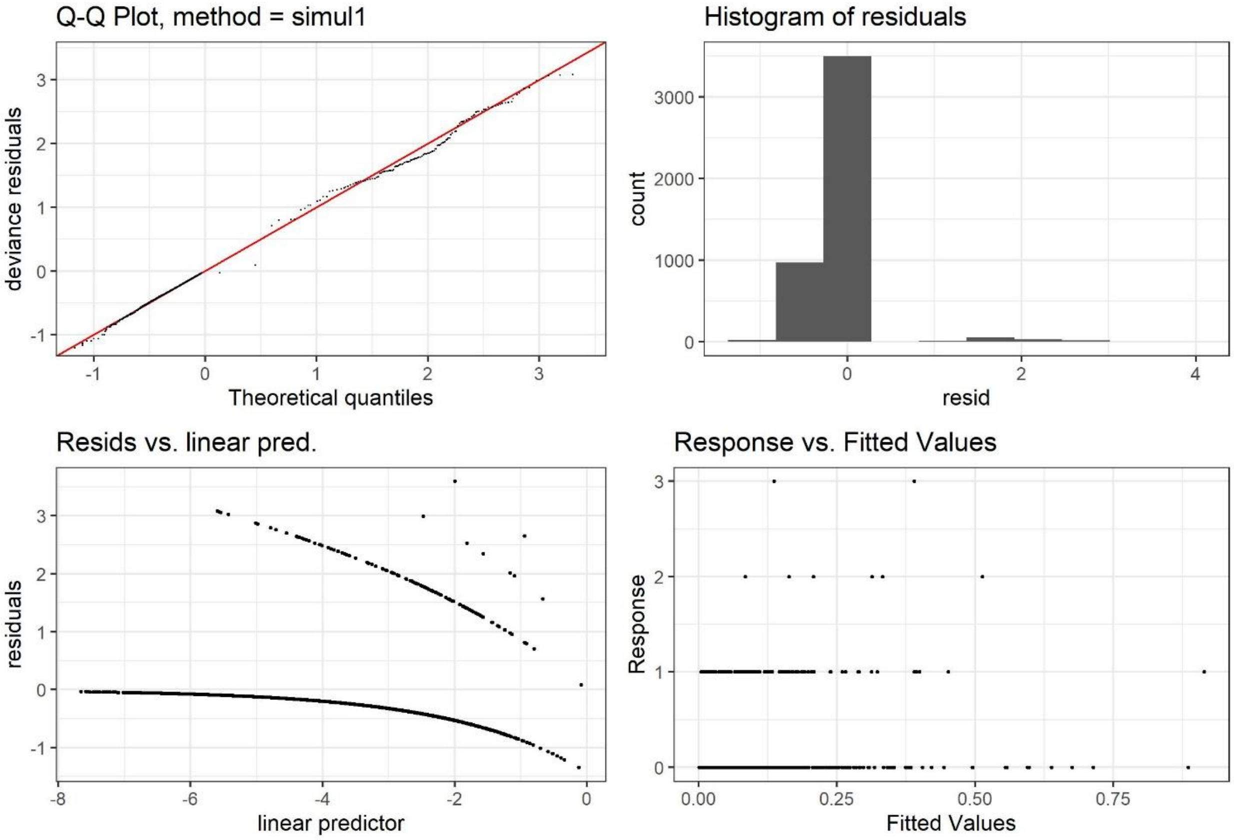


Figure V.2.1.3-3. Diagnostic plots of the selected generalised additive model of the encounter rate of bottlenose dolphin groups in Summer for the period 2001 – 2017.

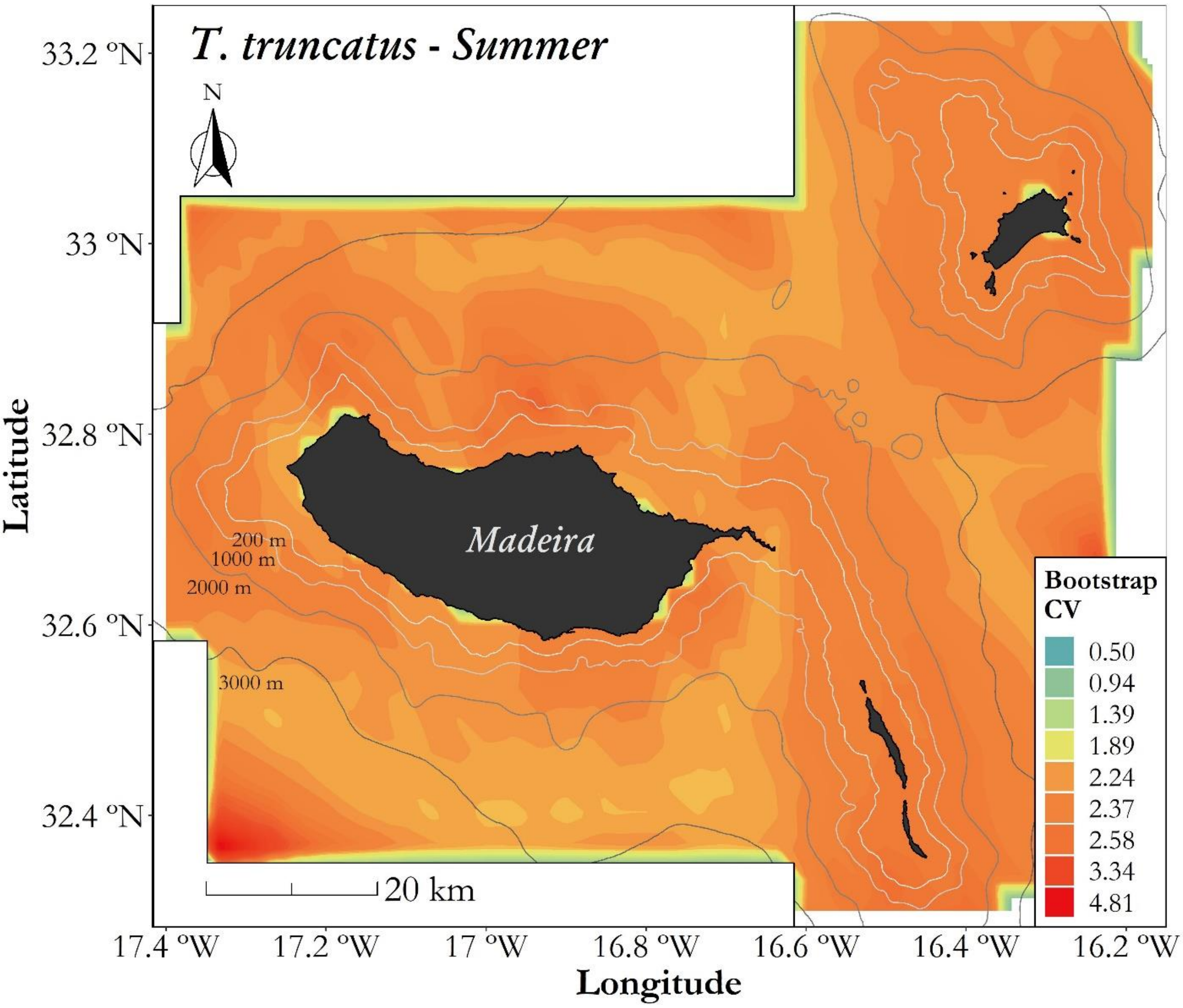


Figure V.2.1.3-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of bottlenose dolphins in Summer in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.4. *Tursiops truncatus - Autumn*

Model of encounter rates of groups

Table V.2.1.4-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-4.3268	0.2983	-14.504	<0.001*
Survey type SLS-RD	0.6629	0.3728	1.778	0.076
Survey type ALS	-0.5057	0.4864	-1.04	0.299
Survey type NSS	1.1588	0.3933	2.946	0.003*
Survey type WWO	0.7896	0.3501	2.255	0.024*
Survey type FO	-	-	-	-
*Significant at α = 0.05				

Table V.2.1.4-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Maximum depth	3.5605	9	2.173	<0.001*
Beaufort	0.9054	5	1.841	0.0014*
Effort	2.933	9	1.328	0.004*
*Significant at α = 0.05				

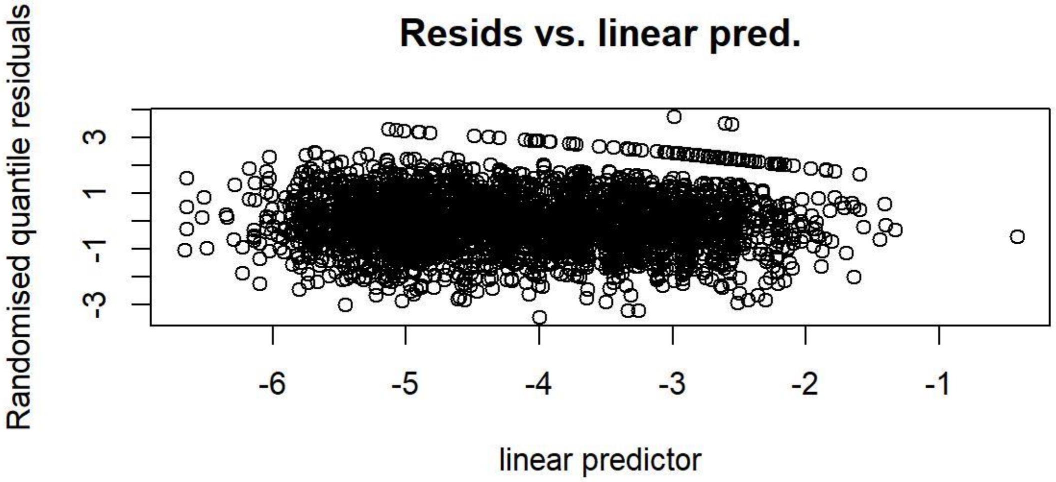


Figure V.2.1.4-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of bottlenose dolphin groups in Autumn to check heteroskedasticity.

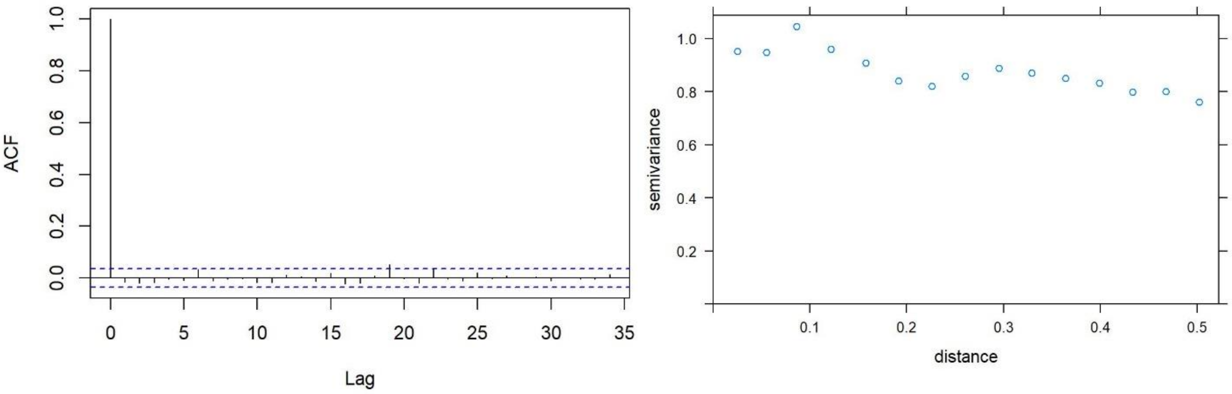


Figure V.2.1.4-2. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of bottlenose dolphin groups in Autumn for the period 2001-2017.

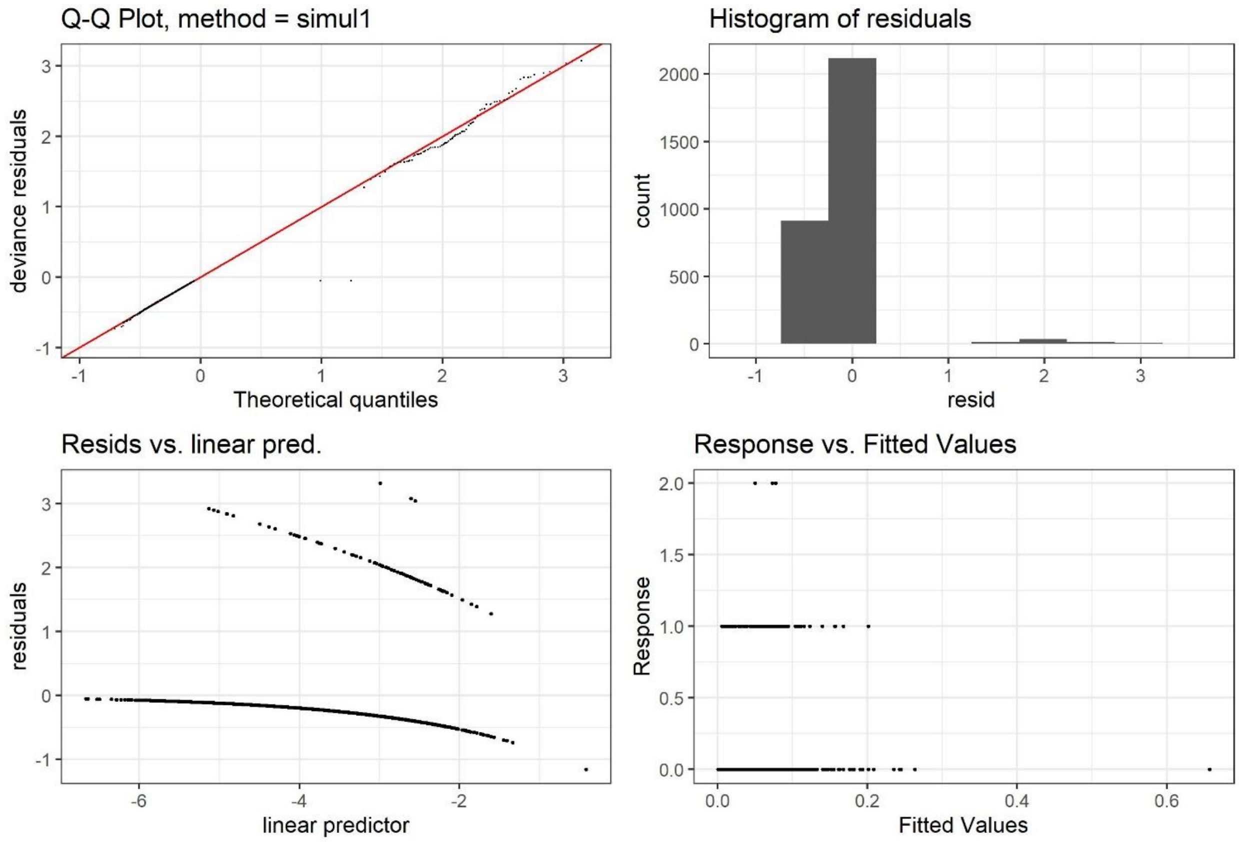


Figure V.2.1.4-3. Diagnostic plots of the selected generalised additive model of the encounter rate of bottlenose dolphin groups in Autumn for the period 2001 – 2017.

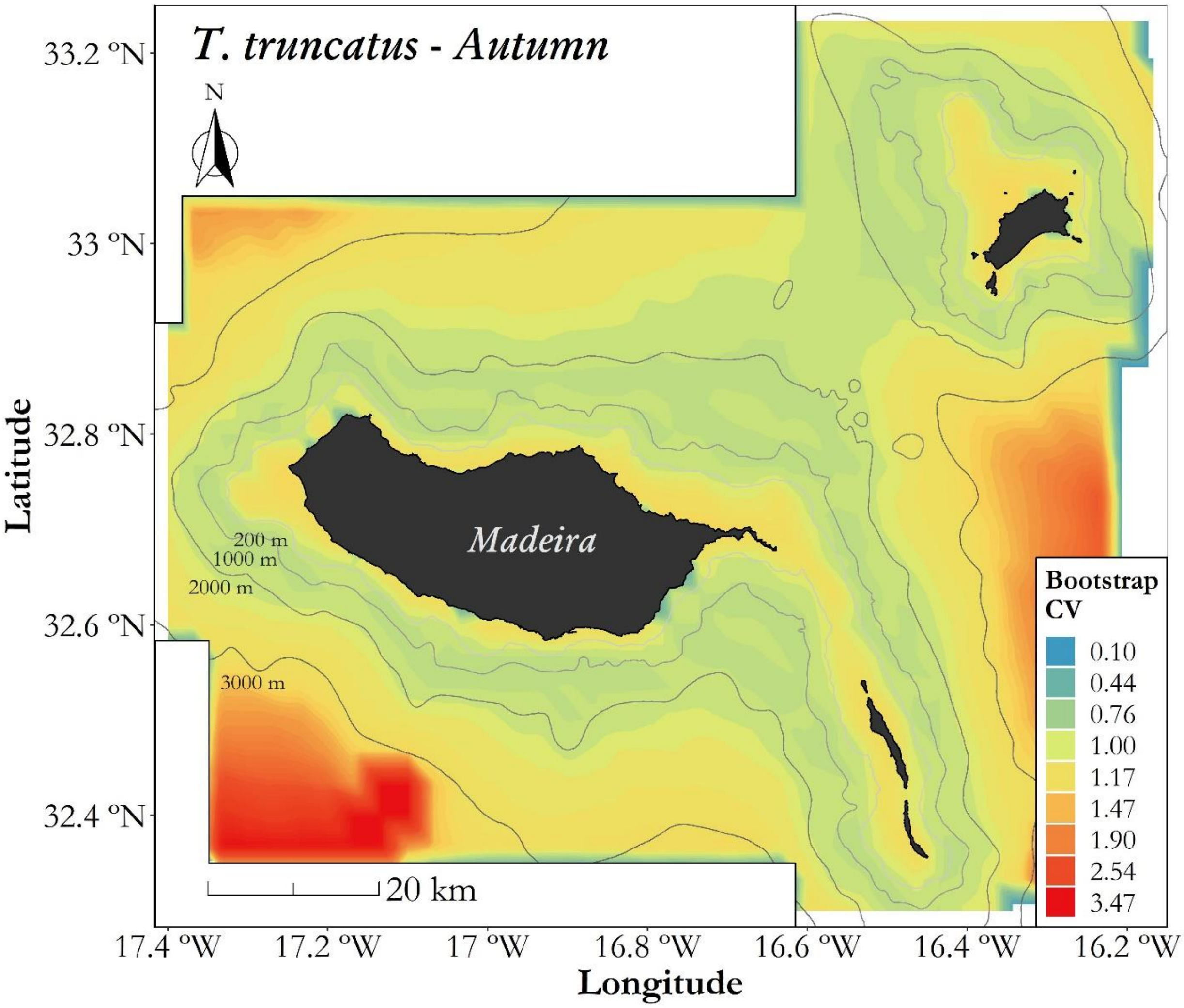


Figure V.2.1.4-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of bottlenose dolphins in Autumn in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.5 Stenella frontalis - Winter

Model of encounter rates of groups

Table V.2.1.5-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-4.5160	0.3804	-11.8730	<0.001*
Survey type SLS-RD	-	-	-	-
Survey type ALS	-1.0410	0.6628	-1.5710	0.116
Survey type NSS	-0.1305	0.5061	-0.2580	0.797
Survey type WWO	0.1928	0.6755	0.2850	0.775
Survey type FO	-49.0700	7962000	0	1
*Significant at α = 0.05				

Table V.2.1.5-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Minimum aspect	1.3473	8	0.305	0.1439
Distance to 3000m isobath	0.8683	9	0.607	0.01*
Mld 2001-17 Winter	0.2863	9	0.046	0.223
Maximum slope	0.7984	9	0.385	0.036*
Month	0.1114	2	0.061	0.2915
Year	2.8509	11	0.747	0.025*
*Significant at α = 0.05				

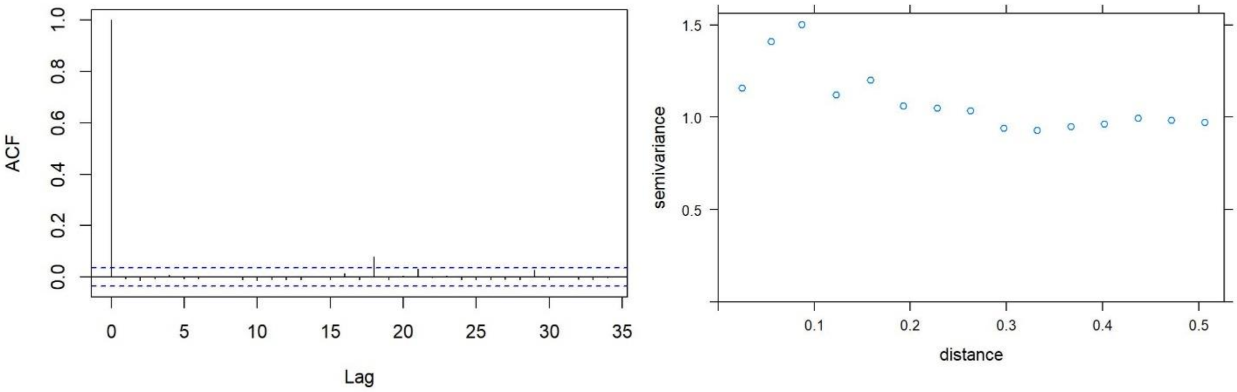


Figure V.2.1.5 -1. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of spotted dolphin groups in Winter for the period 2001-2017.

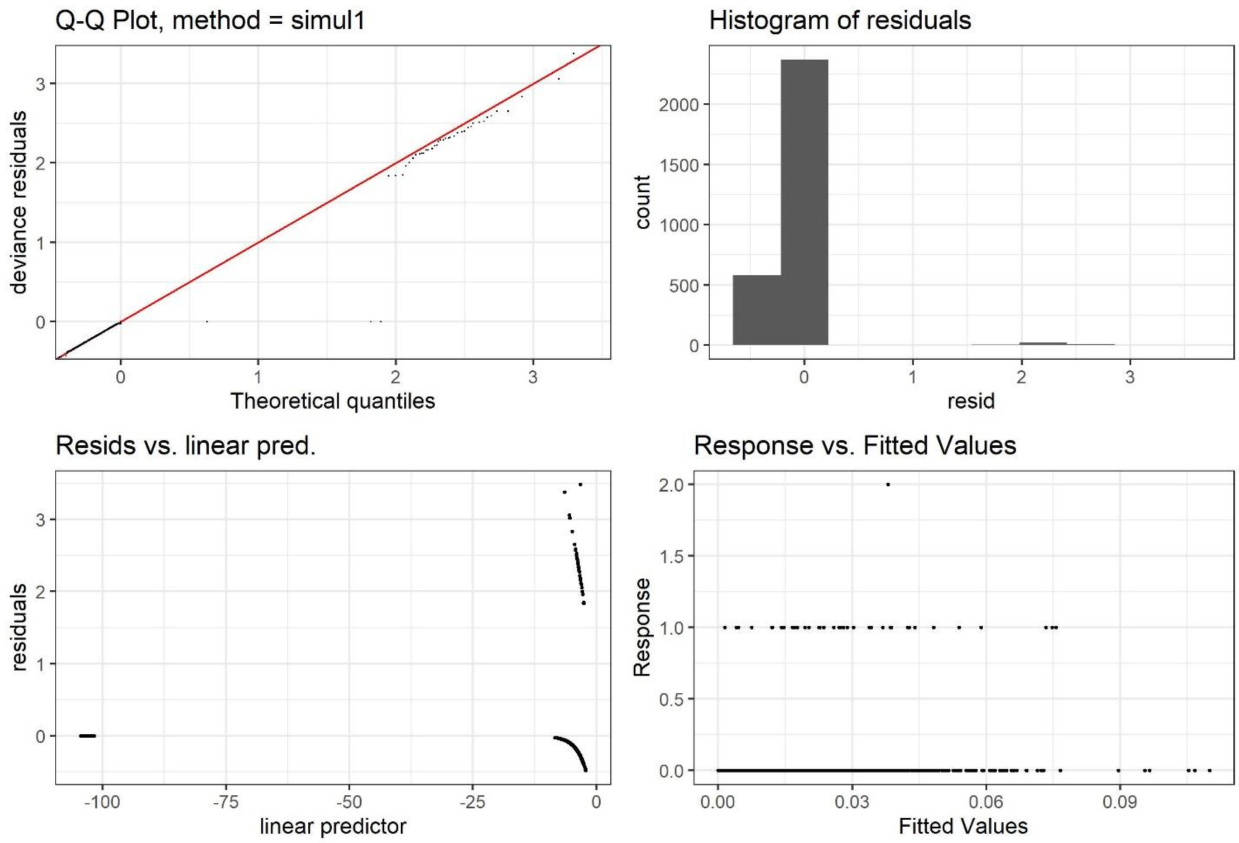


Figure V.2.1.5-2. Diagnostic plots of the selected generalised additive model of the encounter rate of spotted dolphin groups in Winter for the period 2001 – 2017.

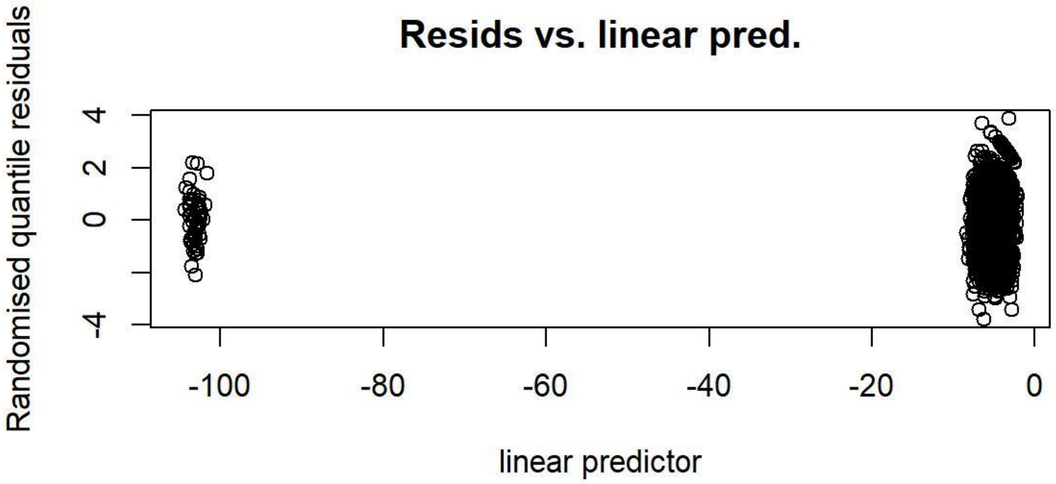


Figure V.2.1.5-3. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of spotted dolphin groups in Winter to check heteroskedasticity.

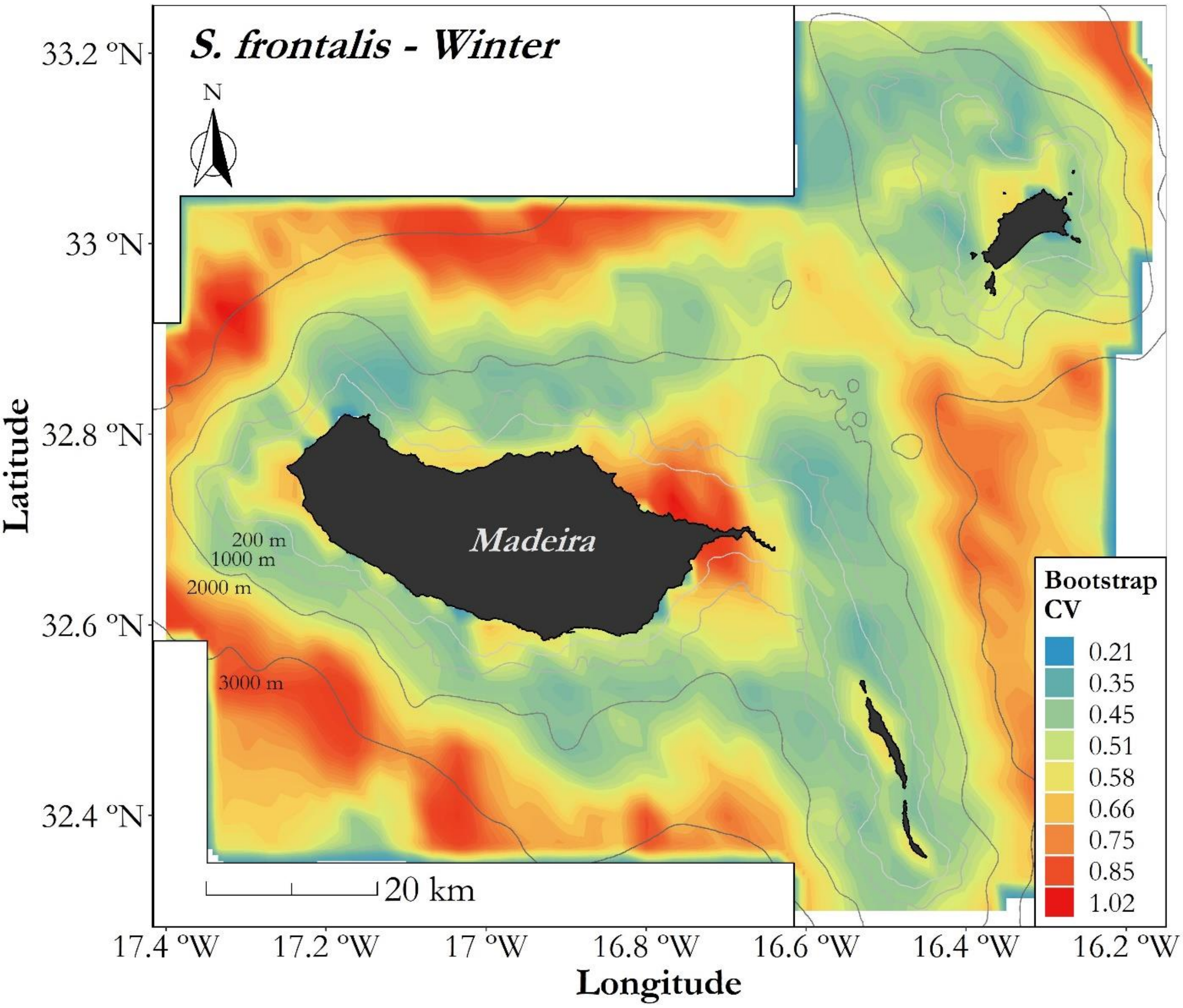


Figure V.2.1.5-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of spotted dolphins in Winter in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.6 Stenella frontalis - Spring

Model of encounter rates of groups

Table V.2.1.6-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-4.3998	0.2374	-18.533	<0.001*
Survey type SLS-RD	-	-	-	-
Survey type ALS	-2.2401	0.7298	-3.069	0.0022*
Survey type NSS	0.2767	0.3153	0.878	0.380
Survey type WWO	0.8251	0.3276	2.519	0.012*
Survey type FO	-0.7064	0.5109	-1.383	0.17
*Significant at $\alpha = 0.05$				

Table V.2.1.6-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Slope area	0.9606	9	1.331	<0.001*
Chl-a 2001-17 Spring	0.8319	9	0.472	0.016*
Poc 2001-17 Spring	0.8964	9	0.682	0.004*
Sst 2001-17 Spring	0.9308	9	0.743	<0.005*
Month	1.1646	2	12.661	<0.001*
Effort	4.5095	9	3.685	<0.001*
*Significant at $\alpha = 0.05$				

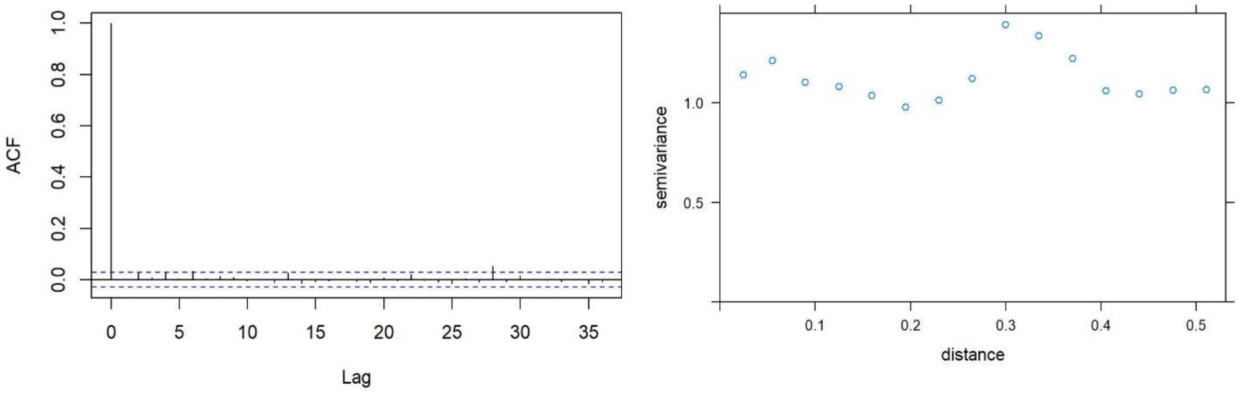


Figure V.2.1.6-1. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of spotted dolphin groups in Spring for the period 2001-2017.

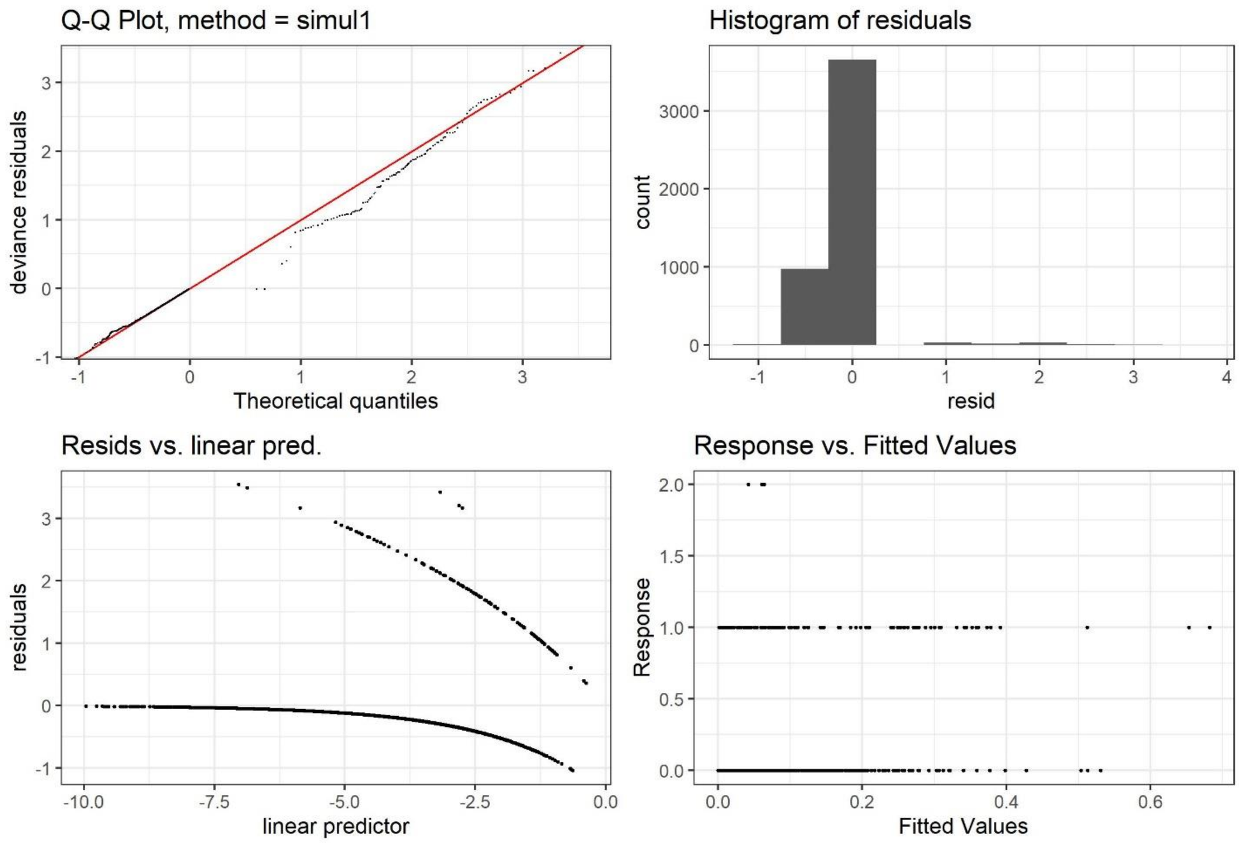


Figure V.2.1.6-2. Diagnostic plots of the selected generalised additive model of the encounter rate of spotted dolphins in Spring for the period 2001 – 2017.

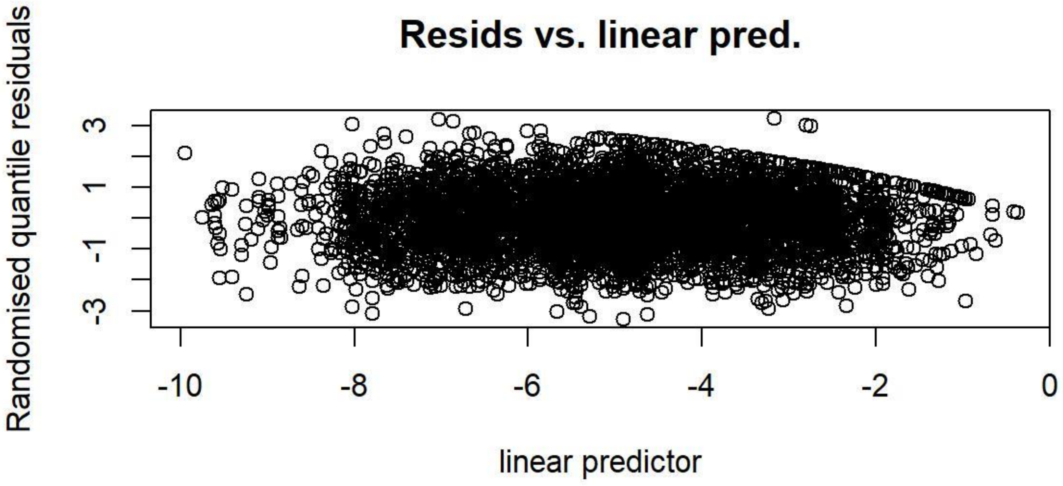


Figure V.2.1.6-3. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of spotted dolphins in Spring to check heteroskedasticity.

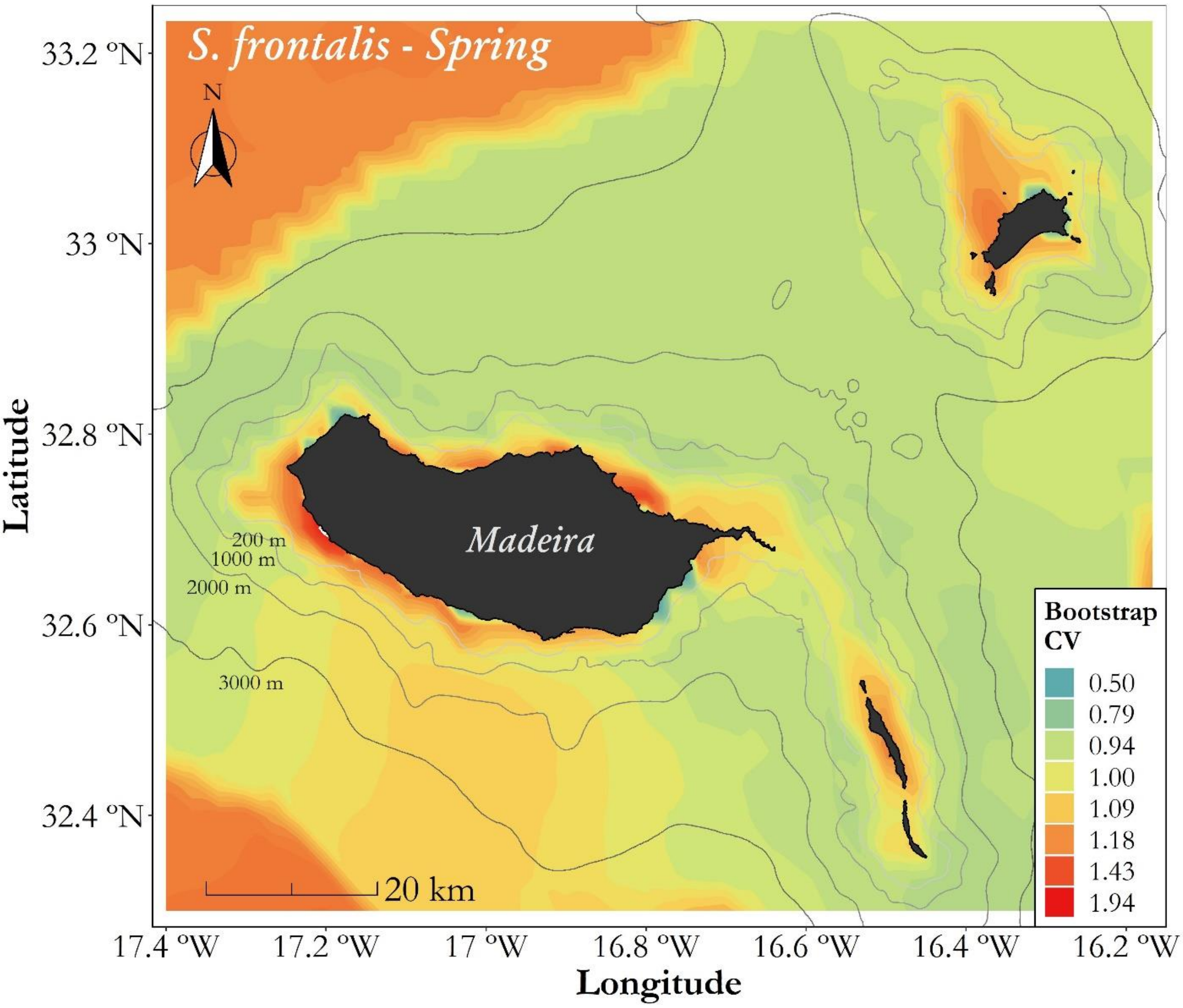


Figure V.2.1.6-4 Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of spotted dolphins in Spring in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.7 *Stenella frontalis - Summer*

Model of encounter rates of groups

Table V.2.1.7-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-3.9240	0.2276	-17.242	<0.001*
Survey type SLS-RD	-0.2000	0.4490	-0.4450	0.656
Survey type ALS	-1.3600	0.3860	-3.5240	<0.001*
Survey type NSS	0.6973	0.2829	2.4650	0.014*
Survey type WWO	1.5520	0.2813	5.5180	<0.001*
Survey type FO	-83.300	7989000	0.0000	0.9999
*Significant at α = 0.05				

Table V.2.1.7-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Average aspect	2.0486	8	0.779	0.026*
Beaufort	0.7706	5	0.668	0.037*
Contour index	1.0492	9	2.419	<0.001*
Effort	5.3871	9	6.136	<0.001*
Month	1.1167	2	8.984	<0.001*
*Significant at α = 0.05				

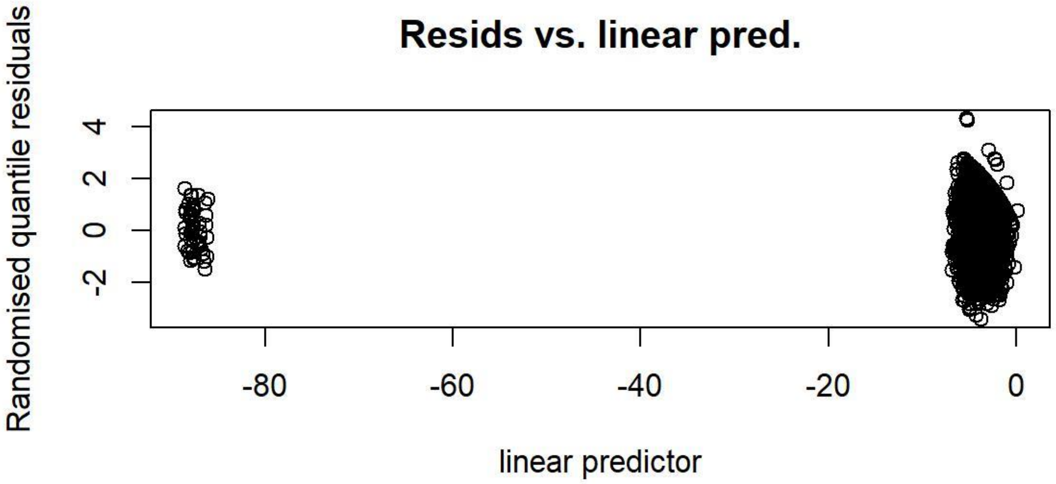


Figure V.2.1.7-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of spotted dolphins in Summer to check heteroskedasticity.

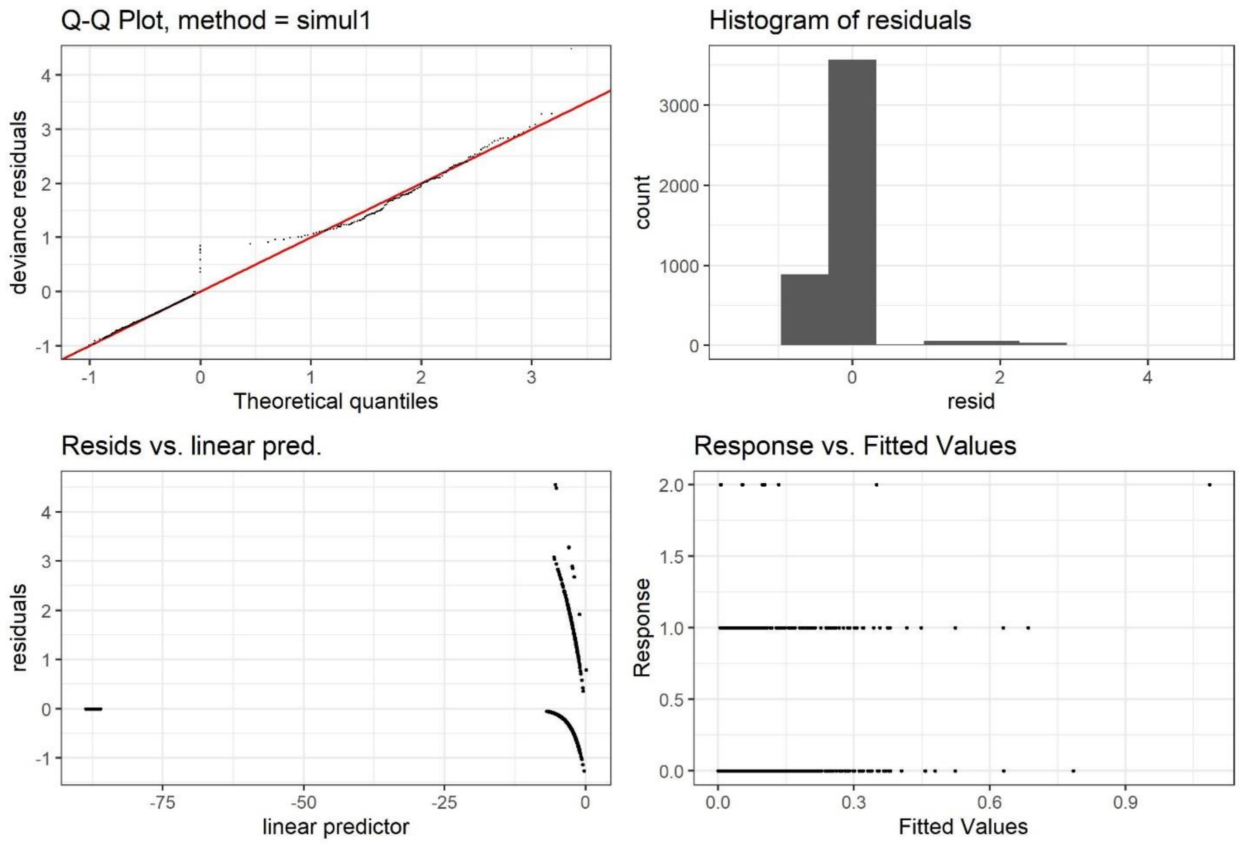


Figure V.2.1.7-2. Diagnostic plots of the selected generalised additive model of the encounter rate of spotted dolphins in Summer for the period 2001-2017.

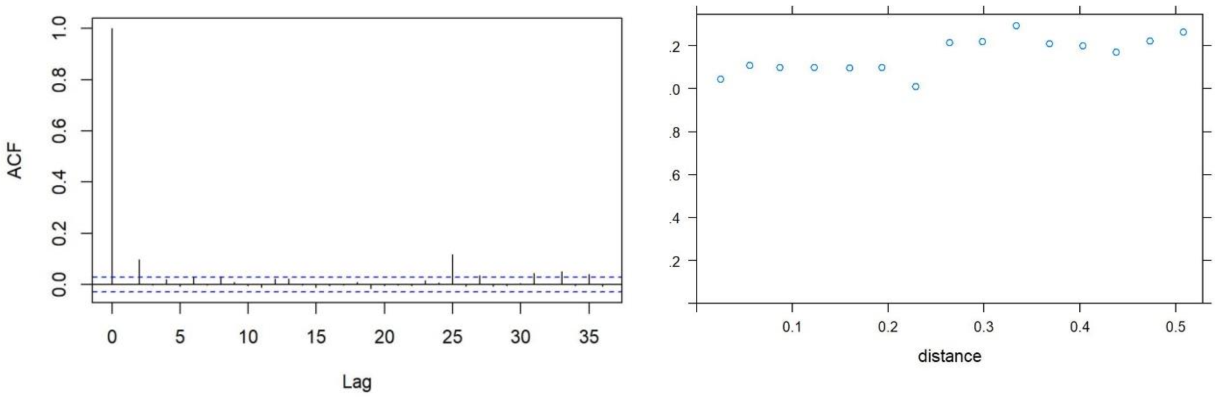


Figure V.2.1.7-3. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of spotted dolphin groups in Summer for the period 2001-2017.

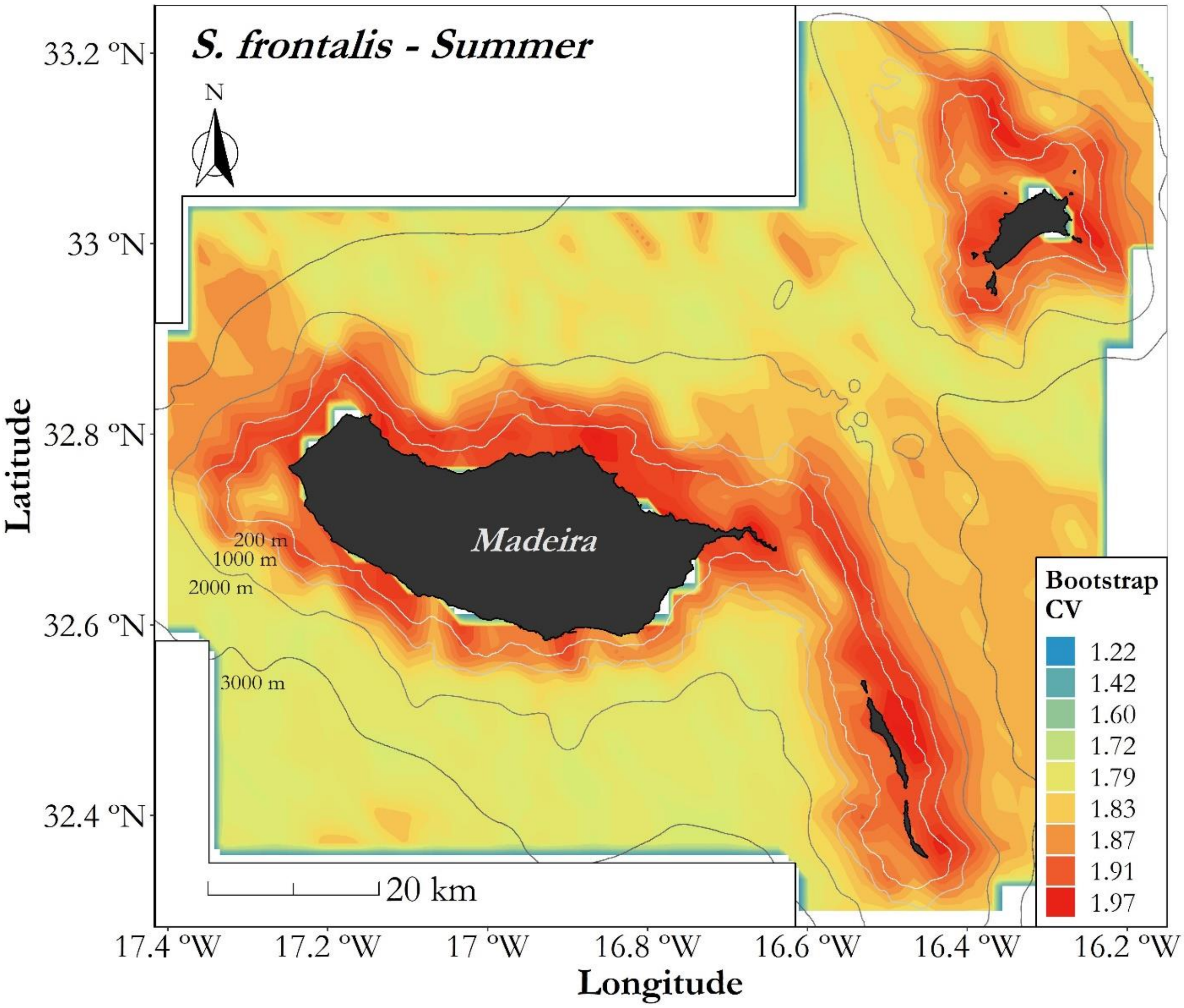


Figure V.2.1.7-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of spotted dolphins in Summer in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.8 Stenella frontalis - Autumn

Model of encounter rates of groups

Table V.2.1.8-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-6.7038	0.5998	-11.177	<0.001*
Survey type SLS-RD	0.2108	0.4644	0.454	0.650
Survey type ALS	-0.6572	0.4618	-1.423	0.155
Survey type NSS	0.2916	0.5929	0.492	0.623
Survey type WWO	1.1039	0.4088	2.701	0.007*
Survey type FO	-	-	-	-
*Significant at $\alpha = 0.05$				

Table V.2.1.8-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Distance to slope	0.8864	9	0.771	0.008*
Sst-a 2001-17 Autumn	0.95	9	0.967	0.002*
*Significant at $\alpha = 0.05$				

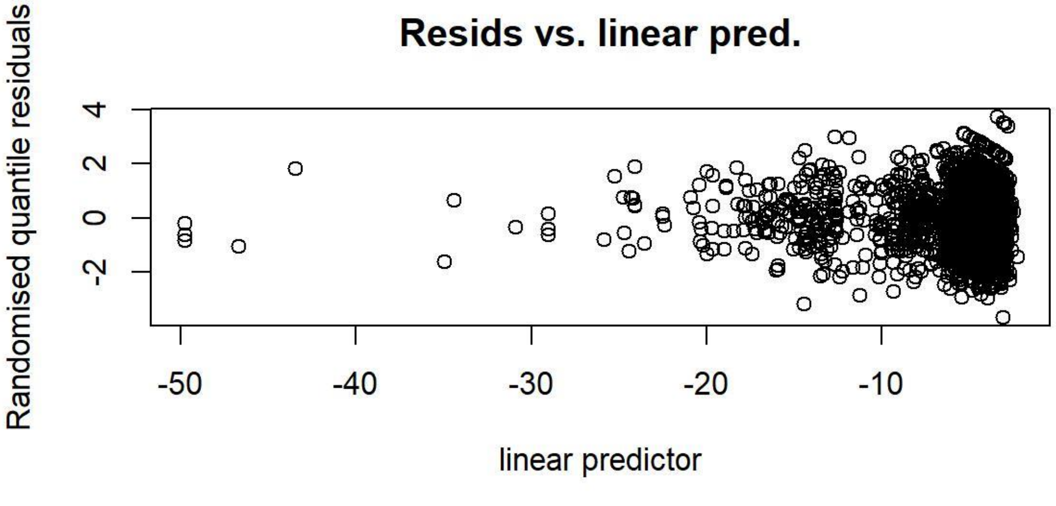


Figure V.2.1.8-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of spotted dolphin groups in Autumn to check heteroskedasticity.

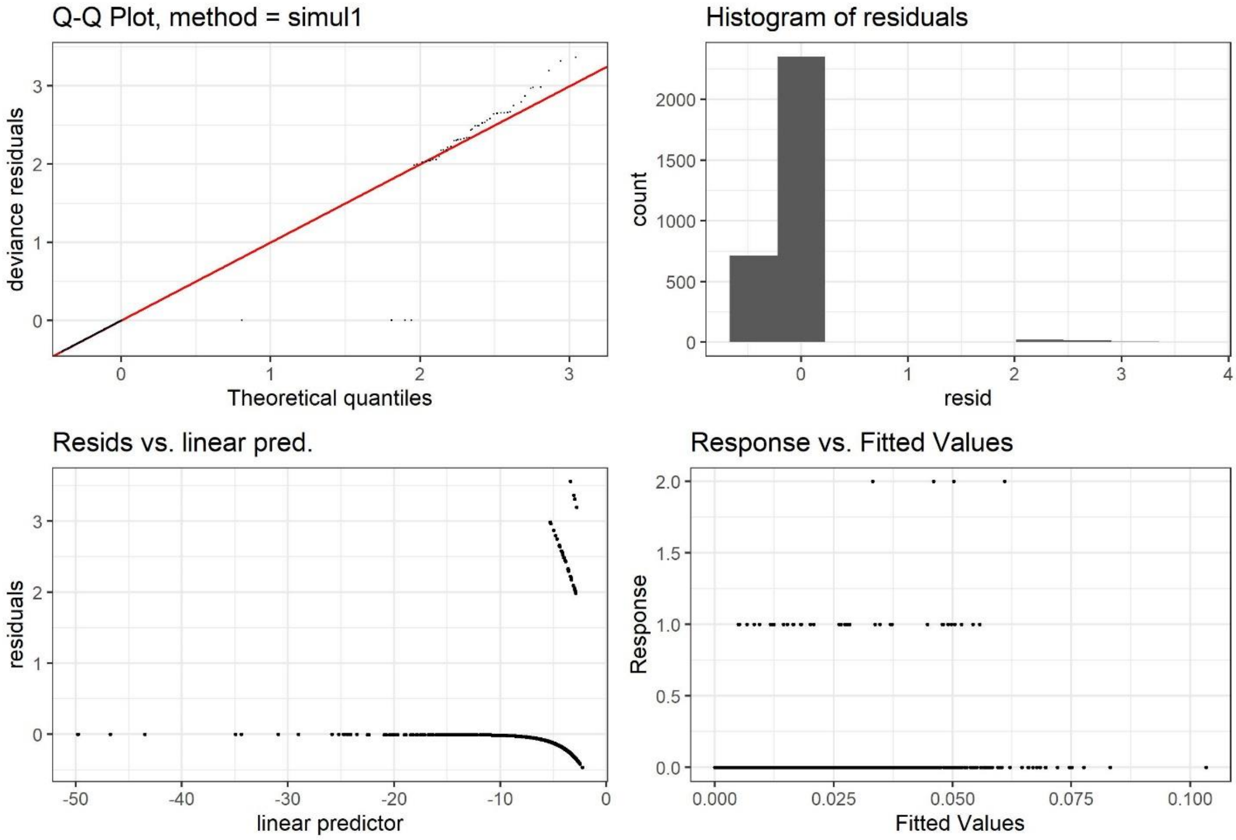


Figure V.2.1.8-2. Diagnostic plot of the selected generalised additive model of the encounter rate of spotted dolphin groups in Autumn for the period 2001-2017.

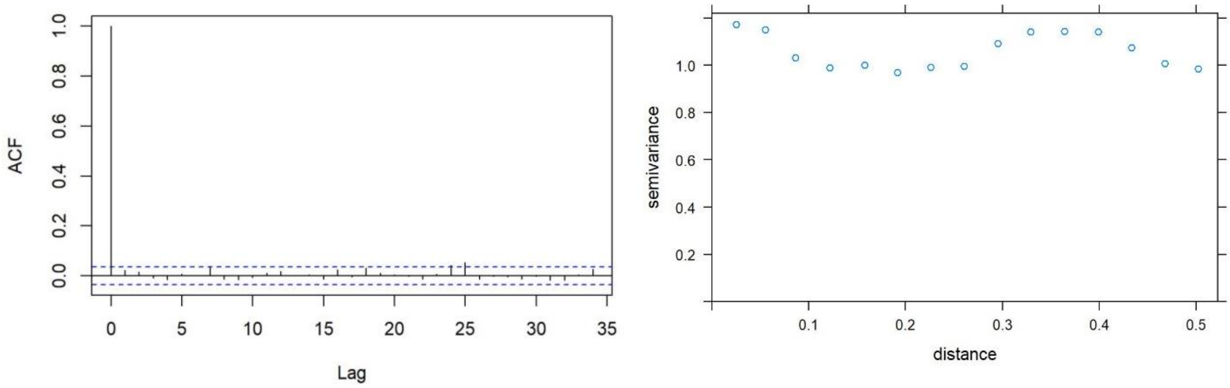


Figure V.2.1.8-3. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of spotted dolphin groups in Autumn for the period 2001-2017.

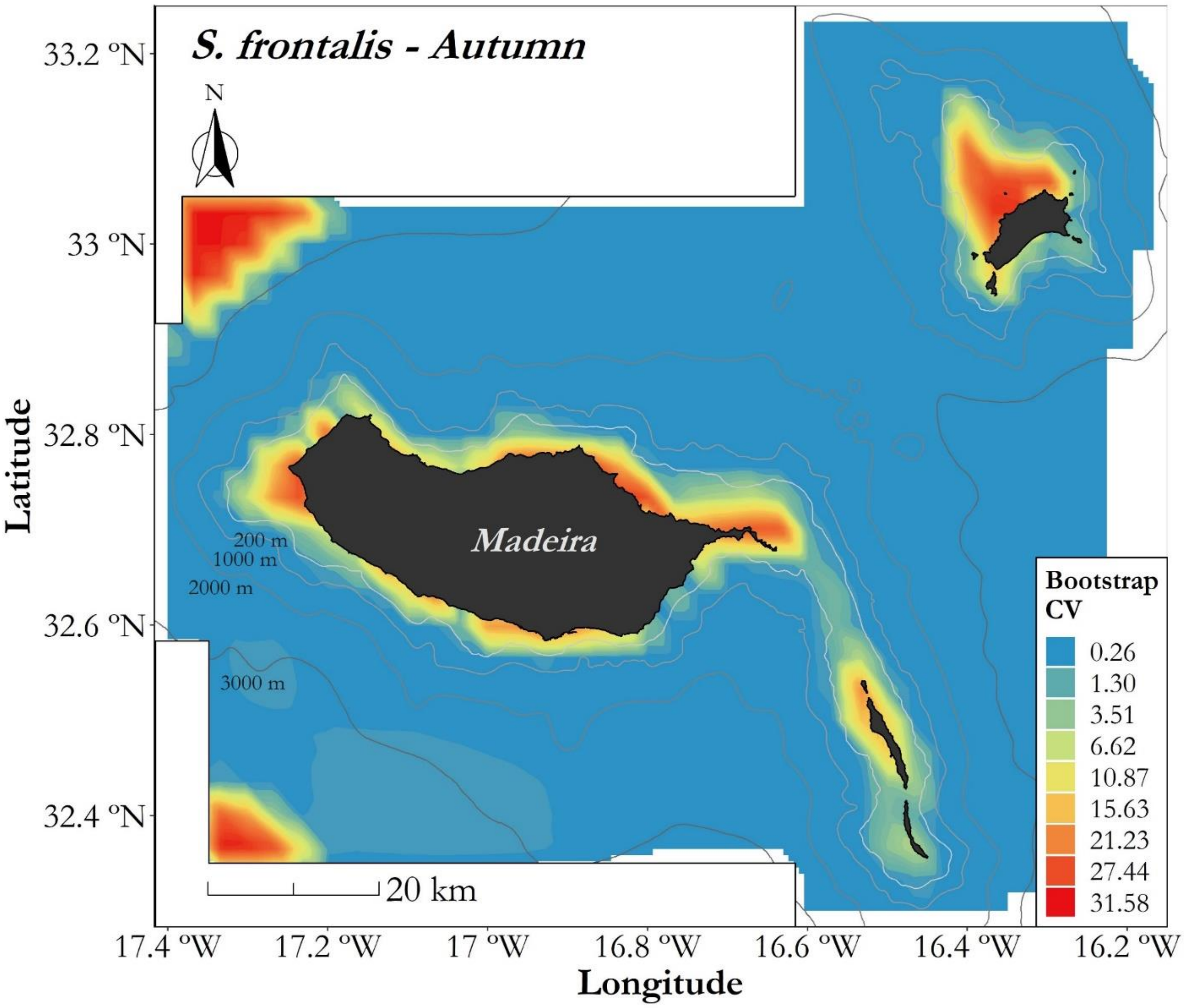


Figure V.2.1.8-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of spotted dolphins in Autumn in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.9 Delphinus delphis - Winter

Model of encounter rates of groups

Table V.2.1.9-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-3.4110	0.1767	-19.3110	<0.001*
Survey type SLS-RD	-	-	-	-
Survey type ALS	-0.4965	0.2461	-2.0170	0.044*
Survey type NSS	0.6875	0.2578	2.6670	0.008*
Survey type WWO	0.7030	0.2754	2.5520	0.01*
Survey type FO	-83.5700	7921000	0	0.999
*Significant at α = 0.05				

Table V.2.1.9-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Sst 2001-17 Winter	0.9488	9	1.048	0.001*
Beaufort	0.9549	4	2.690	<0.001*
Effort	3.0249	9	2.574	<0.001*
Month	1.1593	2	11.638	<0.001*
*Significant at α = 0.05				

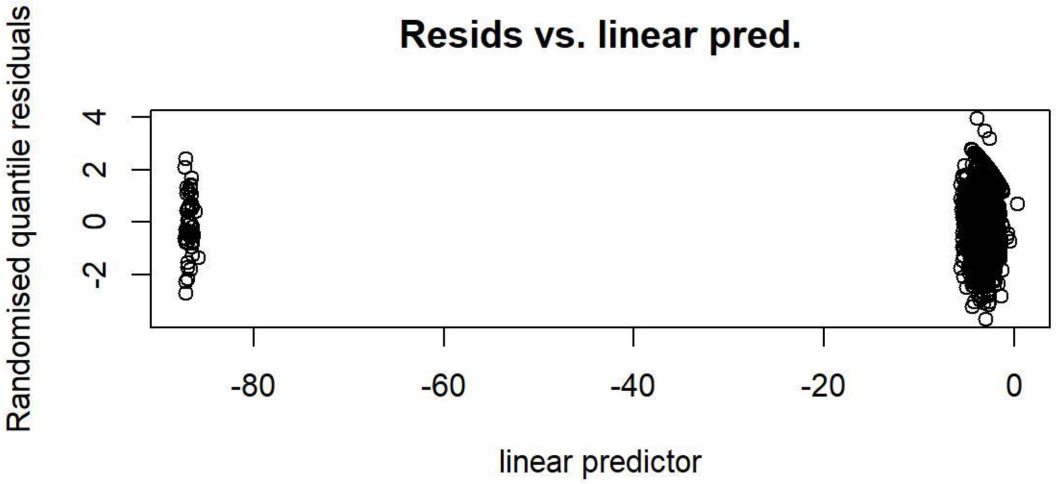


Figure V.2.1.9-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of common dolphin groups in Winter to check heteroskedasticity.

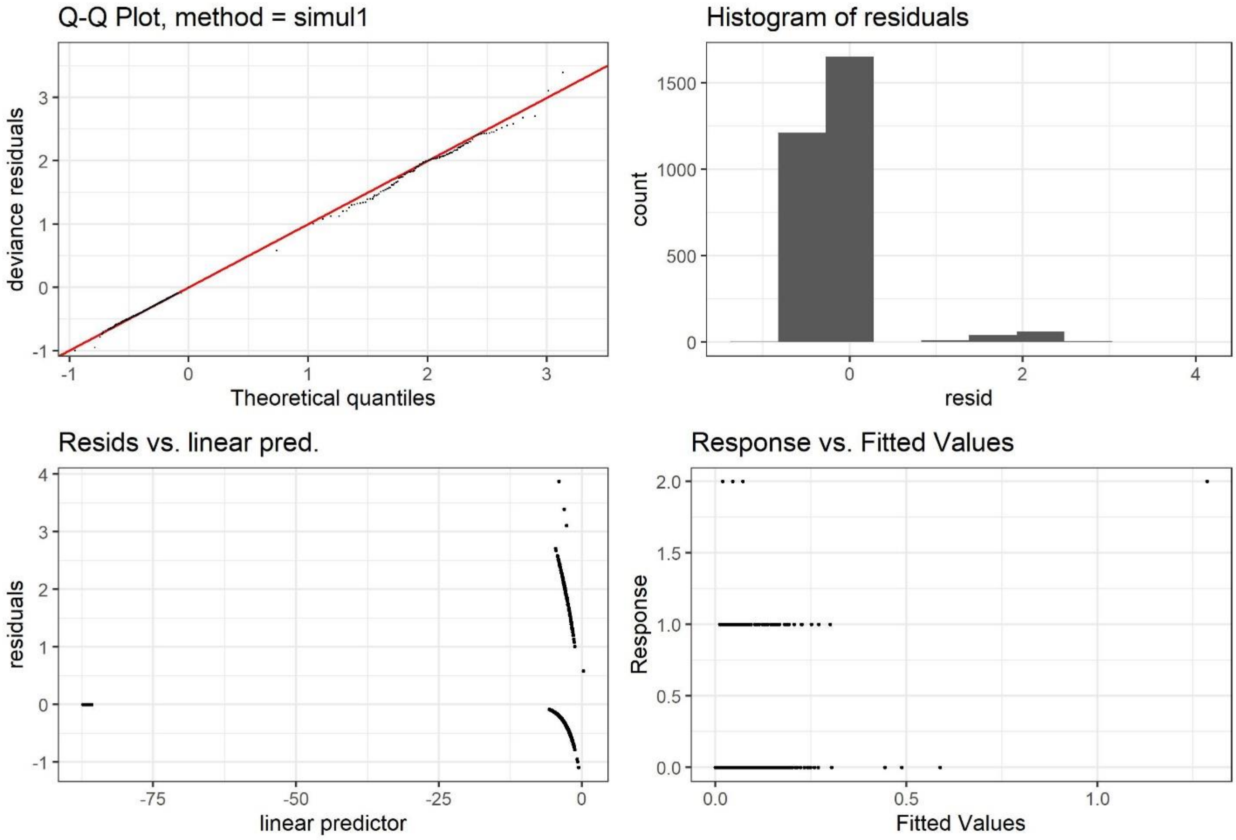


Figure V.2.1.9-2. Diagnostic plot of the selected generalised additive model of the encounter rate of common dolphin groups in Winter for the period 2001-2017.

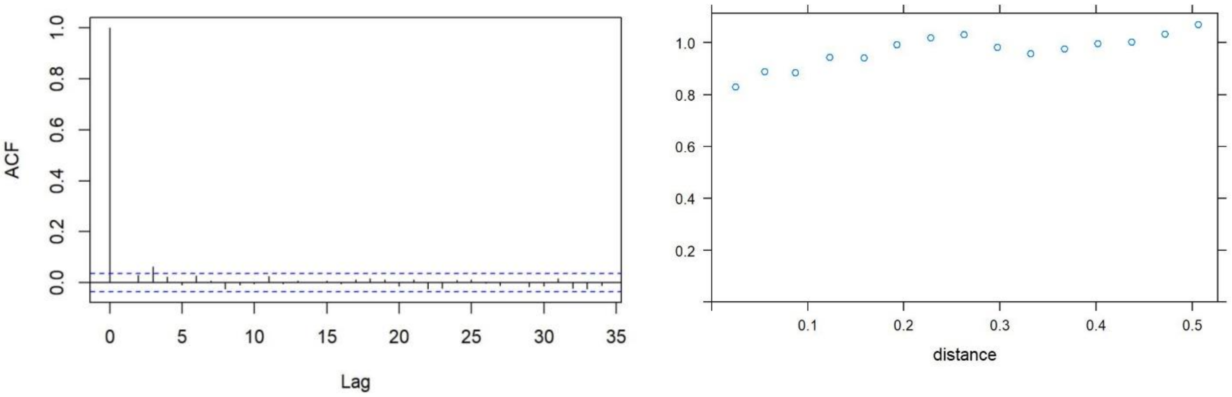


Figure V.2.1.9-3. Temporal auto-correlation regression plot from “acf” function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of common dolphin groups in Winter for the period 2001-2017.

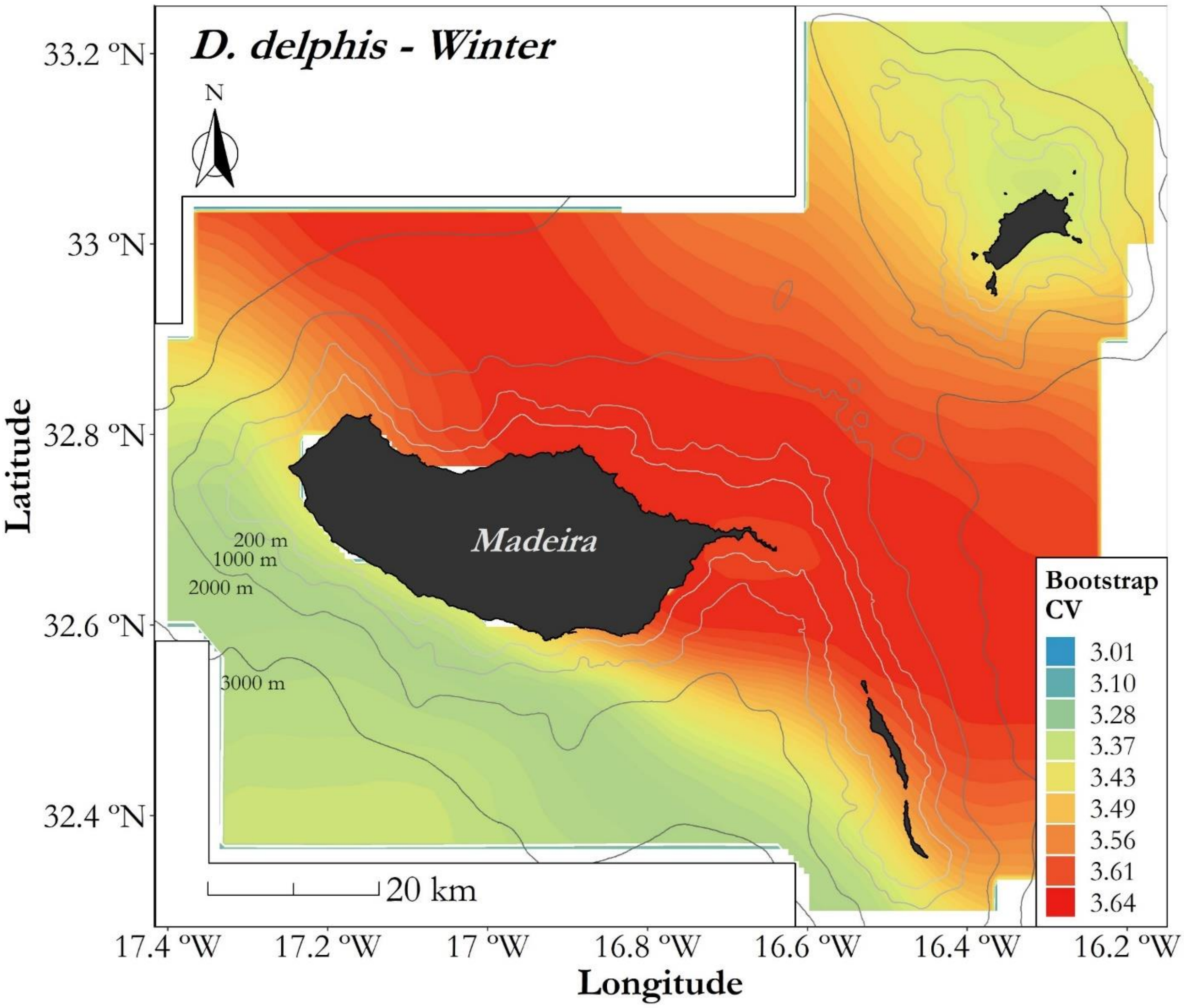


Figure V.2.1.9-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of common dolphins in Winter in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.10 Delphinus delphis - Spring

Model of encounter rates of groups

Table V.2.1.10-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-3.25542	0.14201	-22.924	<0.001*
Survey type SLS-RD	-	-	-	-
Survey type ALS	-1.32278	0.26978	-4.903	<0.001*
Survey type NSS	-0.16626	0.23963	-0.694	0.488
Survey type WWO	0.15055	0.25679	0.586	0.558
Survey type FO	-0.07193	0.19342	-0.372	0.710
*Significant at $\alpha = 0.05$				

Table V.2.1.10-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Minimum aspect	1.6285	8	0.540	0.049*
Maximum slope	0.897	9	0.767	0.005*
Effort	4.078	9	3.653	<0.001*
Month	1.693	2	30.891	<0.001*
Sst-a 2001-17 Spring	0.8235	9	0.445	0.02*
*Significant at $\alpha = 0.05$				

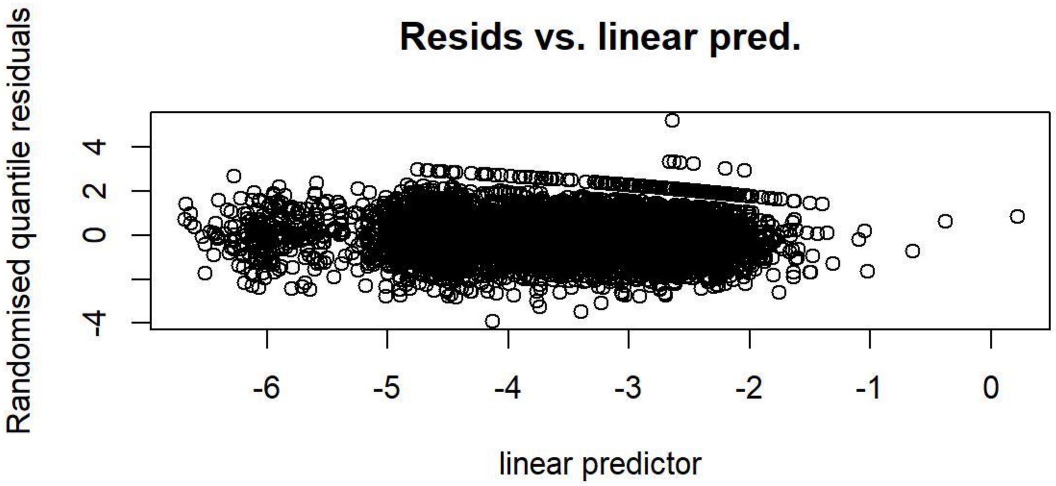


Figure V.2.1.10-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of common dolphin group in Spring to check heteroskedasticity.

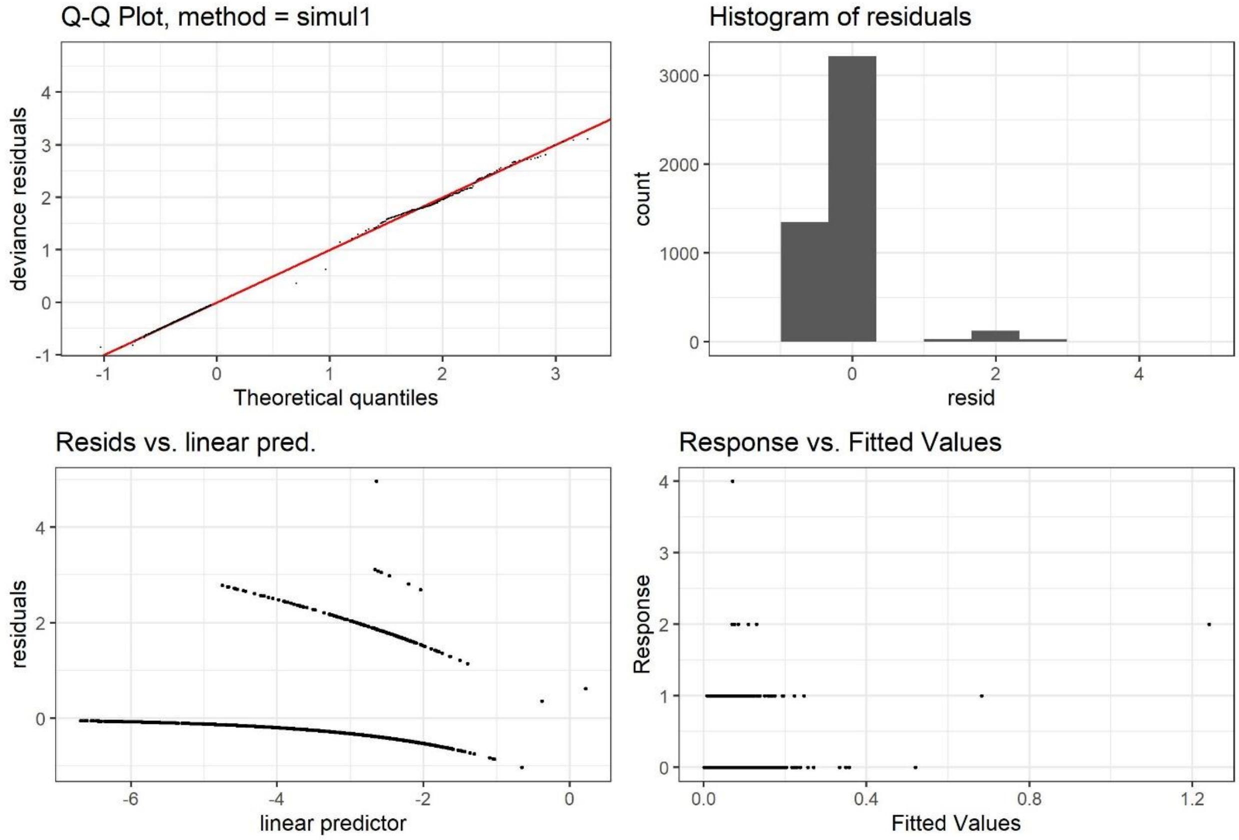


Figure V.2.1.10-2. Diagnostic plot of the selected generalised additive model of the encounter rate of common dolphin groups in Spring for the period 2001-2017.

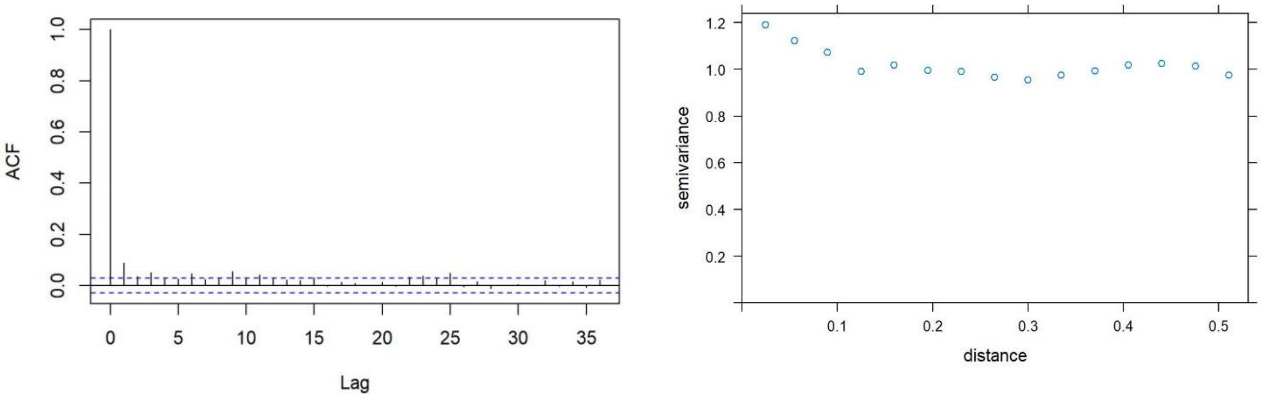


Figure V.2.1.10-3. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of common dolphin groups in Spring for the period 2001-2017.

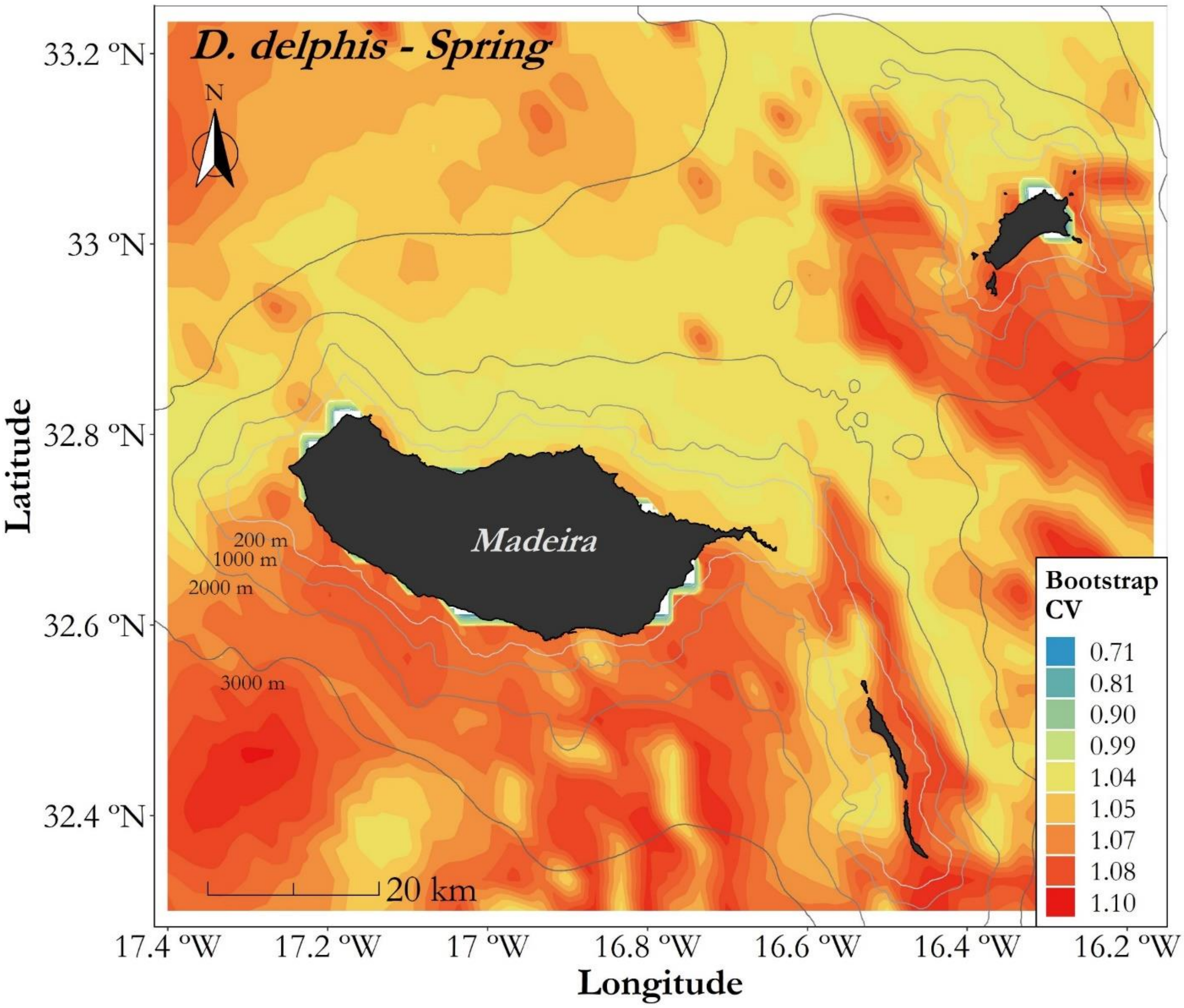


Figure V.2.1.10-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of common dolphins in Spring in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.11. Globicephala macrorhynchus - Winter

Model of encounter rates of groups

Table V.2.1.11-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-296.40	371.50	-0.7980	0.4251
Survey type SLS-RD	-	-	-	-
Survey type ALS	-0.6416	0.6645	-0.9660	0.3343
Survey type NSS	0.9178	0.4829	1.9010	0.0574
Survey type WWO	-0.6346	0.6207	-1.022	0.3067
Survey type FO	-44.52	7926000	0	1
*Significant at α = 0.05				

Table V.2.1.11-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Slope area	0.7963	9	0.072	0.3664
Maximum aspect	2.8100	8	1.965	<0.001*
Distance of 3000m isobath	0.4836	9	0.102	0.165272
Month	0.4153	2	0.344	0.195212
Year	0.8252	11	0.325	0.035*
Effort	1.8674	9	2.264	<0.001*
*Significant at α = 0.05				

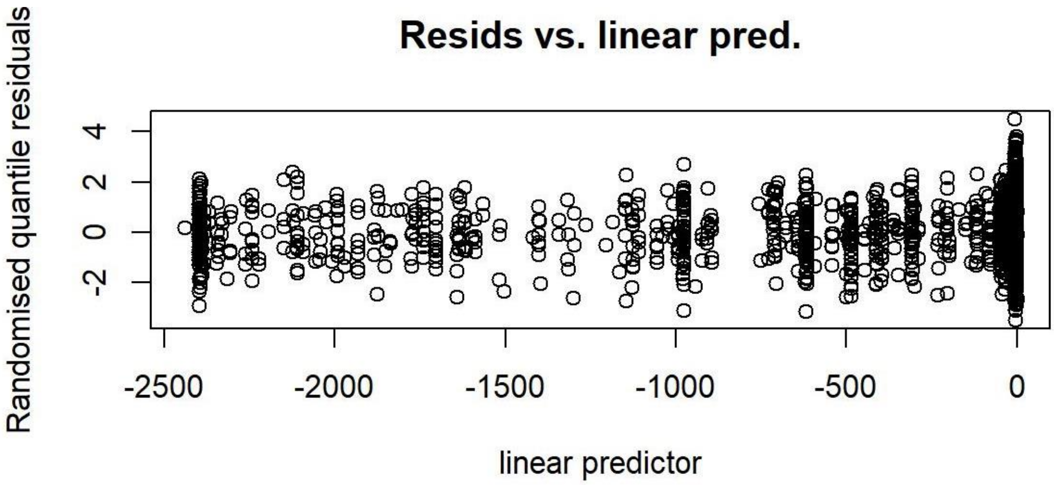


Figure V.2.1.11-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of short-finned pilot whale groups in Winter to check heteroskedasticity.

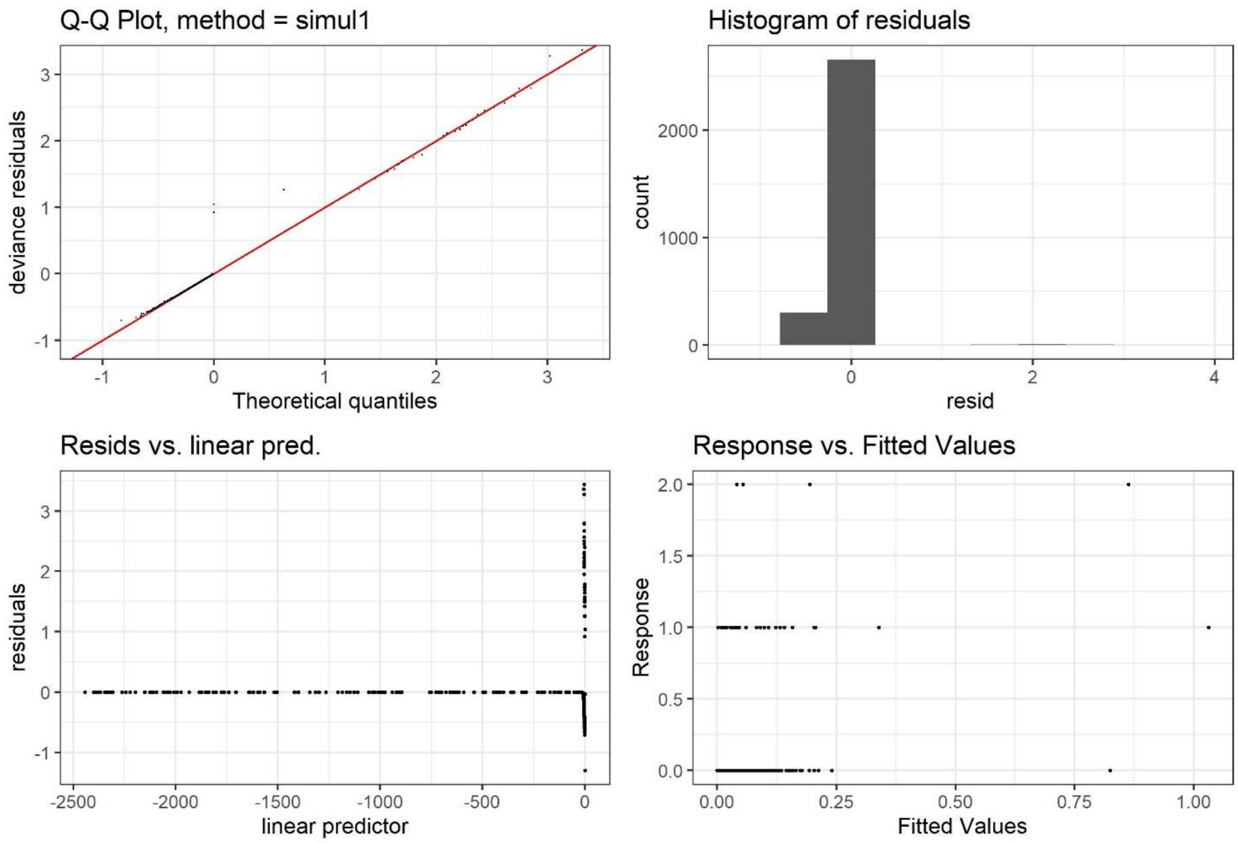


Figure V.2.1.11-2. Diagnostic plot of the selected generalised additive model of the encounter rate of short-finned pilot whale groups in Winter for the period 2001 – 2017.

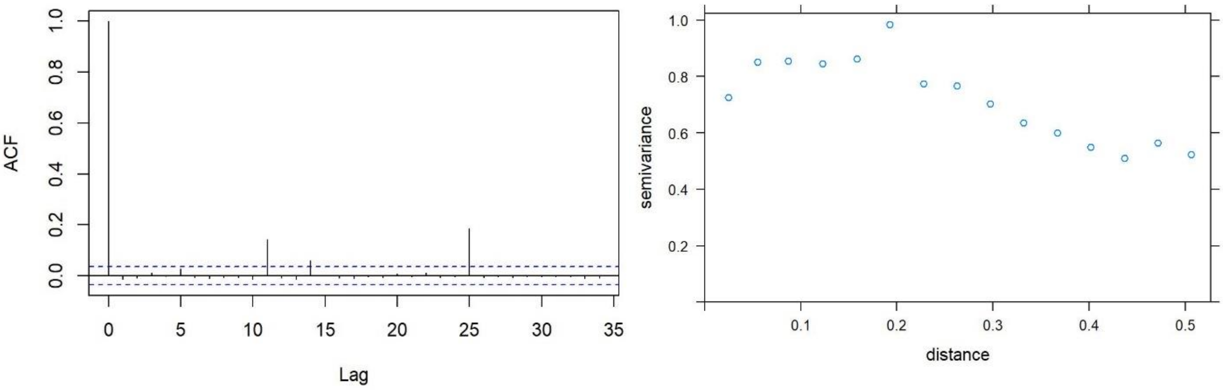


Figure V.2.1.11-3. Temporal auto-correlation regression plot from “acf” function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of short-finned pilot whale groups in Winter for the period 2001-2017.

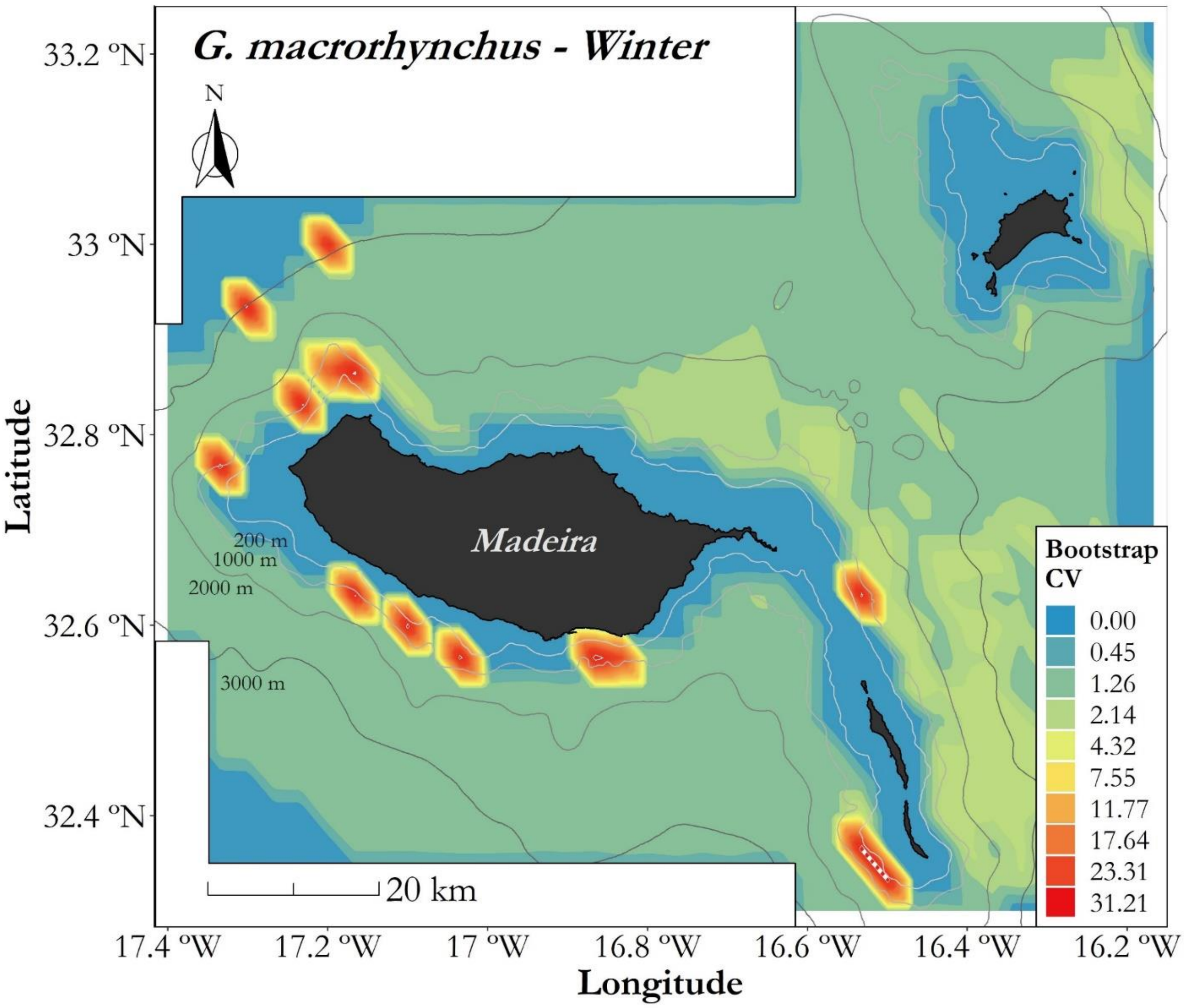


Figure V.2.1.11-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of short-finned pilot whales in Winter in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.12. Globicephala macrorhynchus - Spring

Model of encounter rates of groups

Table V.2.1.12-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-6.97616	0.42787	-16.305	<0.001*
Survey type SLS-RD	-	-	-	-
Survey type ALS	-0.9484	0.77851	-1.218	0.223
Survey type NSS	0.01909	0.47218	0.04	0.968
Survey type WWO	-0.25995	0.54918	-0.473	0.636
Survey type FO	0.03491	0.69045	0.051	0.96
*Significant at α = 0.05				

Table V.2.1.12-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Beaufort	0.9508	4	2.432	0.0011*
Distance 1500m isobath	0.9124	9	0.991	0.0016*
Minimum slope	0.9563	9	1.249	<0.001*
*Significant at α = 0.05				

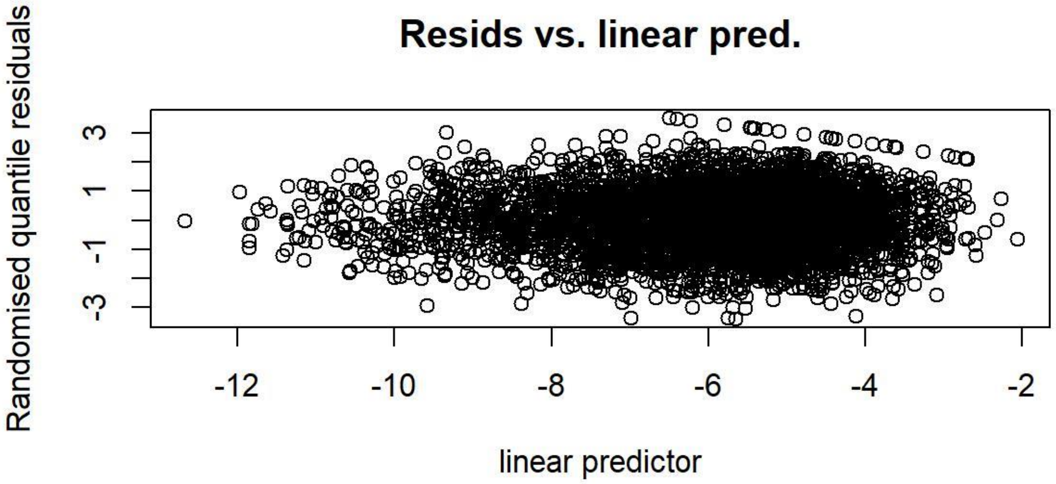


Figure V.2.1.12-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of short-finned pilot whale groups in Spring to check heteroskedasticity.

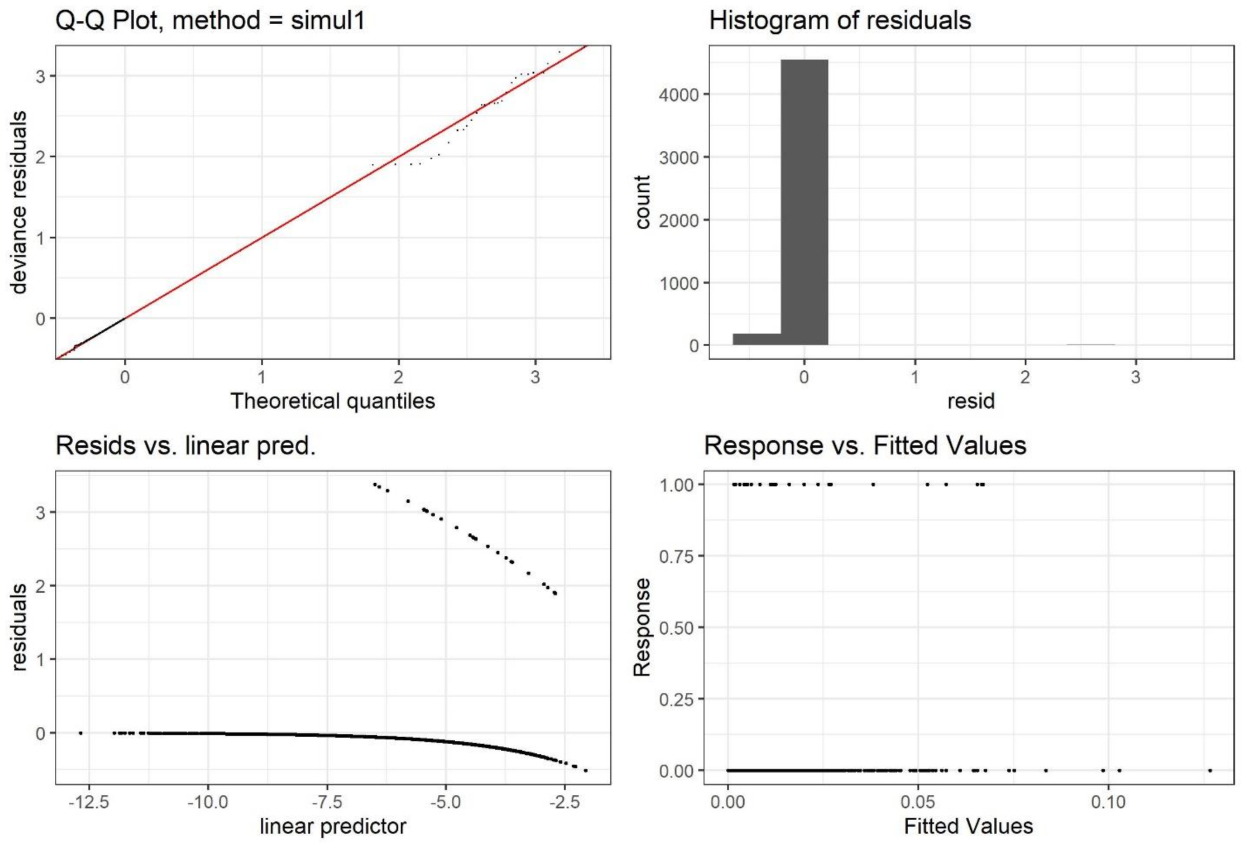


Figure V.2.1.12-2. Diagnostic plots of the selected generalised additive model of the encounter rate of short-finned pilot whale groups in Spring for the period 2001-2017.

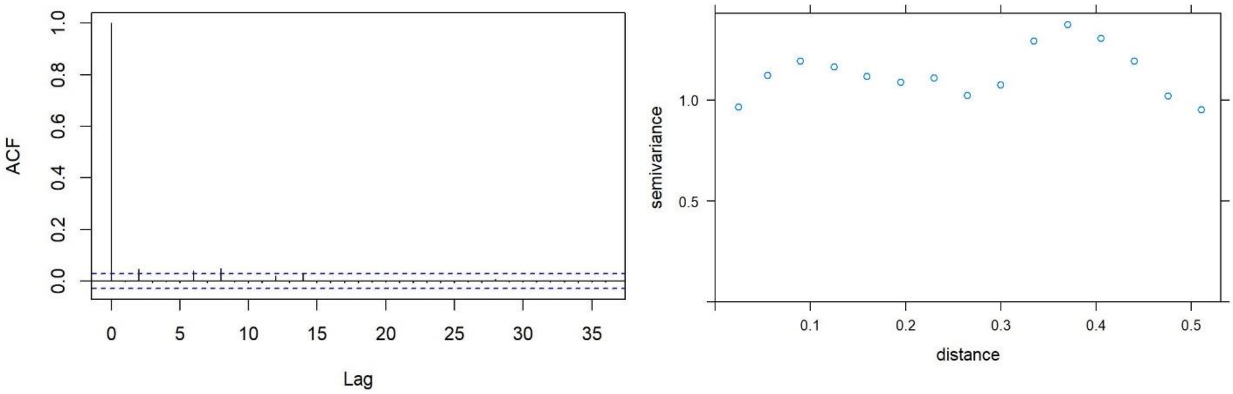


Figure V.2.1.12-3. Temporal auto-correlation regression plot from “acf” function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of short-finned pilot whale groups in Spring for the period 2001-2017.

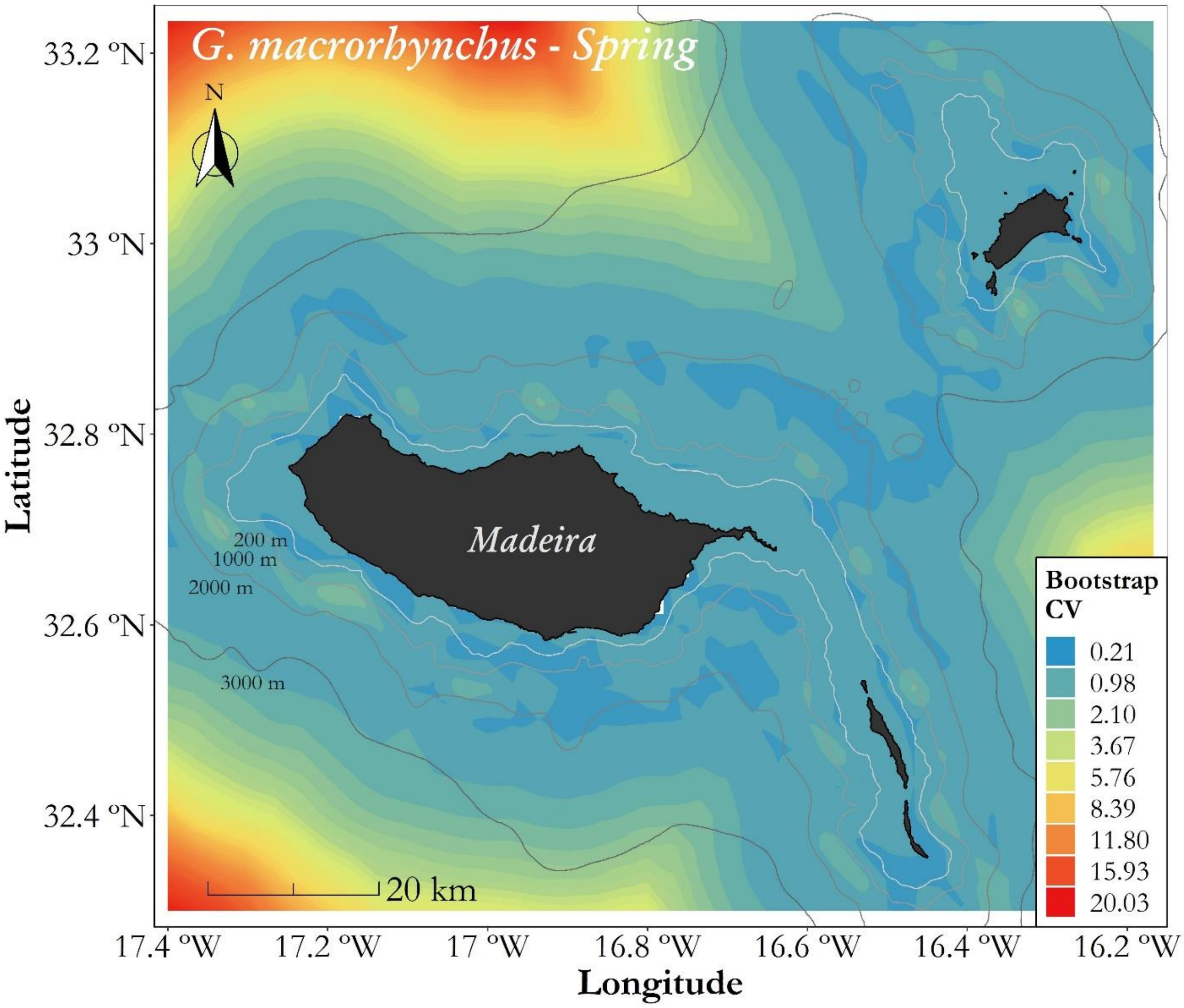


Figure V.2.1.12-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of short-finned pilot whales in Spring in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.13. Globicephala macrorhynchus - Summer

Model of encounter rates of groups

Table V.2.1.13-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-6.7170	0.7421	-9.05	<0.001*
Survey type SLS-RD	-0.0840	0.4694	0.179	0.858
Survey type ALS	-1.3990	0.6522	-2.144	0.0321*
Survey type NSS	0.3676	0.3845	0.956	0.339
Survey type WWO	0.9029	0.3820	2.363	0.018*
Survey type FO	-83.880	8006000	0	1
*Significant at α = 0.05				

Table V.2.1.13-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Distance to slope	0.925	7	1.541	<0.001*
Average aspect	2.8732	8	1.011	0.024*
Mld 2001-17 Summer	0.8107	9	0.458	0.023*
Effort	6.1454	9	5.833	<0.001*
Month	1.0851	2	7.595	<0.001*
*Significant at α = 0.05				

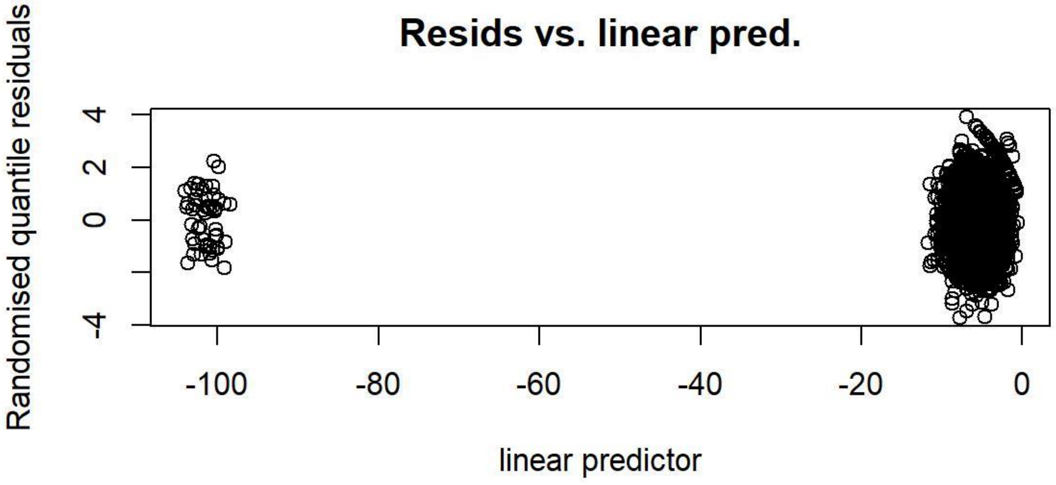


Figure V.2.1.13-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of short-finned pilot whale groups in Summer to check heteroskedasticity.

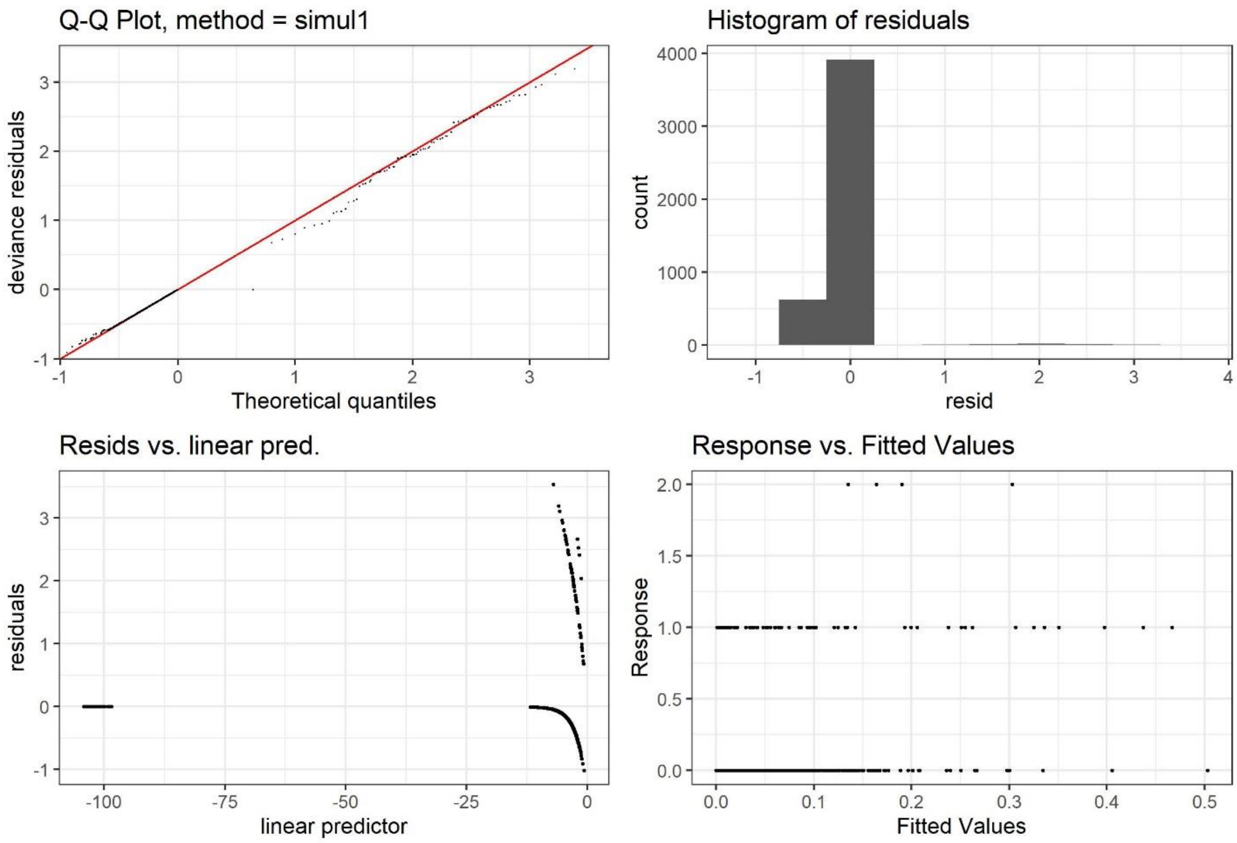


Figure V.2.1.13-2. Diagnostic plots of the selected generalised additive model of the encounter rate of short-finned pilot whale groups in Summer for the period 2001-2017.

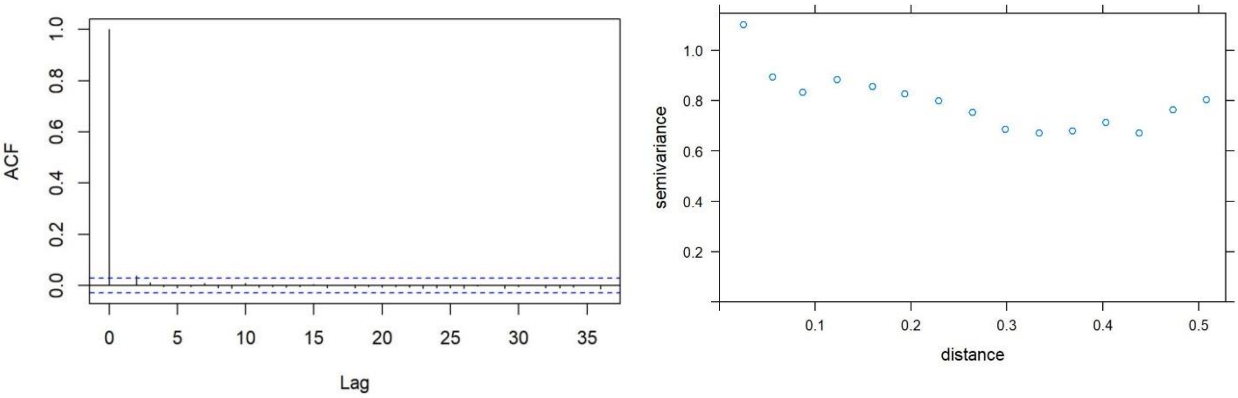


Figure V.2.1.13-3. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of short-finned pilot whale groups in Summer for the period 2001-2017.

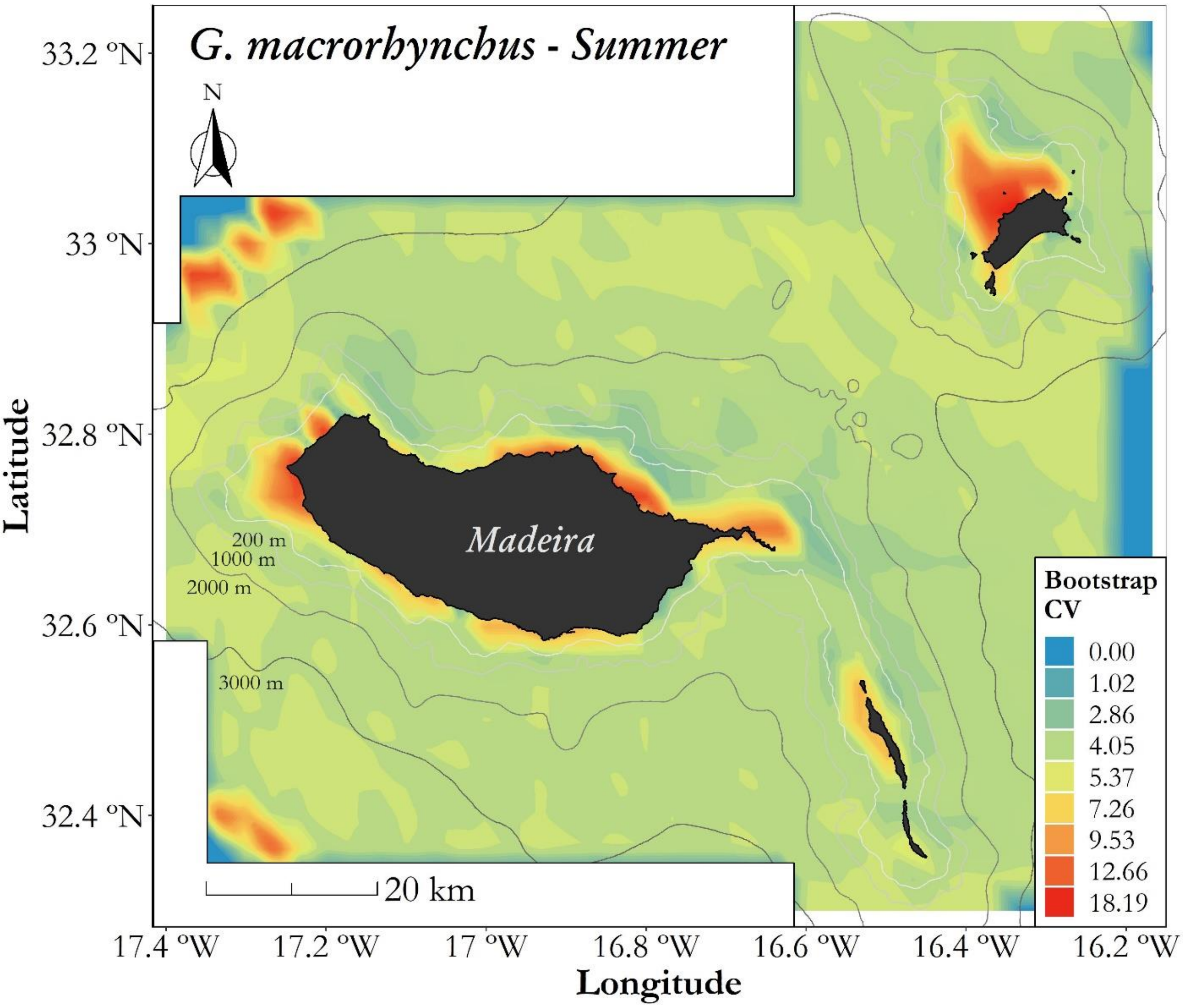


Figure V.2.1.13-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of short-finned pilot whales in Summer in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.14. Globicephala macrorhynchus - Autumn

Model of encounter rates of groups

Table V.2.1.14-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-5.3276	0.4195	-12.699	<0.001*
Survey type SLS-RD	1.0721	0.5335	2.01	0.045*
Survey type ALS	-0.8075	0.6774	-1.192	0.233
Survey type NSS	1.6036	0.4406	3.639	<0.001*
Survey type WWO	1.2475	0.4674	2.669	0.008*
Survey type FO	-	-	-	-
*Significant at α = 0.05				

Table V.2.1.14-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Maximum aspect	2.8087	8	1.610	0.002*
Beaufort	0.8714	5	1.317	0.006*
Maximum depth	3.7122	9	3.200	<0.001*
Effort	6.2412	9	7.197	<0.001*
Year	0.4405	13	0.058	0.1879
*Significant at α = 0.05				

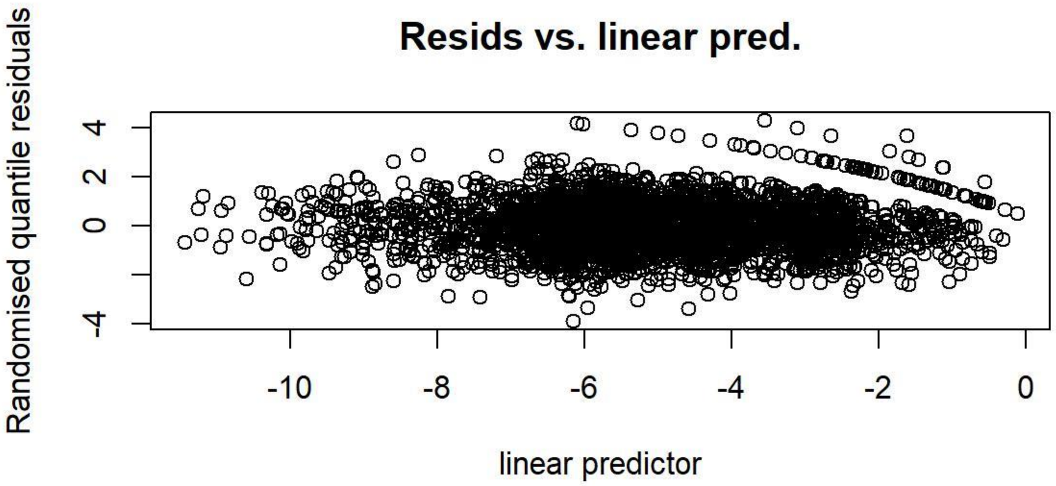


Figure V.2.1.14-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of short-finned pilot whale groups in Autumn to check heteroskedasticity.

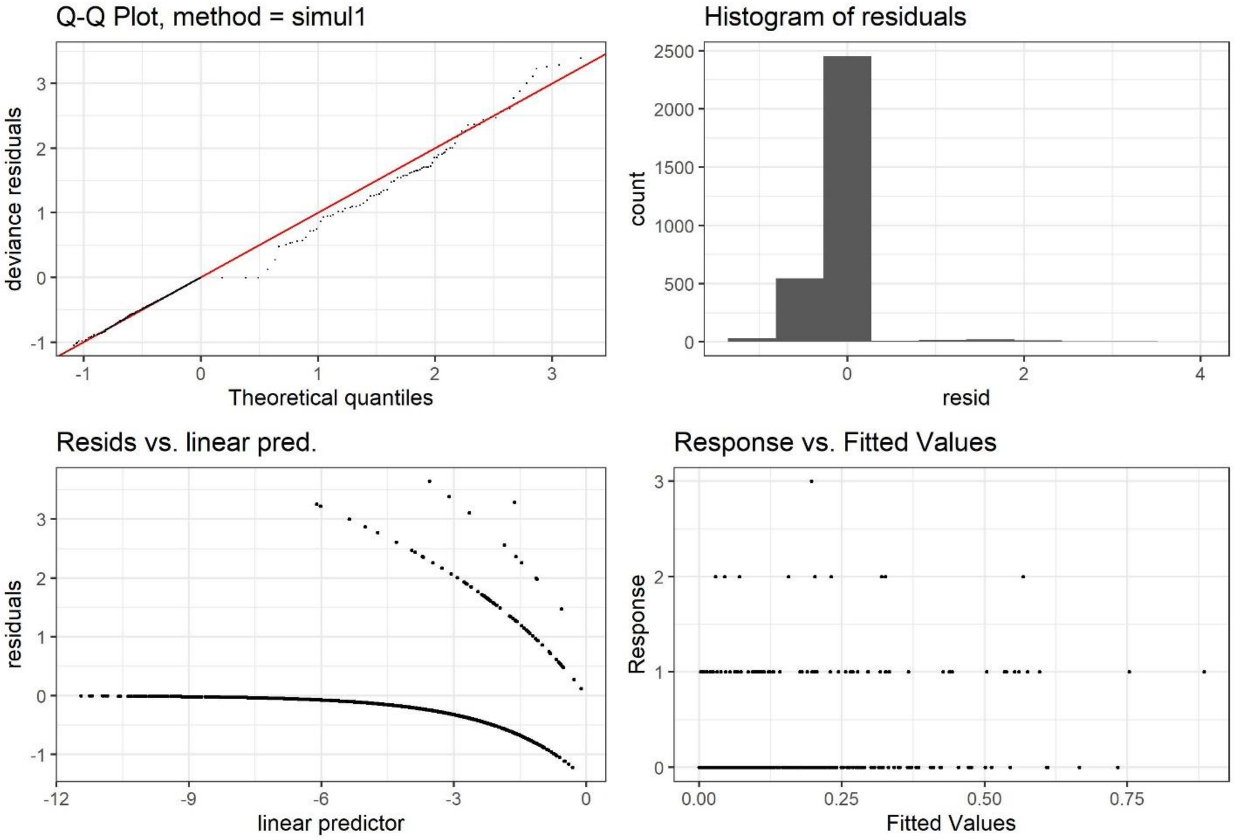


Figure V.2.1.14-2. Diagnostic plots of the selected generalised additive model of the encounter rate of short-finned pilot whale groups in Autumn for the period 2001 – 2017.

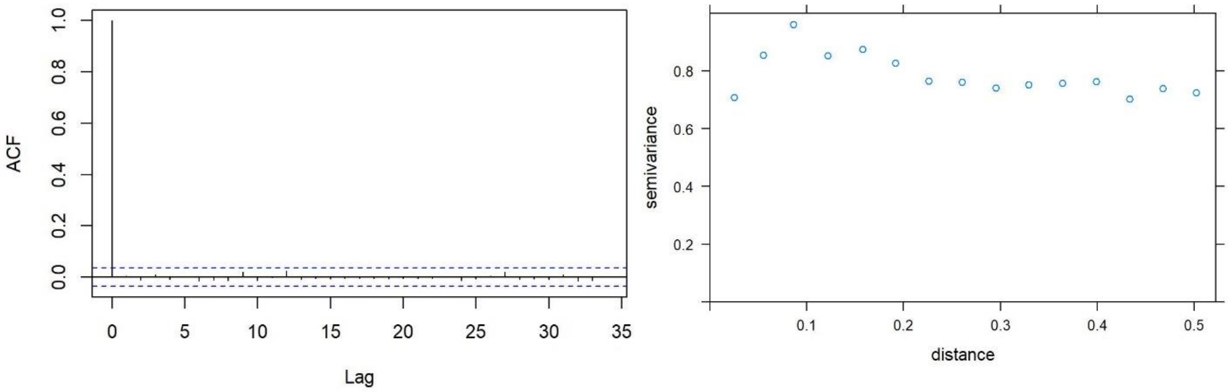


Figure V.2.1.14-3. Temporal auto-correlation regression plot from “acf” function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of short-finned pilot whale groups in Autumn for the period 2001-2017.

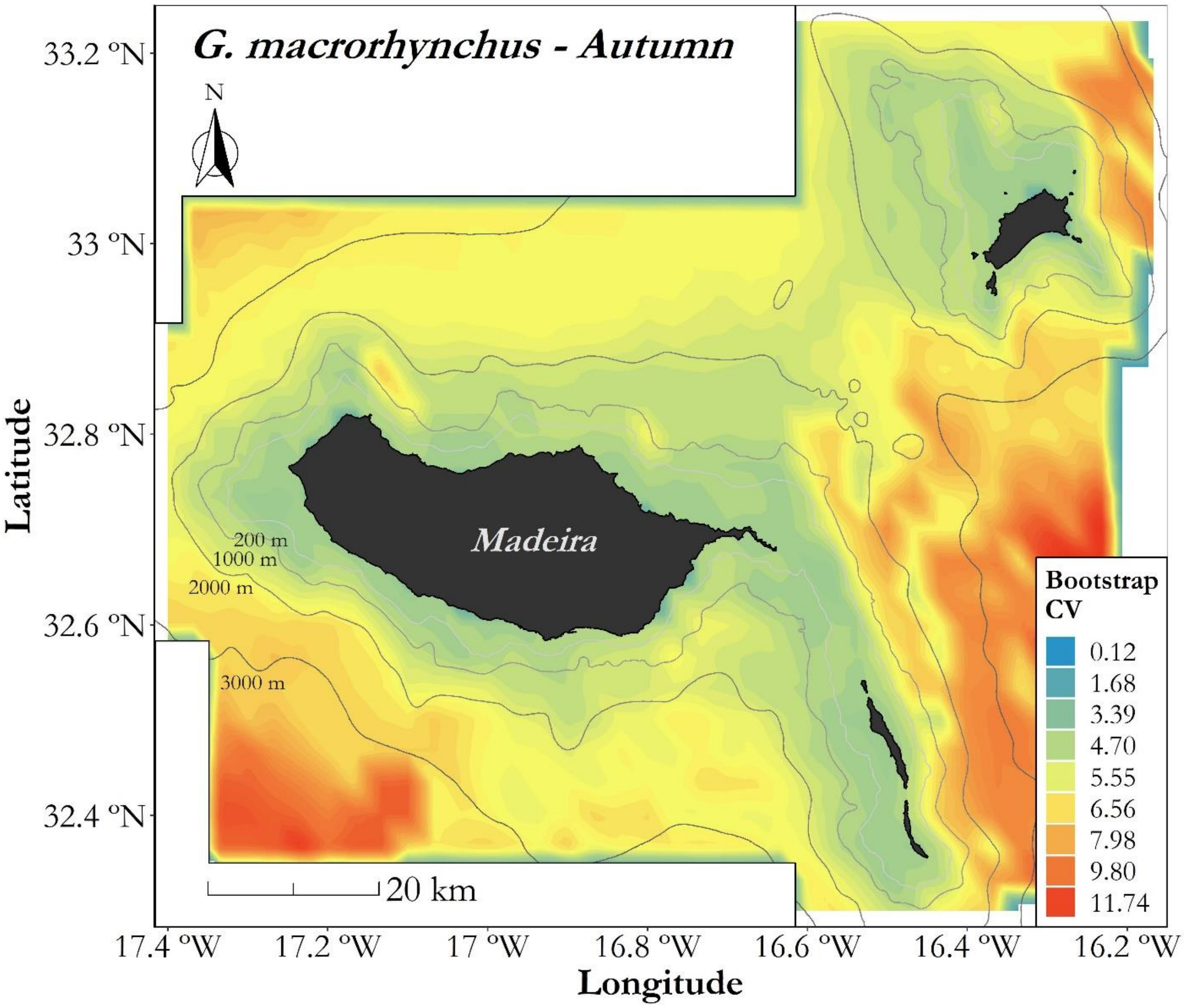


Figure V.2.1.14-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of short-finned pilot whales in Autumn in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.15. Balaenoptera edeni - Spring

Model of encounter rates of groups

Table V.2.1.15-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-6.5710	1.0610	-6.193	<0.001*
Survey type SLS-RD	-	-	-	-
Survey type ALS	-706.53	396482	0	0.999
Survey type NSS	2.4960	1.1180	2.2320	0.026*
Survey type WWO	3.2900	1.1010	2.9870	0.003*
Survey type FO	-706.58	631095	-0.0010	0.999
*Significant at α = 0.05				

Table V.2.1.15-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Sst 2004-17 Spring	0.5966	9	0.182	0.096
Effort	2.1814	9	1.268	0.002*
*Significant at α = 0.05				

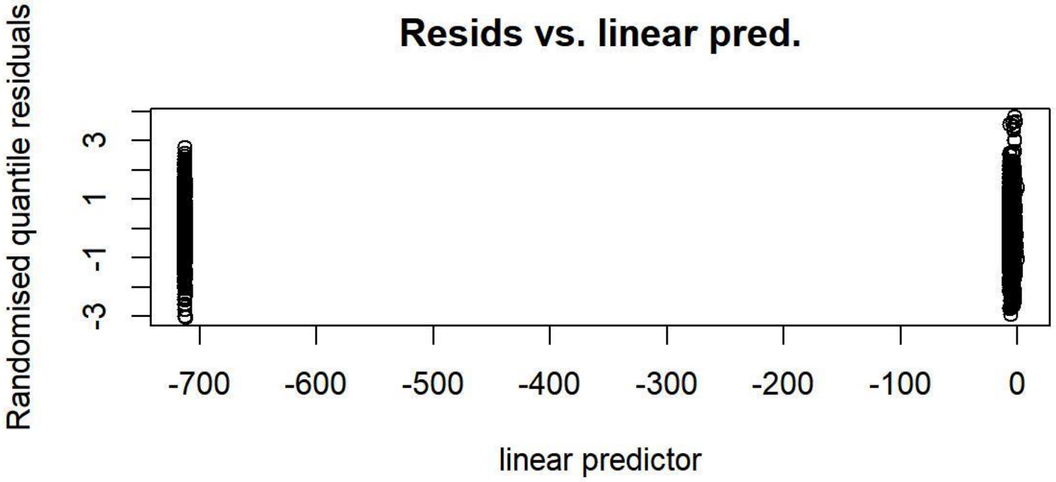


Figure V.2.1.15-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of Bryde's whale groups in Spring to check heteroskedasticity.

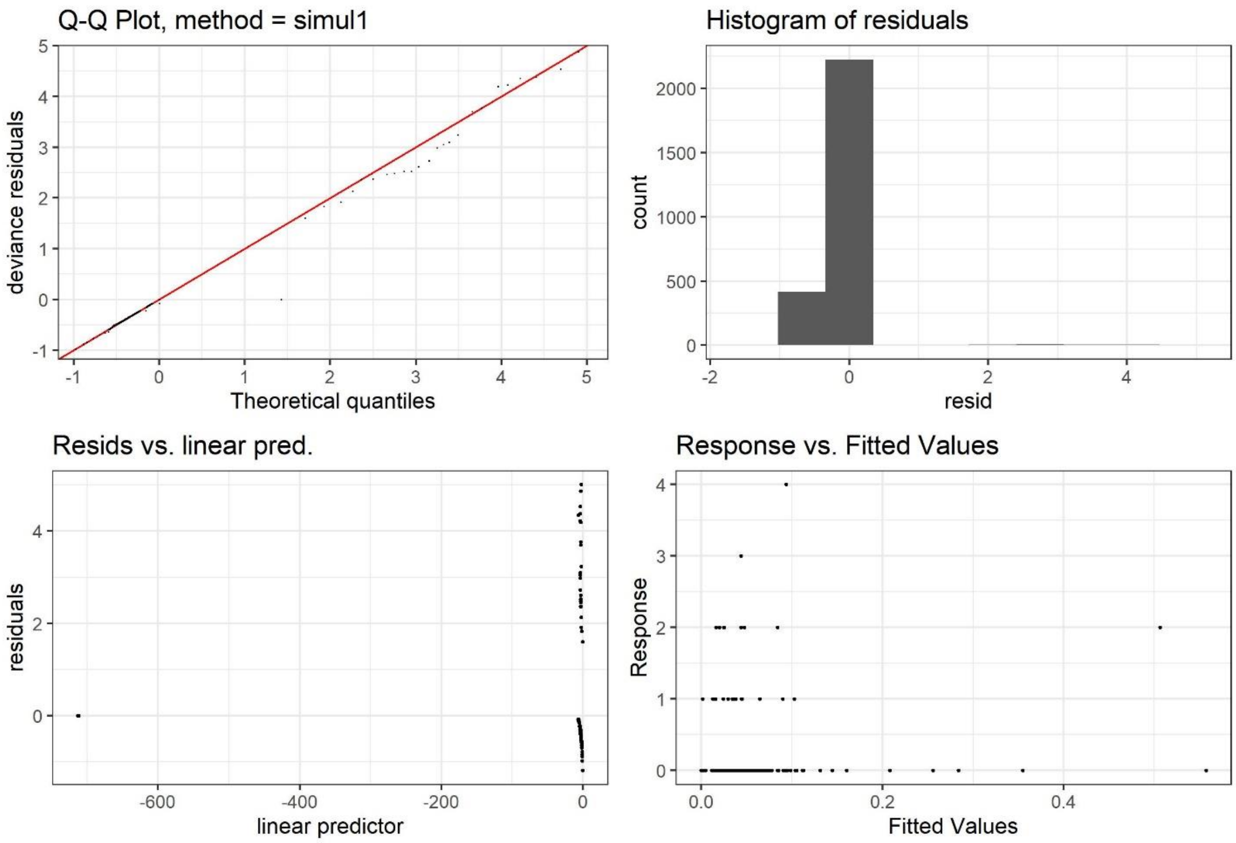


Figure V.2.1.15-2. Diagnostic plots of the selected generalised additive model of the encounter rate of Briyde's whale groups in Spring for the period 2001-2017.

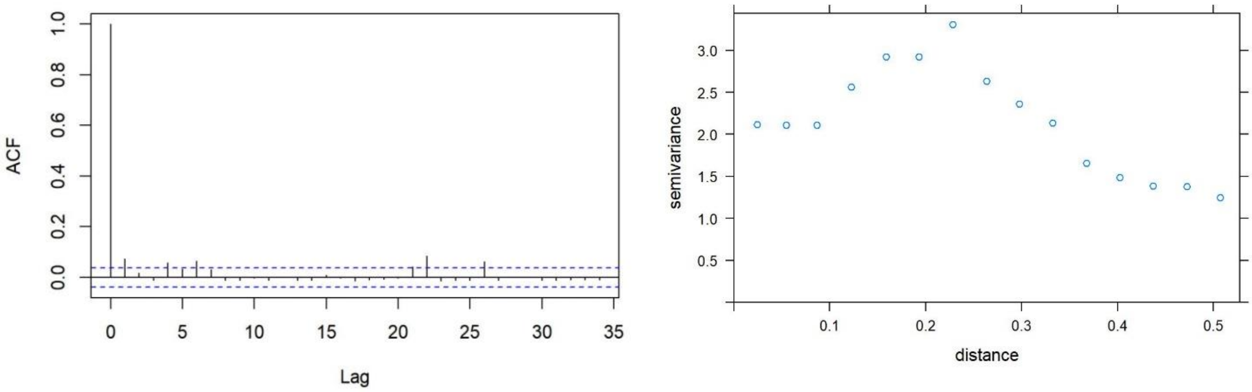


Figure V.2.1.15-3. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of Bryde's whale groups in Spring for the period 2001-2017.

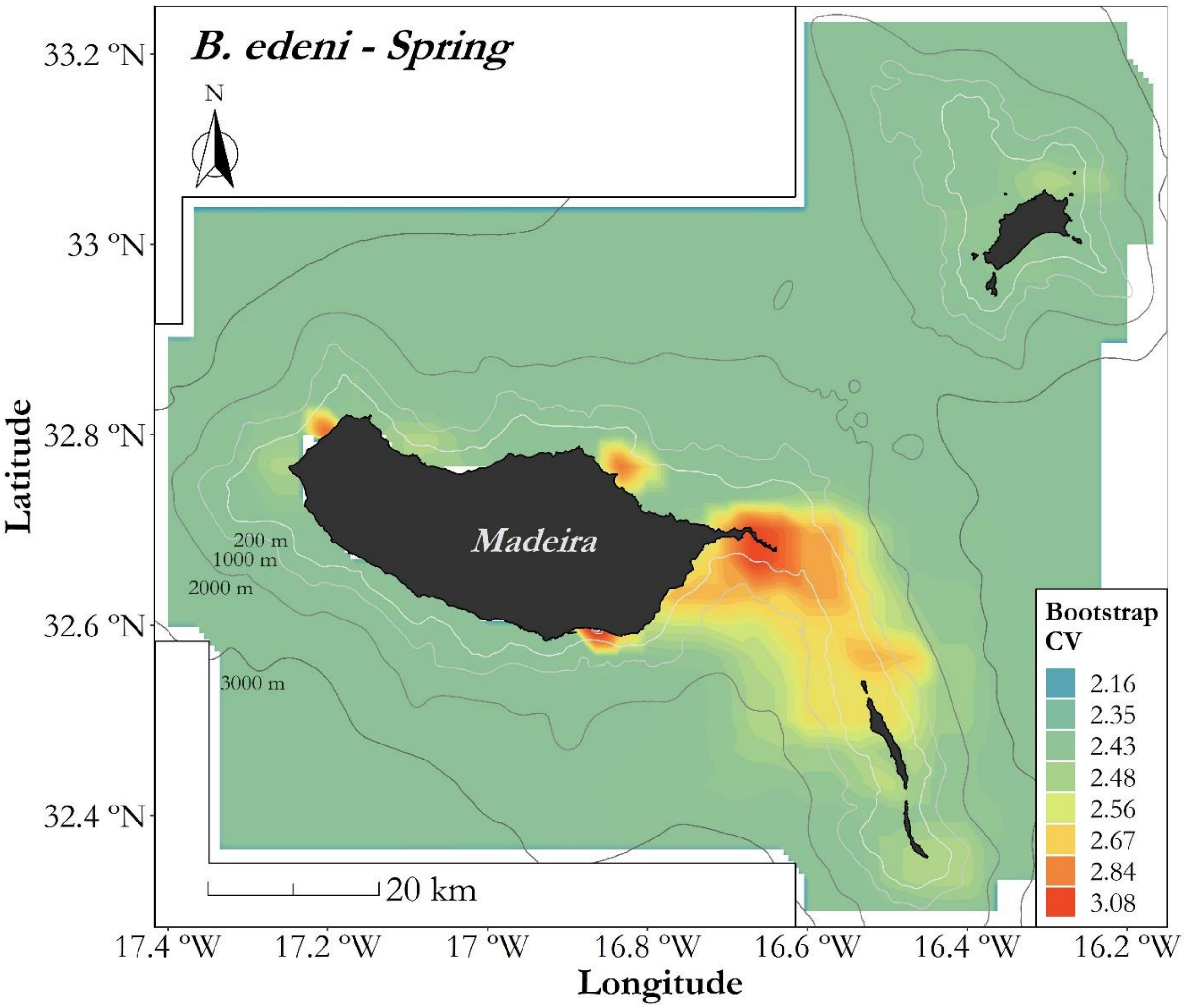


Figure V.2.1.15-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of Bryde's whales in Spring in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.16. Balaenoptera edeni - Summer

Model of encounter rates of groups

Table V.2.1.16-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-6.0375	0.8347	-7.23	<0.001*
Survey type SLS-RD	1.5331	1	2	0.0912
Survey type ALS	1.3167	0.9344	1.409	0.159
Survey type NSS	2.0223	0.8525	2.372	0.018*
Survey type WWO	2.7170	0.8555	3.176	0.0015*
Survey type FO	2.6888	1.3019	2.065	0.039*
*Significant at α = 0.05				

Table V.2.1.16-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Distance to Escarpment, Poc 2004-17 Summer	1.82	29	0.320	0.006*
Effort	4.289	9	3.934	<0.001*
*Significant at α = 0.05				

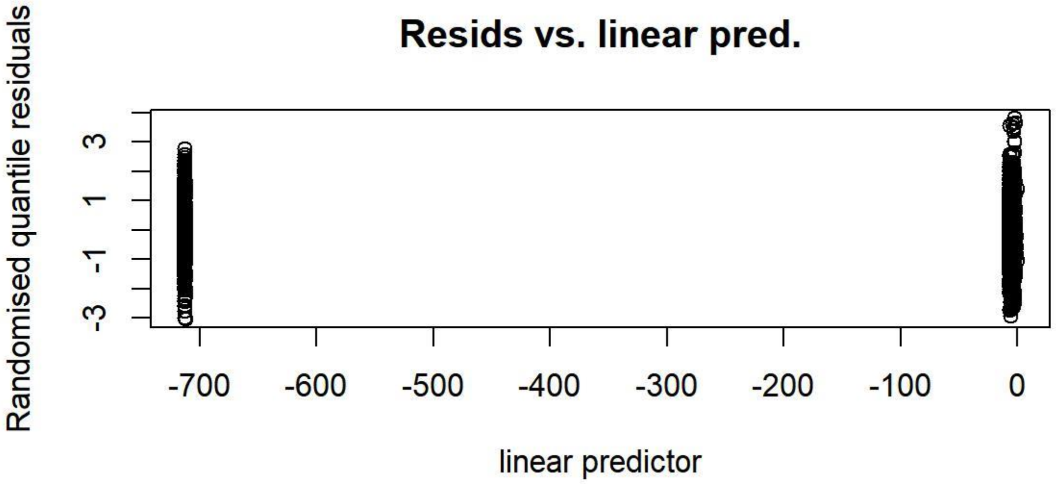


Figure V.2.1.16-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of Bryde's whale groups in Summer to check heteroskedasticity.

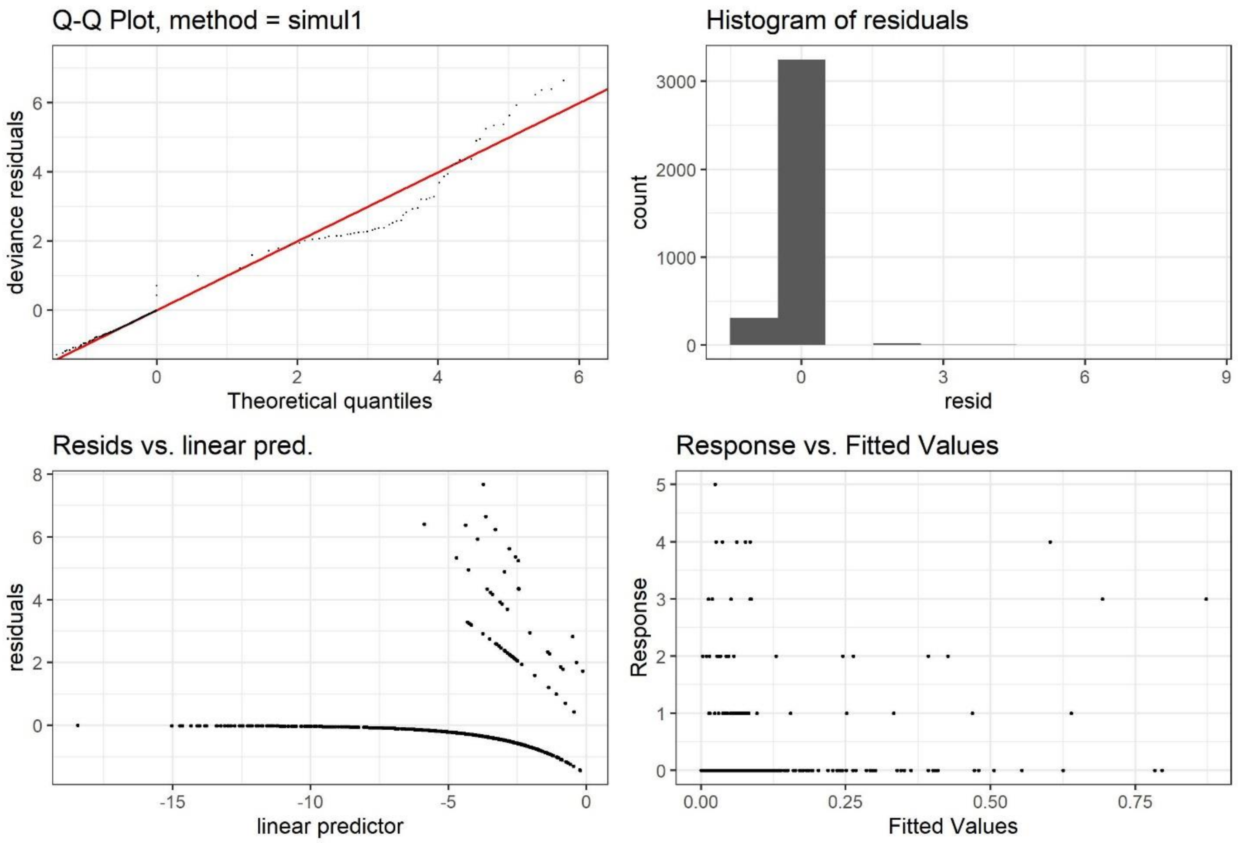


Figure V.2.1.16-2. Diagnostic plots of the selected generalised additive model of the encounter rate of Bryde's whale groups in Summer for the period 2001-2017.

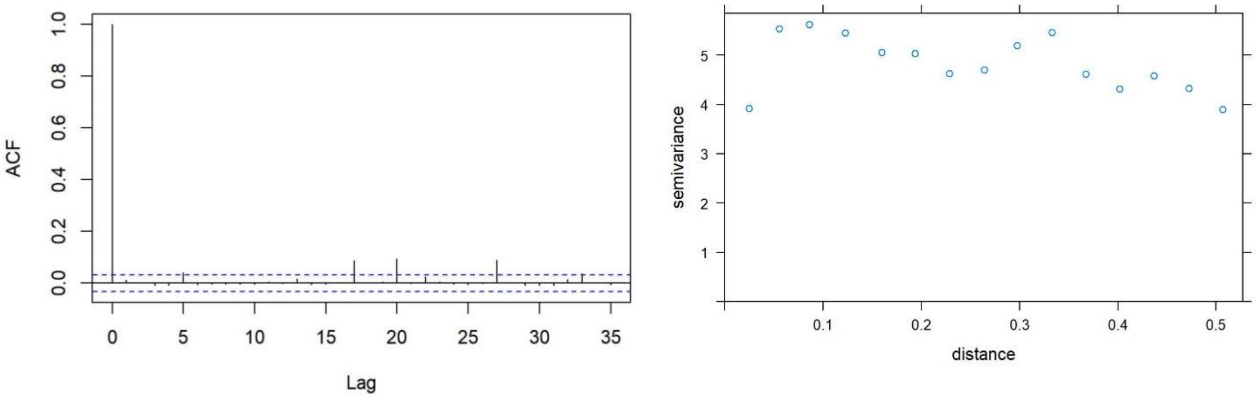


Figure V.2.1.16-3. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of Bryde's whale groups in Summer for the period 2001-2017.

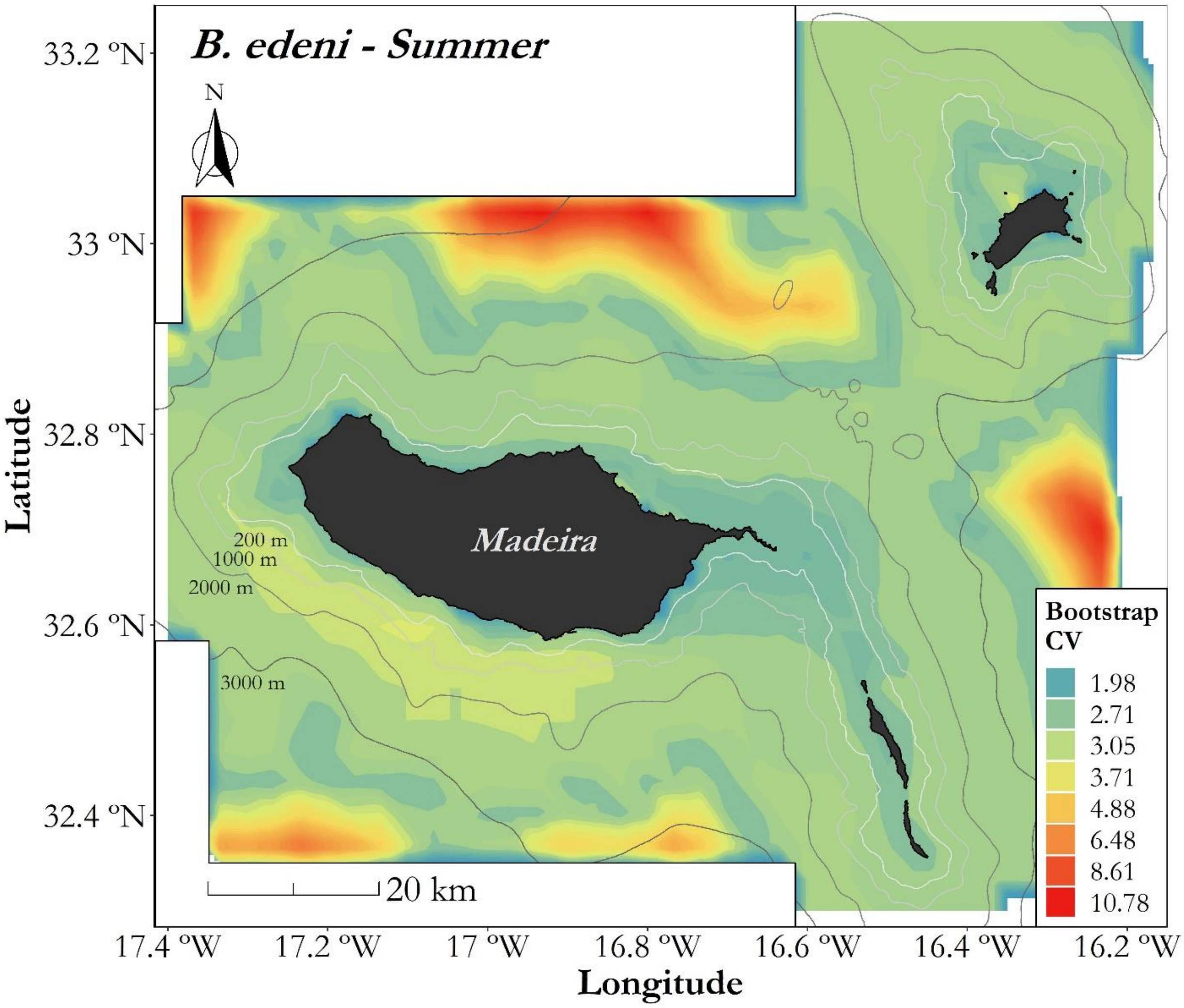


Figure V.2.1.16-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of Bryde's whales in Summer in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.17. *Balaenoptera edeni - Autumn*

Model of encounter rates of groups

Table V.2.1.17-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-5.3914	0.5992	-8.9980	<0.001*
Survey type SLS-RD	0.7986	0.6376	1.2520	0.2105
Survey type ALS	1.1750	0.7109	1.6530	0.099
Survey type NSS	-0.5168	1.0498	-0.4920	0.623
Survey type WWO	0.3790	0.6696	0.5660	0.5714
Survey type FO	-	-	-	-
*Significant at α = 0.05				

Table V.2.1.17-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Distance to 500m isobath	0.9318	9	1.141	<0.001*
Effort	4.5254	9	2.712	<0.001*
*Significant at α = 0.05				

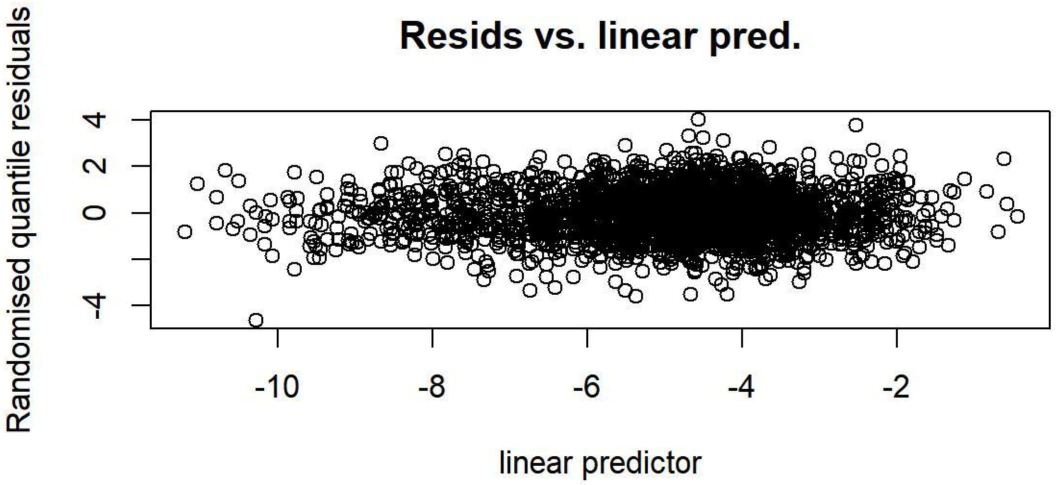


Figure V.2.1.17-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of Bryde's whale groups in Autumn to check heteroskedasticity.

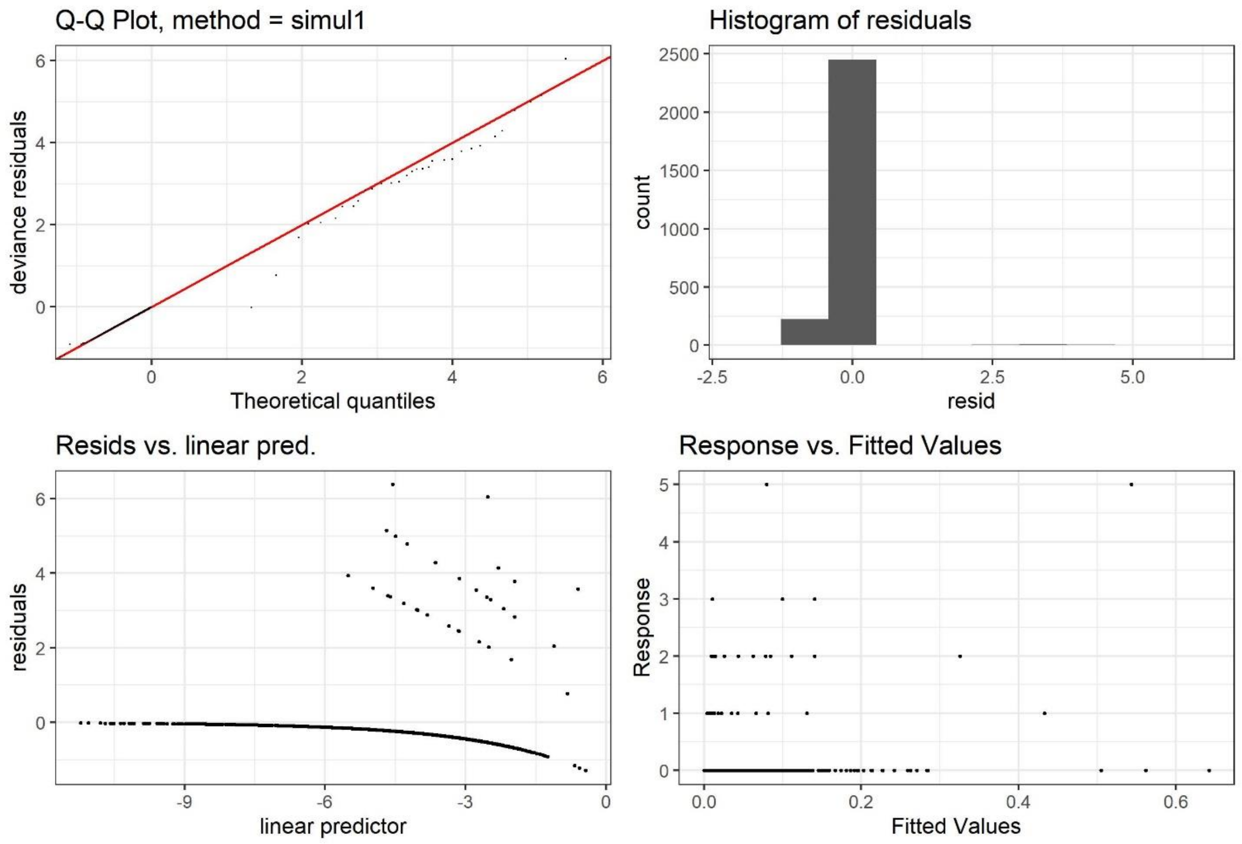


Figure V.2.1.17-2. Diagnostic plots of the selected generalised additive model of the encounter rate of Briyde's whale groups in Autumn for the period 2001-2017.

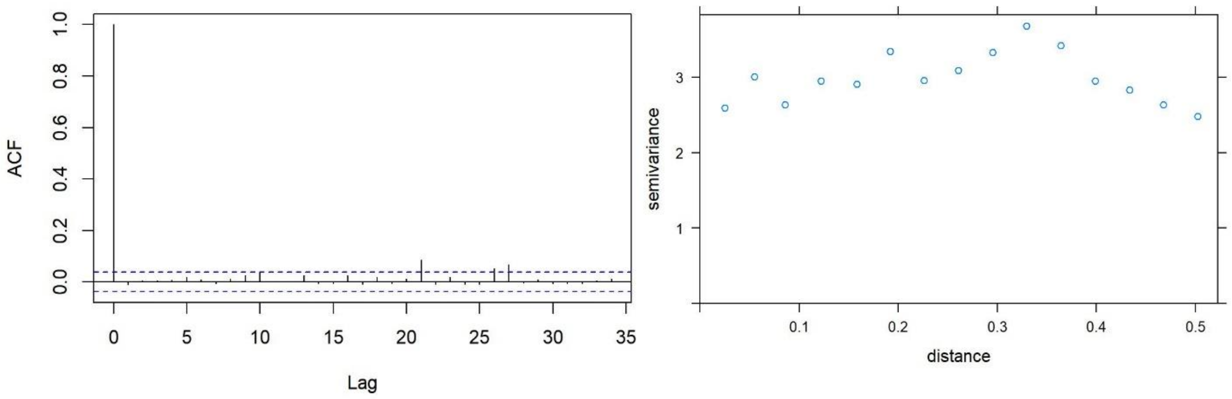


Figure V.2.1.17-3. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of Bryde's whale groups in Autumn for the period 2001-2017.

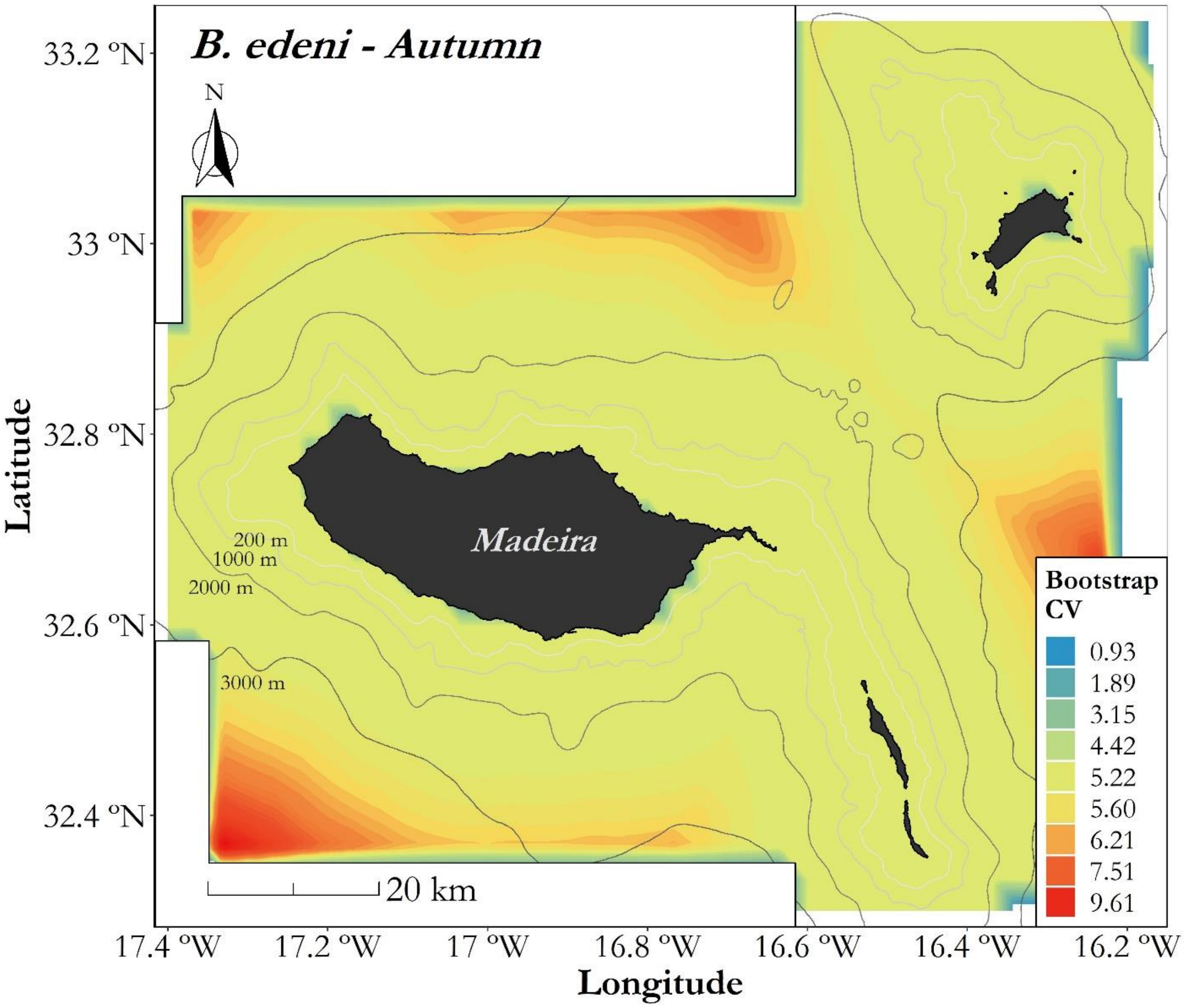


Figure V.2.1.17-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of Bryde's whales in Autumn in the Madeira inshore waters for the period 2001 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.18. Balaenoptera edeni – June/July, no time-lag (June/July)

Model of encounter rates of groups

Table V.2.1.18-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-6.564	1.123	-5.845	<0.001*
Survey type SLS-RD	-	-	-	-
Survey type ALS	-269.09	168724.633	-0.002	0.99873
Survey type NSS	2.535	1.141	2.223	0.0263*
Survey type WWO	3.948	1.233	3.201	0.0014*
Survey type FO	3.17	1.537	2.063	0.039*
*Significant at α = 0.05				

Table V.2.1.18-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Escarpment area	0.7932	9	0.328	0.052
Maximum slope	0.0000	9	0.0000	0.5434
Sst-a 2004-17 Jun/Jul	0.9578	9	1.262	<0.001*
Year	0.7631	2	1.147	0.077
Beaufort	0.0001	5	0.0000	0.6416
Effort	0.0017	9	0.0000	0.0019*
*Significant at α = 0.05				

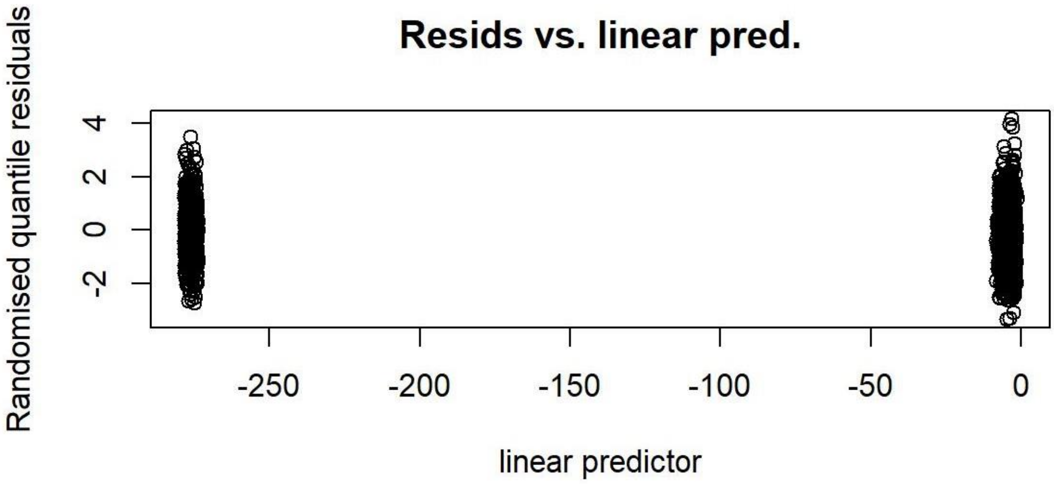


Figure V.2.1.18-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of Bryde's whale groups in June/July, no time-lag (June/July), to check heteroskedasticity.

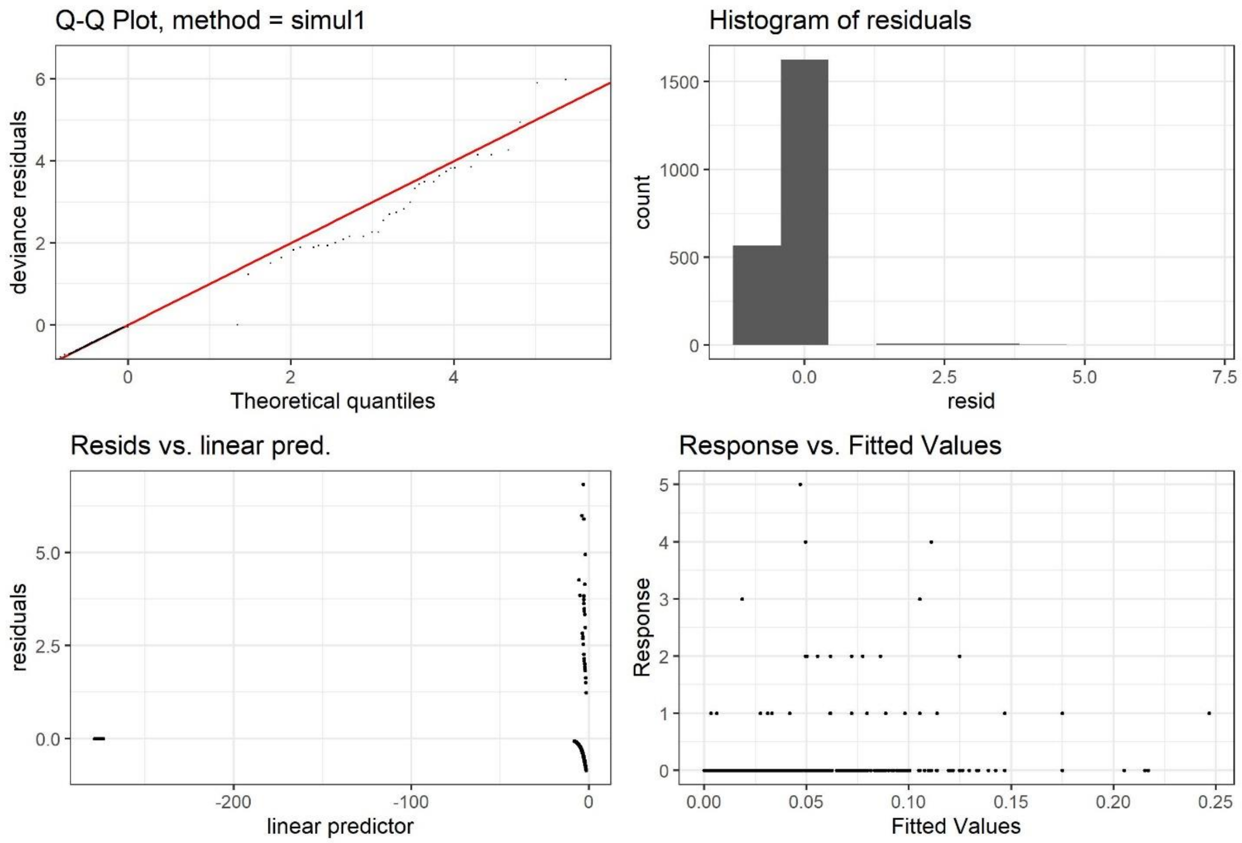


Figure V.2.1.18-2. Diagnostic plots of the selected generalised additive model of the encounter rate of Bryde's whale groups in June/July, no time-lag (June/July), for the period 2004-2017.

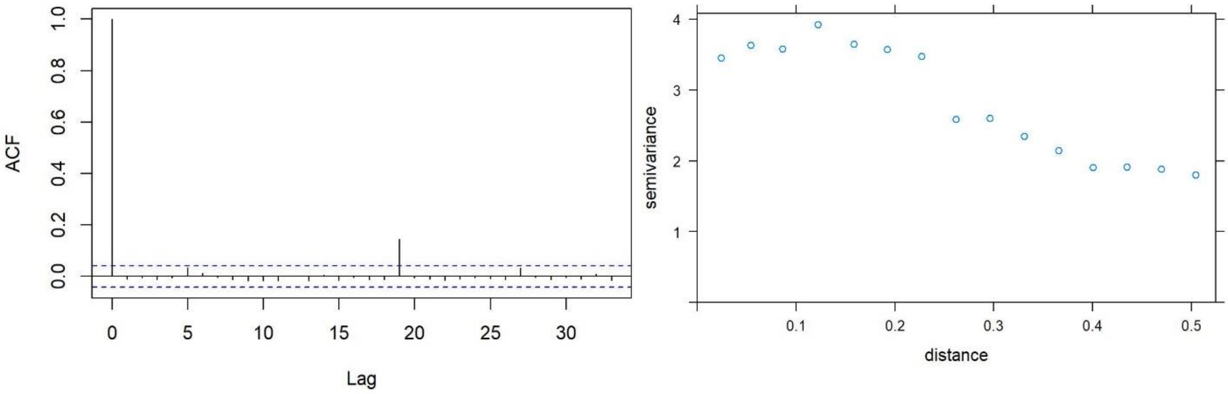


Figure V.2.1.18-3. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of Bryde's whales in June/July, no time-lag (June/July), in the Madeira inshore waters for the period 2004 – 2017, based on encounter rate (animals per km of transect line).

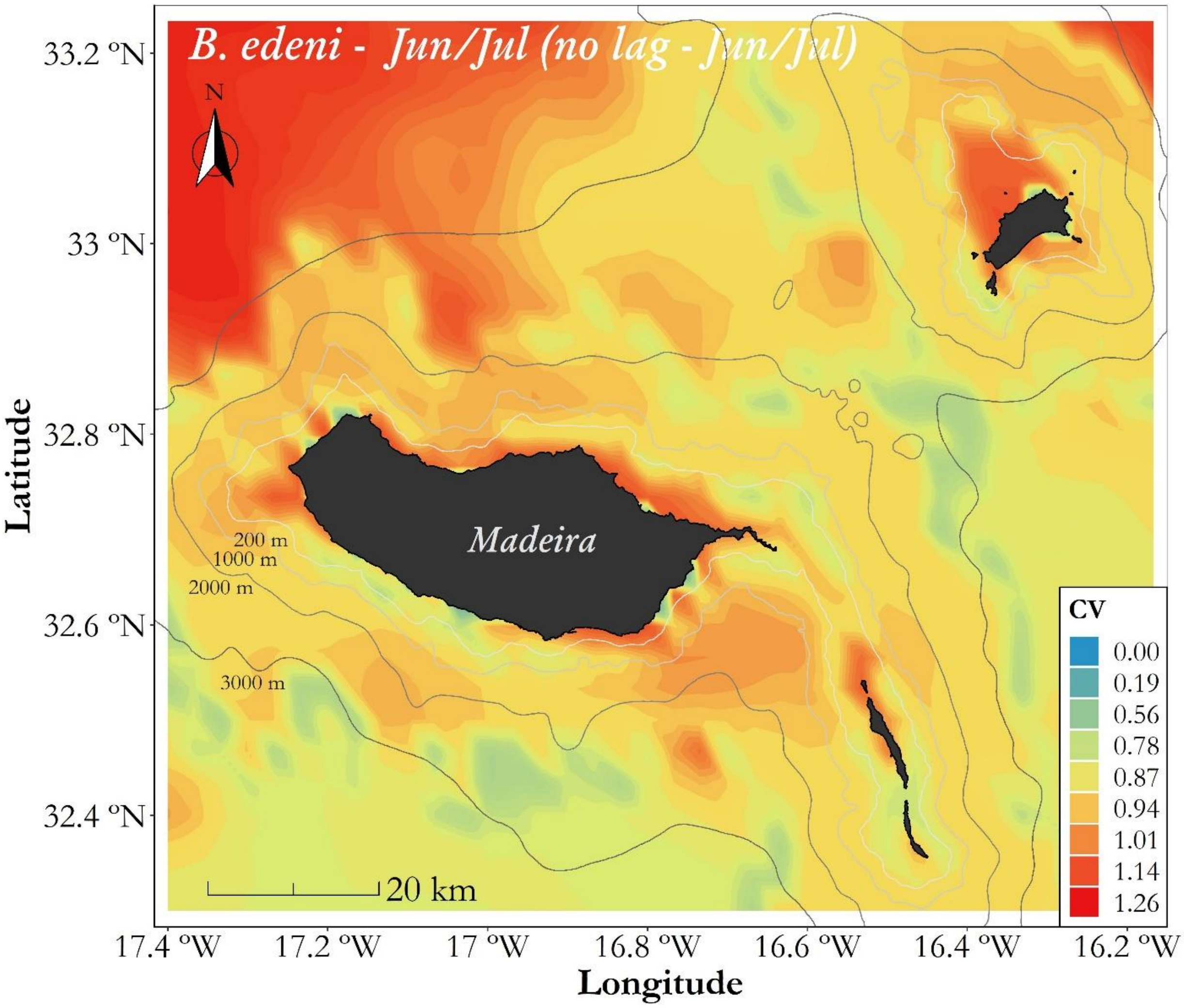


Figure V.2.1.18-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of Bryde's whales in June/July, one-month time-lag (June/July), in the Madeira inshore waters for the period 2004 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.19. Balaenoptera edeni – June/July, one-month time-lag (May/June)

Model of encounter rates of groups

Table V.2.1.19-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-6.6550	1.146	-5.8070	<0.001*
Survey type SLS-RD	-	-	-	-
Survey type ALS	-238.78	161825	-0.0010	0.9988
Survey type NSS	2.2860	1.1460	1.9960	0.046*
Survey type WWO	2.8570	1.1540	2.4770	0.013*
Survey type FO	2.6420	1.5110	1.7480	0.08
*Significant at α = 0.05				

Table V.2.1.19-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Escarpment area	0.9193	9	0.6700	0.006*
Average aspect	1.2529	8	0	0.0827
Slope std dev	0.8827	9	0.6610	0.006*
Chl-a 2004-17 May/Jun	0.8128	9	0	0.024*
Effort	0.0001	9	0.0000	0.538
*Significant at α = 0.05				

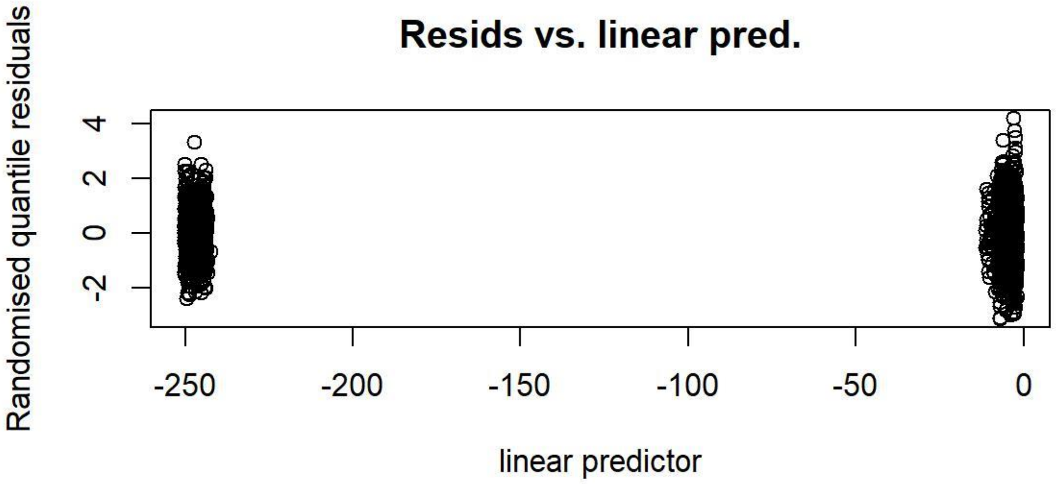


Figure V.2.1.19-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of Bryde's whale groups in June/July, one-month time-lag (May/June), to check heteroskedasticity.

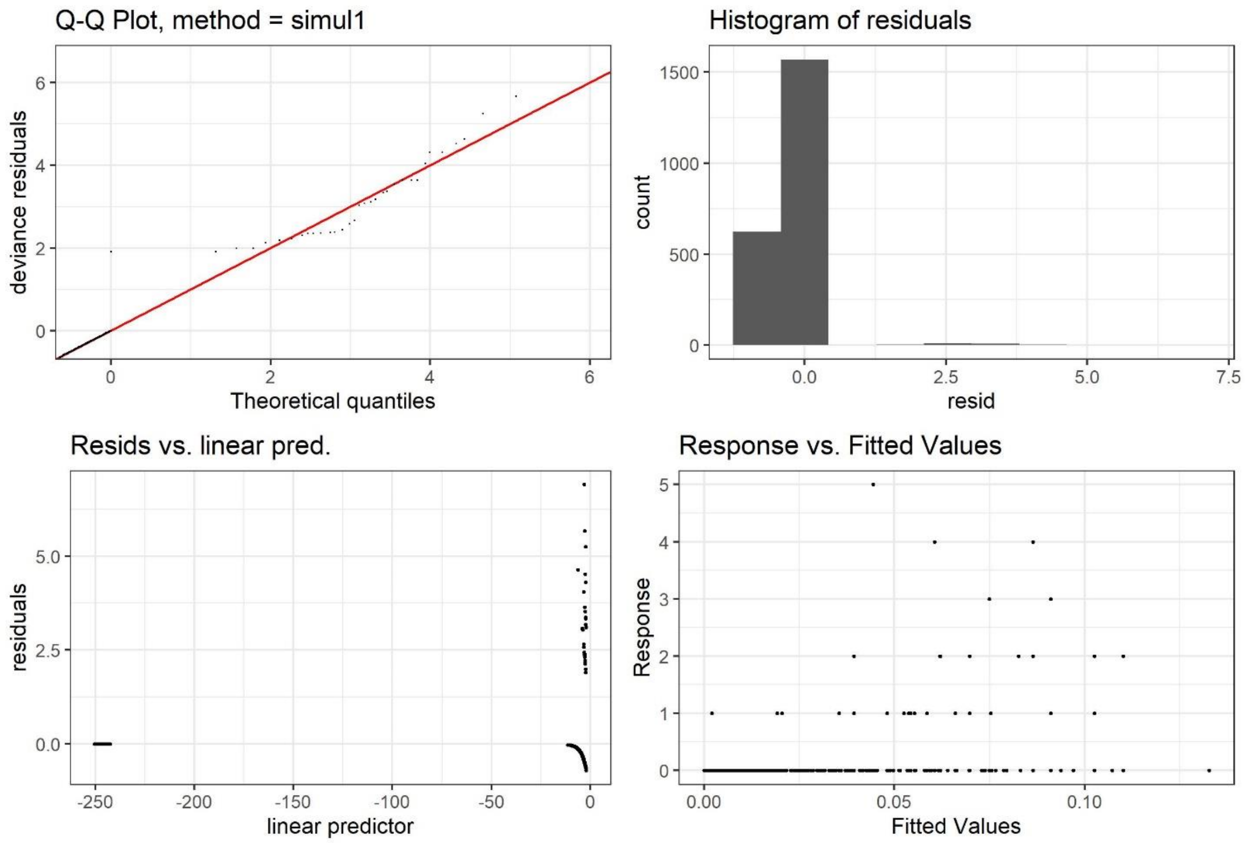


Figure V.2.1.19-2. Diagnostic plots of the selected generalised additive model of the encounter rate of Bryde's whale groups in June/July, one-month time-lag (May/June), for the period 2004-2017.

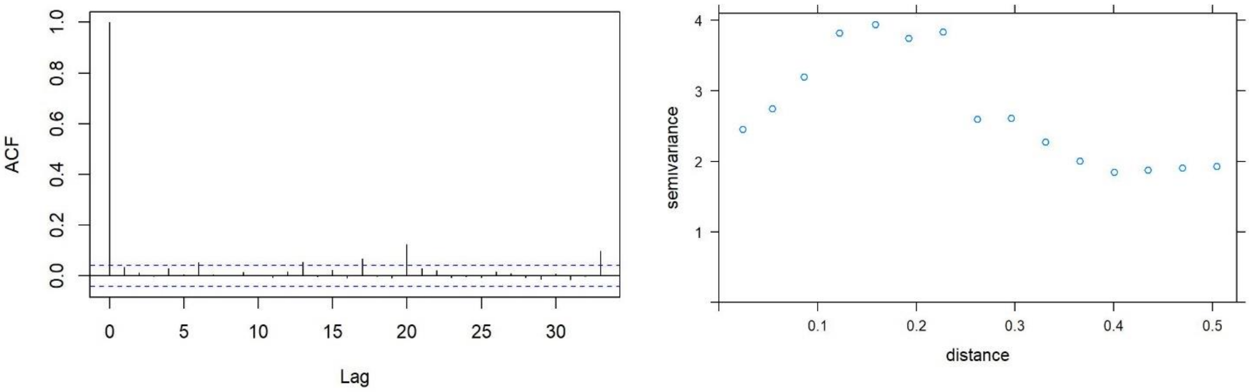


Figure V.2.1.19-3. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of Bryde's whale groups in June/July, one-month time-lag (May/June), for the period 2004-2017.

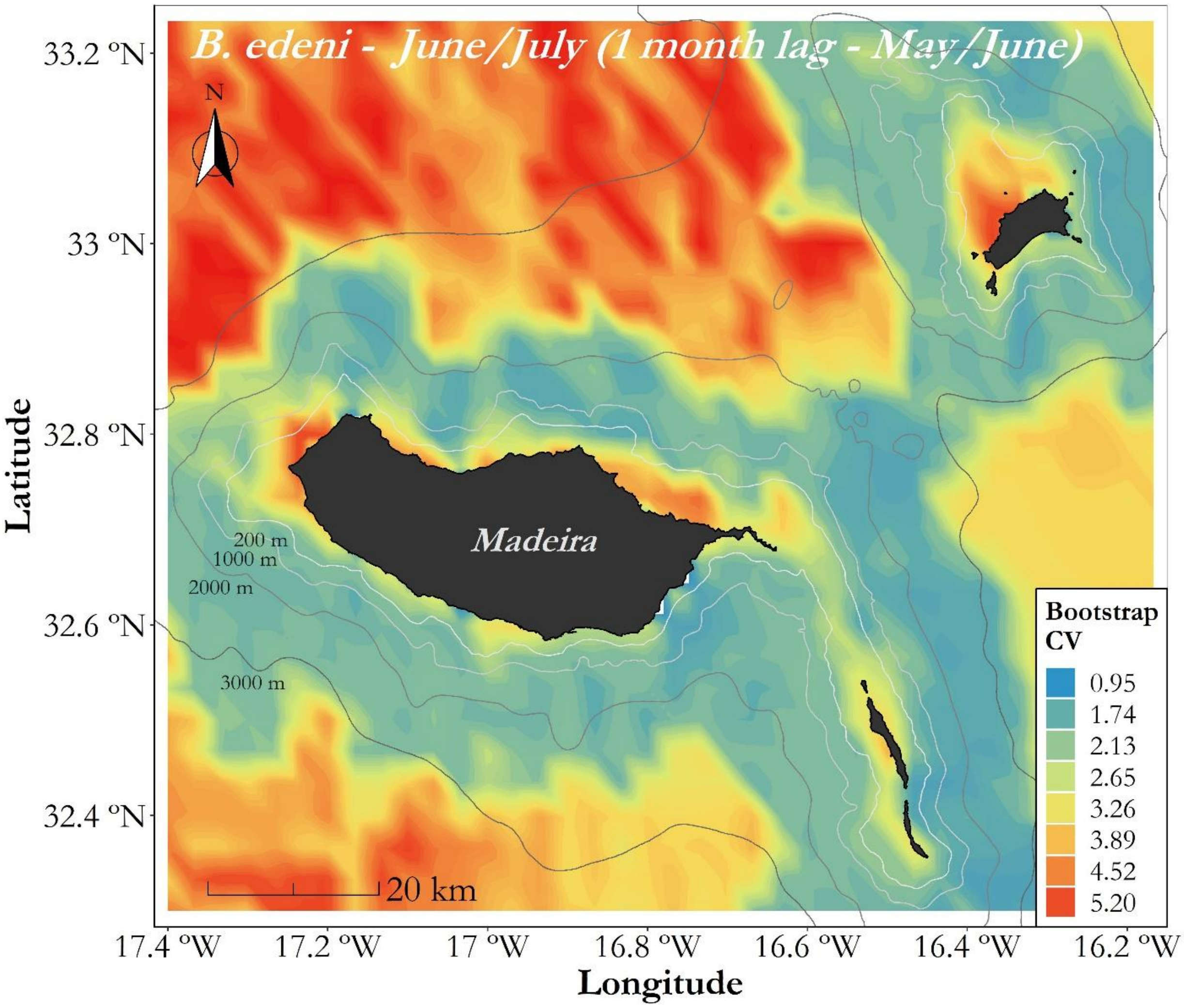


Figure V.2.1.19-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of Bryde's whales in June/July, one-month time-lag (May/June), in the Madeira inshore waters for the period 2004 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.20. Balaenoptera edeni – June/July, two-months' time-lag (Mar/Apr)

Model of encounter rates of groups

Table V.2.1.20-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-8.0820	1.1560	-6.9920	<0.001*
Survey type SLS-RD	-	-	-	-
Survey type ALS	-212.21	161748	-0.0010	0.999
Survey type NSS	2.6290	1.1550	2.2770	0.023*
Survey type WWO	3.9900	1.2480	3.1960	0.001*
Survey type FO	3.0810	1.5630	1.9720	0.049*
*Significant at α = 0.05				

Table V.2.1.20-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Escarpment area	0.9267	9	0.7220	0.006*
Chl-a 2004-17 Mar/Apr	0.9522	9	1.3210	<0.001*
Year	0.7243	12	0.1850	0.079
*Significant at α = 0.05				

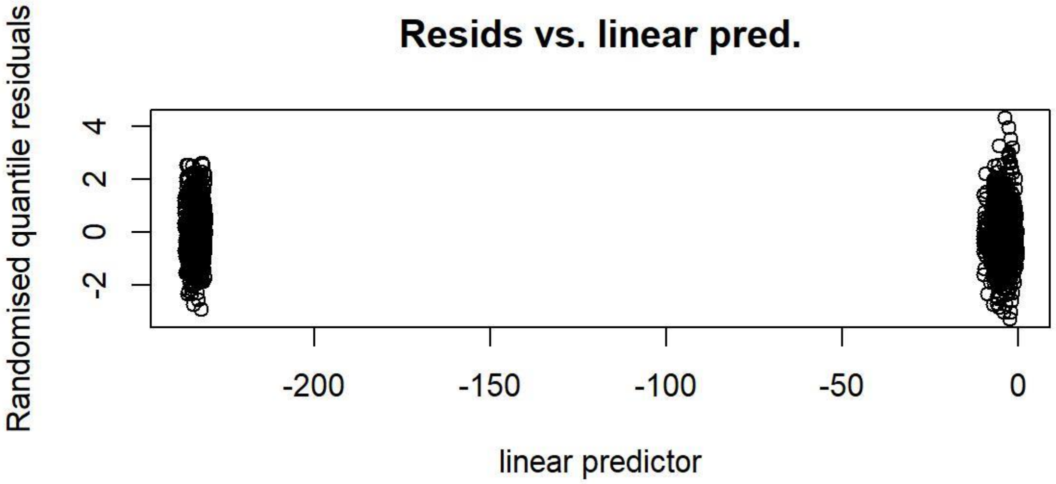


Figure V.2.1.20-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of Bryde's whale groups in June/July, two-months' time-lag (Mar/Apr), to check heteroskedasticity.

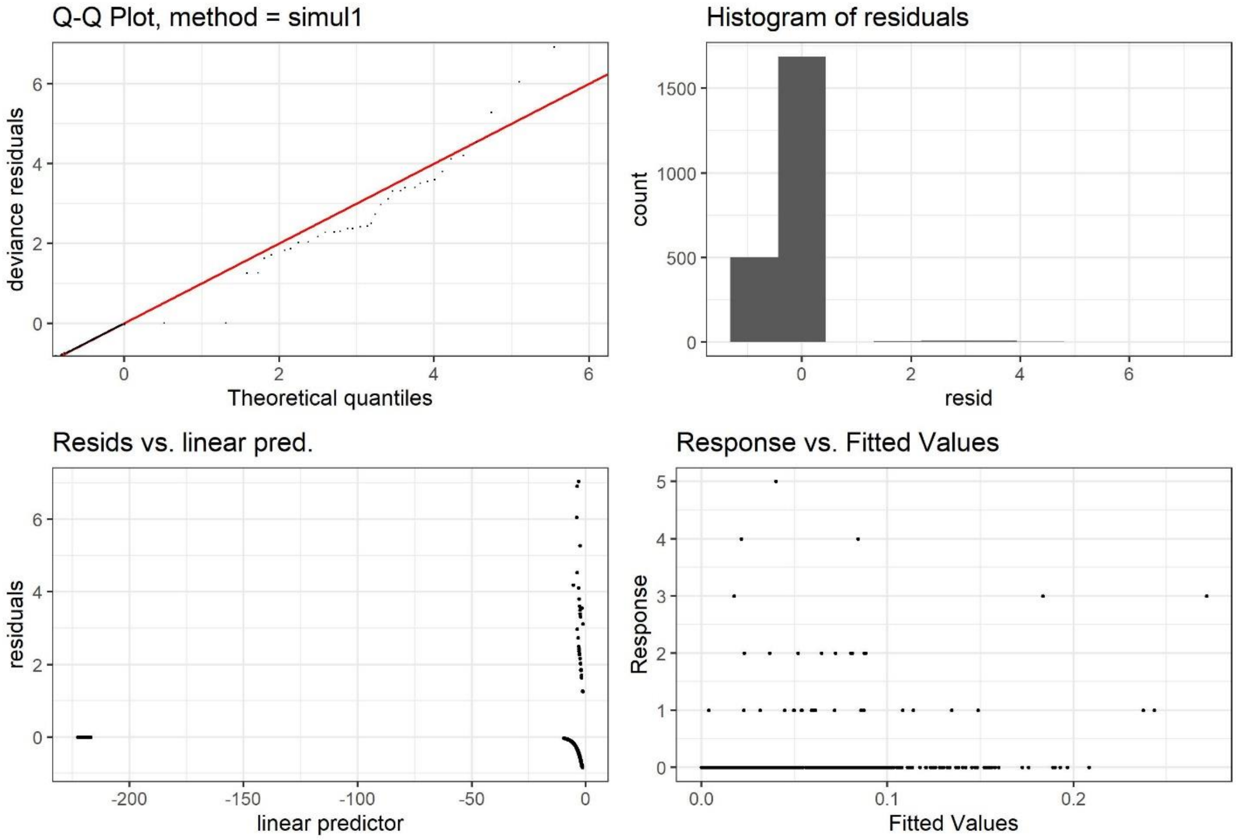


Figure V.2.1.20-2. Diagnostic plots of the selected generalised additive model of the encounter rate of Bryde's whale groups in June/July, two-months' time-lag (Mar/Apr), for the period 2004-2017.

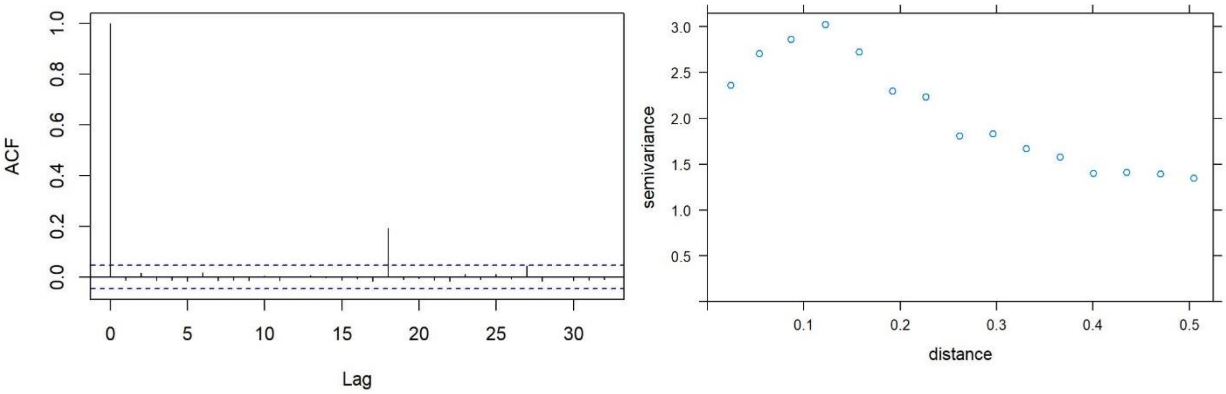


Figure V.2.1.20-3. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of Bryde's whale groups in June/July, two-months' time-lag (Mar/Apr), for the period 2004-2017.

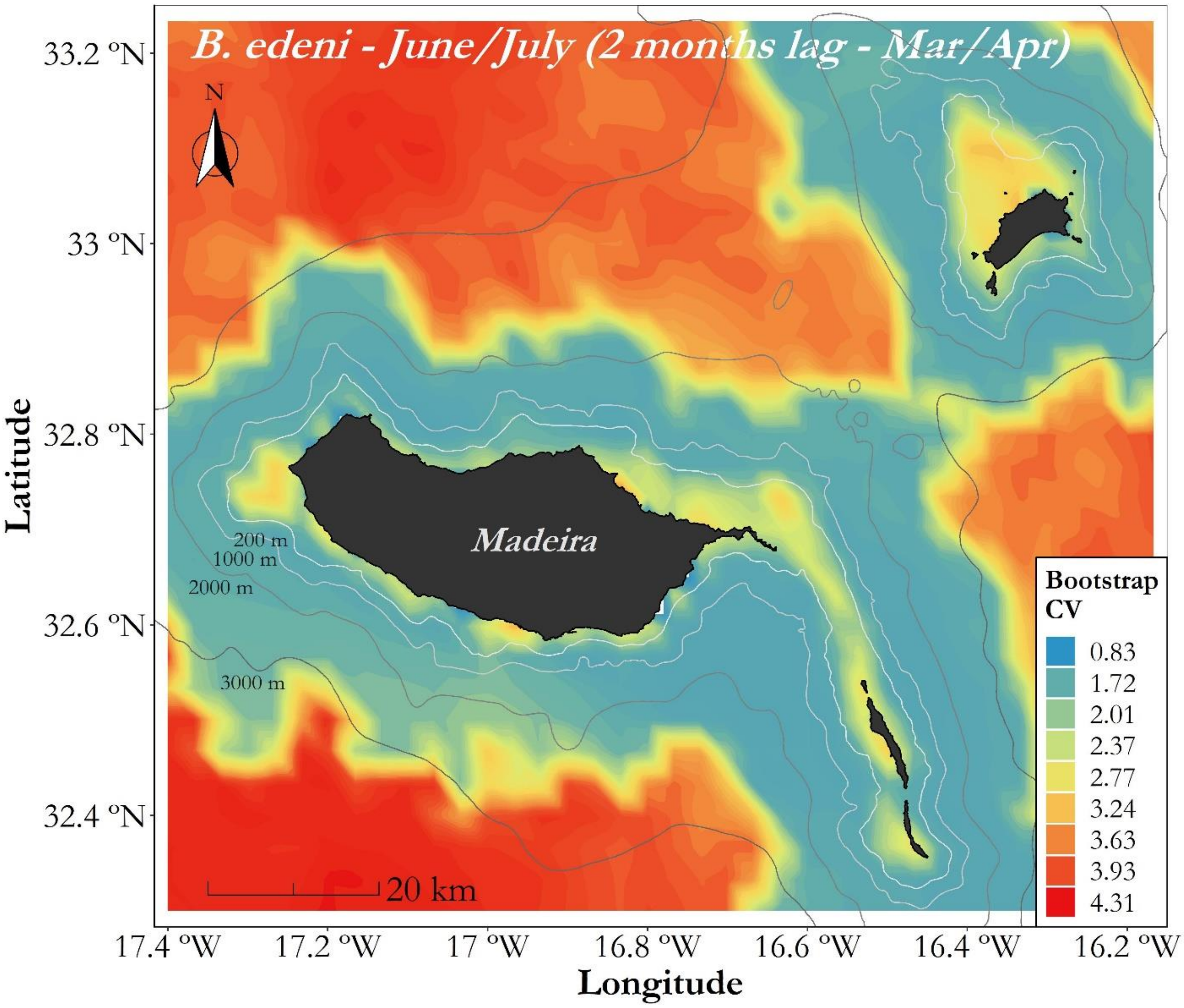


Figure V.2.1.20-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of Bryde's whales in June/July, two-months' time-lag (Mar/Apr), in the Madeira inshore waters for the period 2004 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.21. Balaenoptera edeni – August/September, no time-lag (August/September)

Model of encounter rates of groups

Table V.2.1.21-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-6.0110	0.8393	-7.162	<0.001*
Survey type SLS-RD	0.9529	0.9223	1.033	0.3016
Survey type ALS	1.7110	0.9348	1.830	0.0673
Survey type NSS	1.5440	0.8797	1.755	0.0794
Survey type WWO	2.6220	0.8665	3.026	0.0025*
Survey type FO	-75.060	989800	0.000	0.9999
*Significant at α = 0.05				

Table V.2.1.21-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Distance to escarpment	0.9011	9	0.851	0.003*
Mld 2004-17 Aug/Sept	0.6488	9	0.190	0.102
Pp 2004-17 Aug/Sept	0.9308	9	1.168	<0.001*
Effort	5.3951	9	5.066	<0.001*
*Significant at α = 0.05				

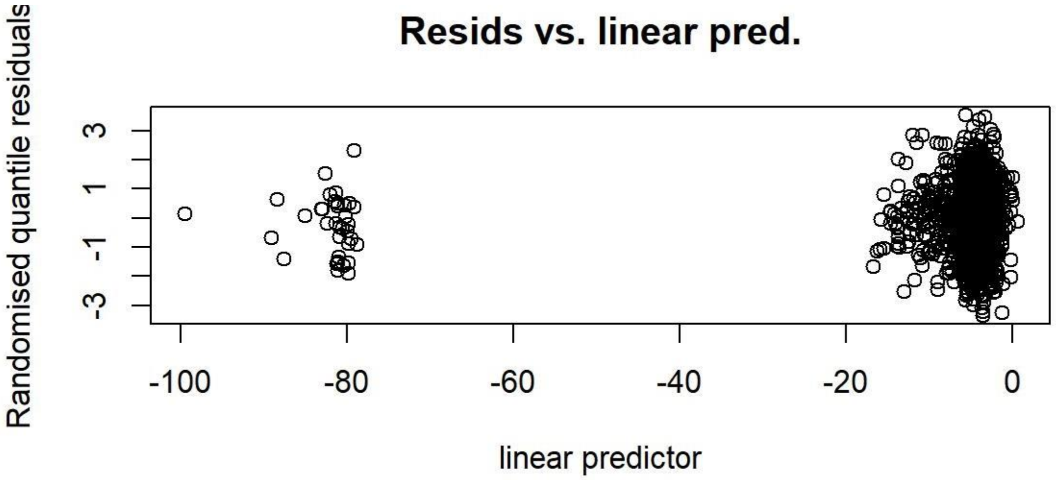


Figure V.2.1.21-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of Bryde's whale groups in Autumn to check heteroskedasticity.

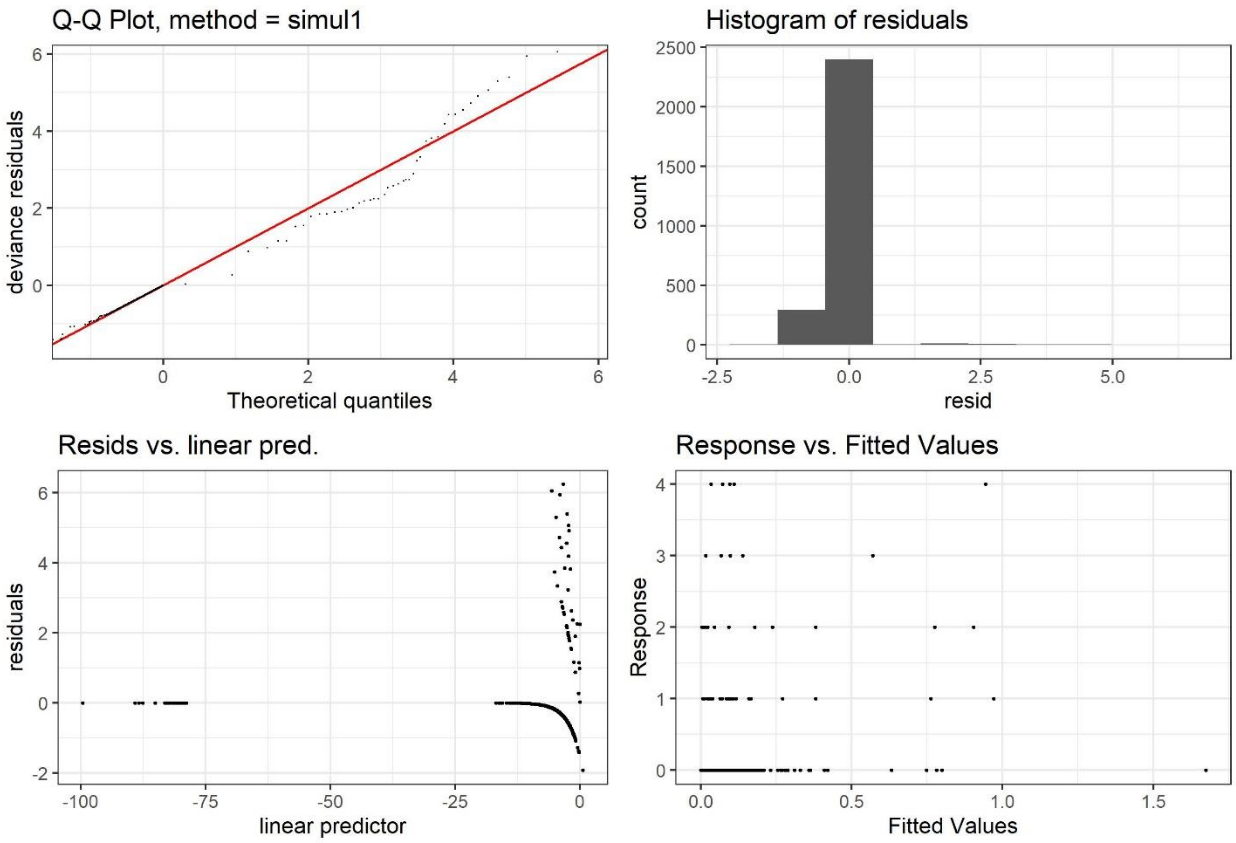


Figure V.2.1.21-2. Diagnostic plots of the selected generalised additive model of the encounter rate of Briyde's whale groups in Autumn for the period 2004-2017.

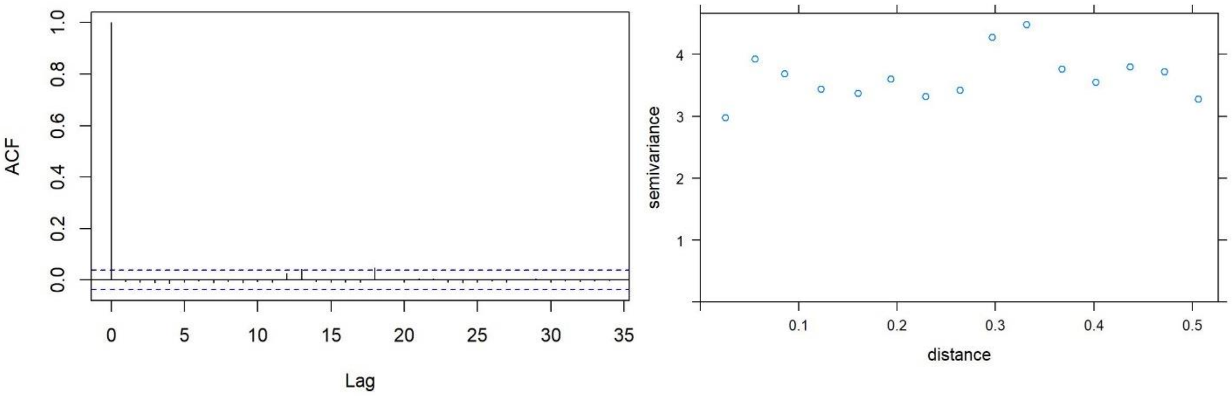


Figure V.2.1.21-3. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of Bryde's whale groups in Autumn for the period 2004-2017.

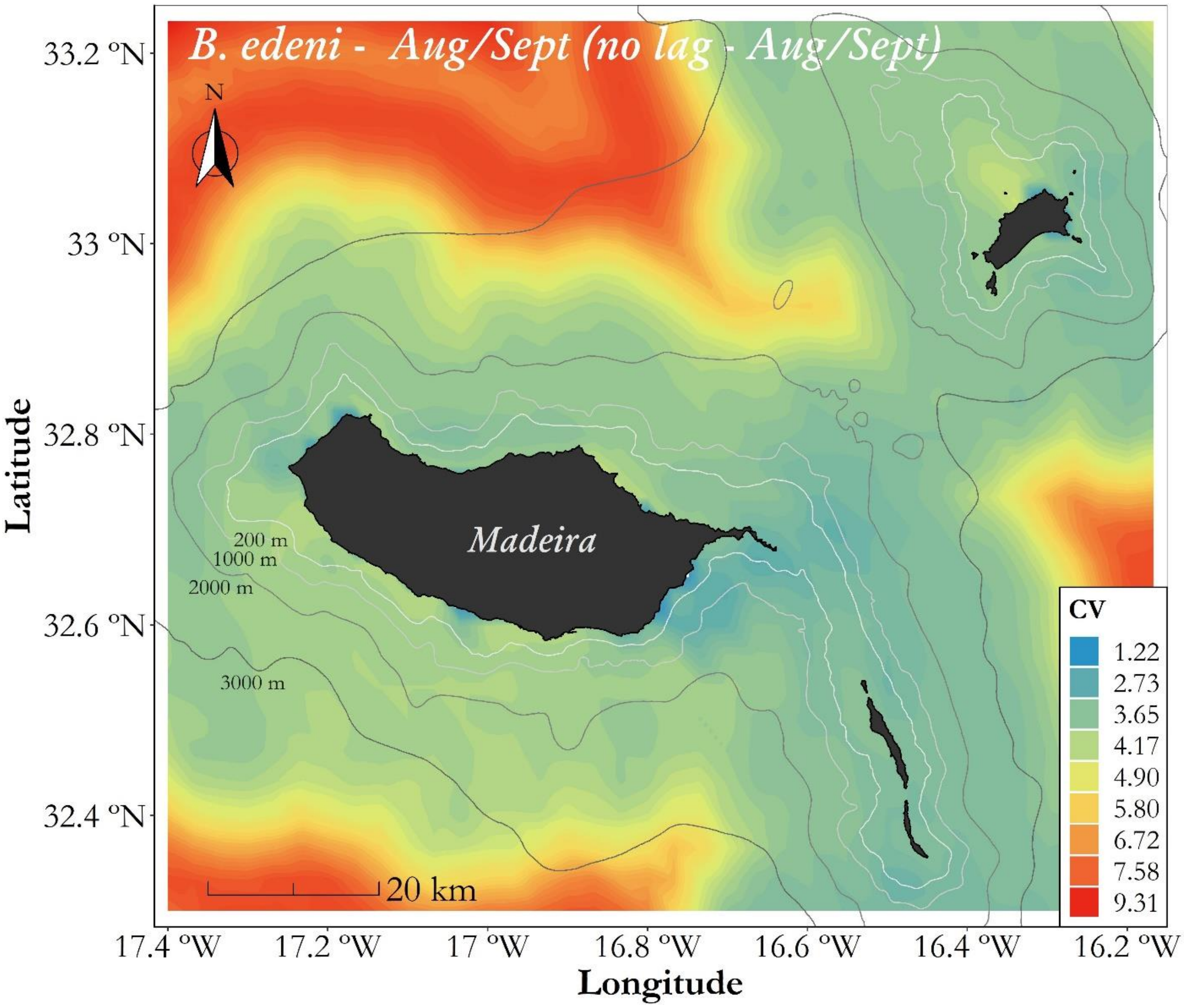


Figure V.2.1.21-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of Bryde's whales in August/September, no time-lag (August/September), in the Madeira inshore waters for the period 2004 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.22. Balaenoptera edeni – August/September, one-month time-lag (July/August)

Model of encounter rates of groups

Table V.2.1.22-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-5.9200	0.8347	-7.0920	<0.001*
Survey type SLS-RD	0.8367	0.9239	0.9060	0.3652
Survey type ALS	1.7090	0.9342	1.8290	0.067
Survey type NSS	1.4160	0.8831	1.6040	0.10892
Survey type WWO	2.6660	0.8717	3.0580	0.002*
Survey type FO	-76.680	993100	0	0.9999
*Significant at α = 0.05				

Table V.2.1.22-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Escarpment area	0.0005	9	0	0.474
Distance to escarpment	0.8907	9	0.764	0.005*
Minimum slope	0.1638	9	0.019	0.307
Poc 2004_17 Jul/Aug	0.9734	9	1.560	<0.001*
Beaufort	0.2560	5	0.064	0.260
Effort	5.2507	9	5.013	<0.001*
*Significant at α = 0.05				

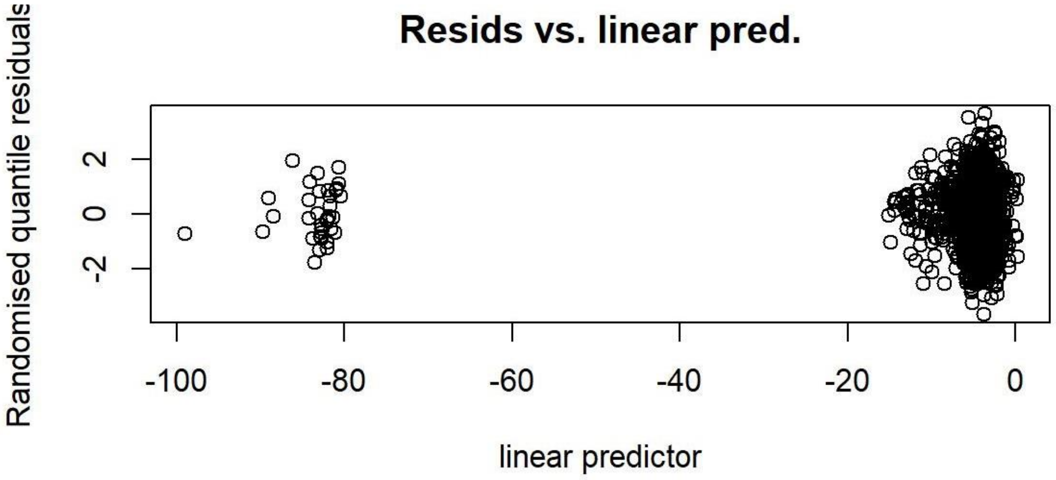


Figure V.2.1.22-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of Bryde's whale groups in August/September, one-month time-lag (July/August), to check heteroskedasticity.

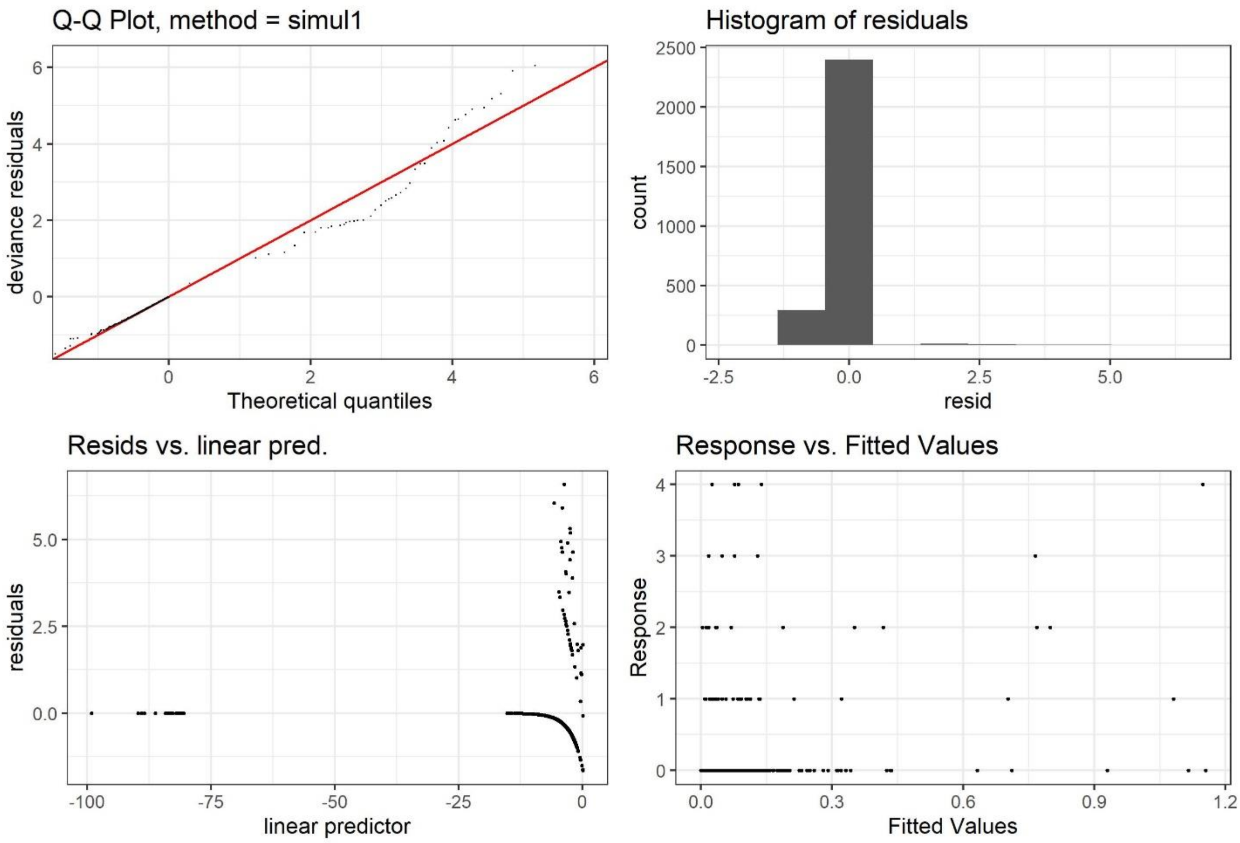


Figure V.2.1.22-2. Diagnostic plots of the selected generalised additive model of the encounter rate of Bryde's whale groups in August/September, one-month time-lag (July/August), for the period 2004-2017.

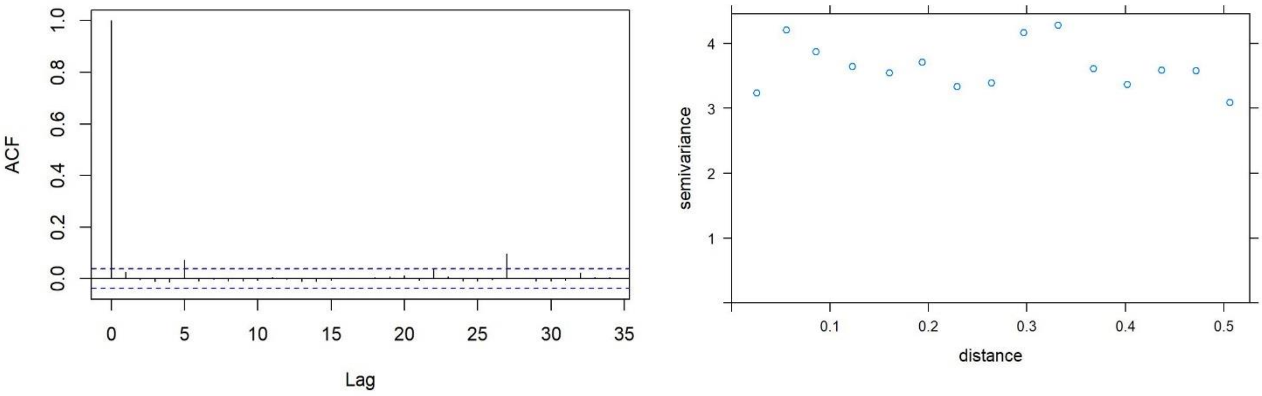


Figure V.2.1.22-3. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of Bryde's whale groups in August/September, one-month time-lag (July/August), for the period 2004-2017.

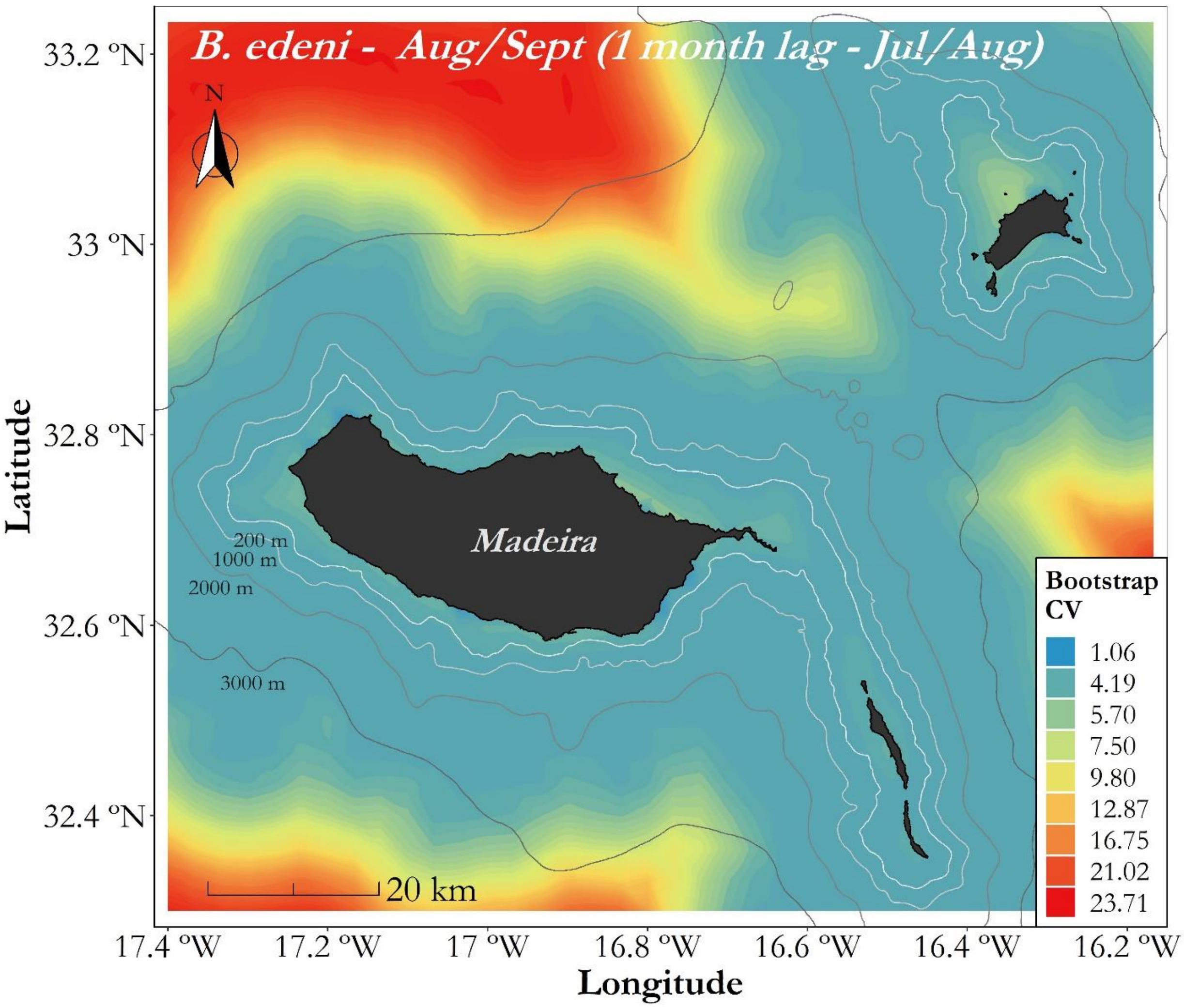


Figure V.2.1.22-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of Bryde's whales in August/September, one-month time-lag (July/August), in the Madeira inshore waters for the period 2004 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.23. Balaenoptera edeni – August/September, two-months' time-lag (May/June)

Model of encounter rates of groups

Table V.2.1.23-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-5.4650	0.8098	-6.7490	<0.001*
Survey type SLS-RD	1.1030	0.9197	1.1990	0.231
Survey type ALS	1.2850	0.9381	1.3700	0.171
Survey type NSS	1.3660	0.8814	1.5500	0.121
Survey type WWO	2.2200	0.8533	2.6020	0.009*
Survey type FO	-81.71	958300	0	0.9999
*Significant at α = 0.05				

Table V.2.1.23-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Escarpment area	0.8214	9	0.410	0.03*
Distance to coast	0.0313	9	0.003	0.347
Mld 2004_17 May/June	0.8169	9	0.443	0.025*
Pp 2004-17 May/June	0.9300	9	0.984	0.001*
Beaufort	0.4592	5	0.159	0.187
Effort	5.3029	9	4.896	<0.001*
*Significant at α = 0.05				

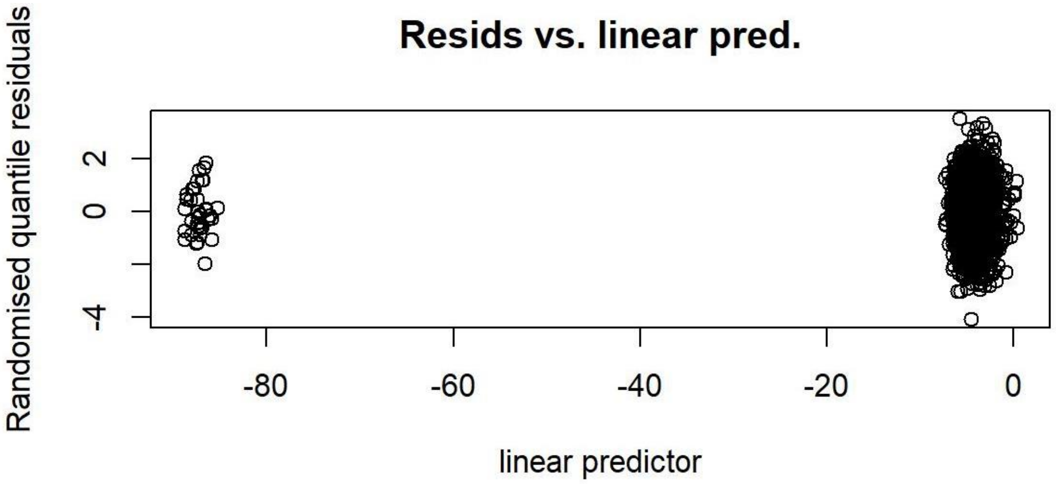


Figure V.2.1.23-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of Bryde's whale groups in August/September, two-months' time-lag (May/June), to check heteroskedasticity.

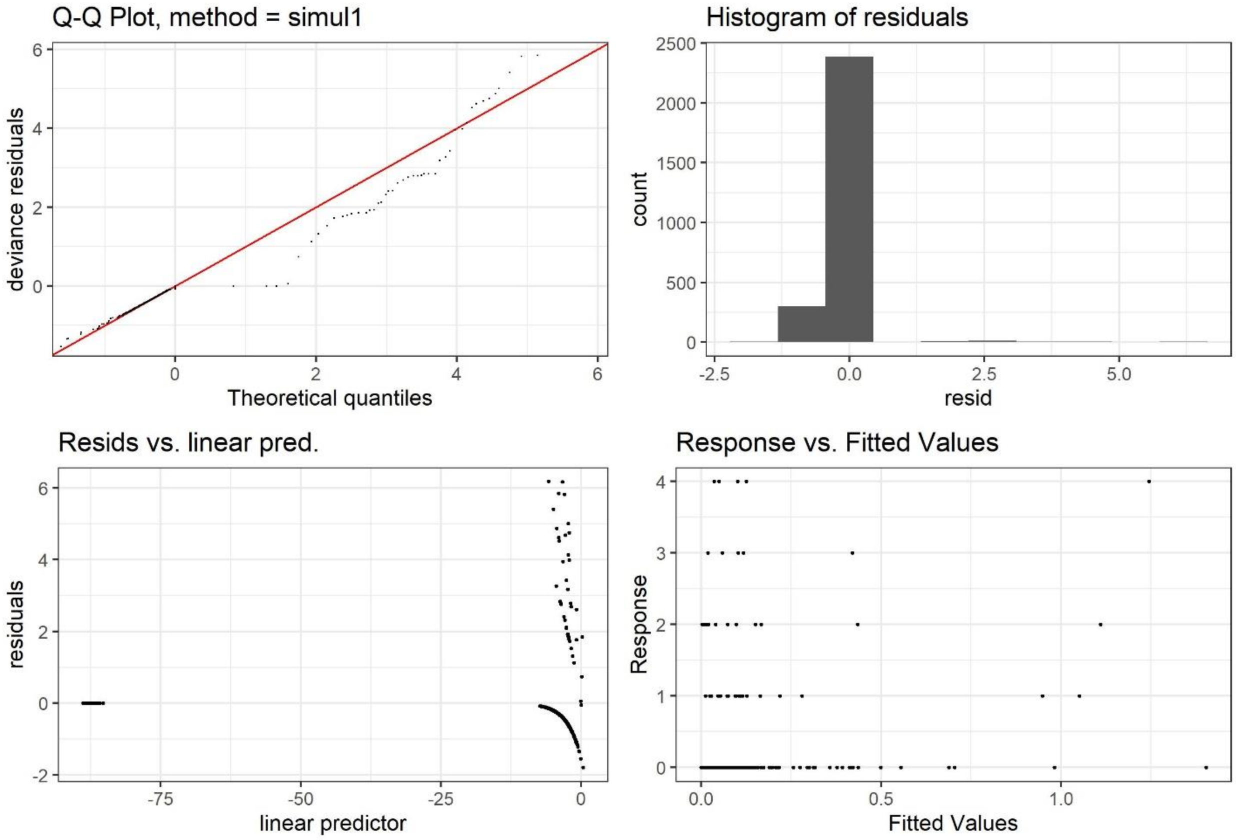


Figure V.2.1.23-2. Diagnostic plots of the selected generalised additive model of the encounter rate of Bryde's whale groups in August/September, two-months' time-lag (May/June), for the period 2004-2017.

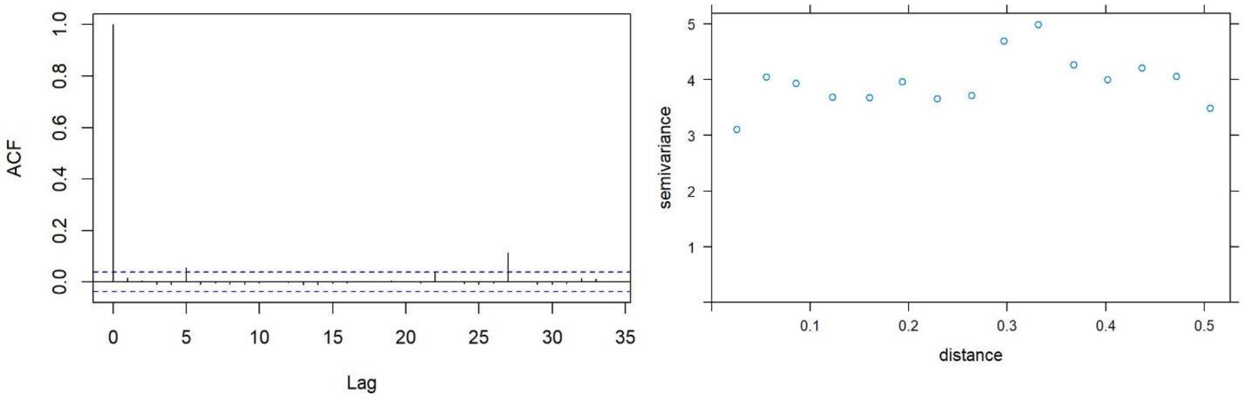


Figure V.2.1.23-3. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of Bryde's whale groups in August/September, two-months' time-lag (May/June), for the period 2004-2017.

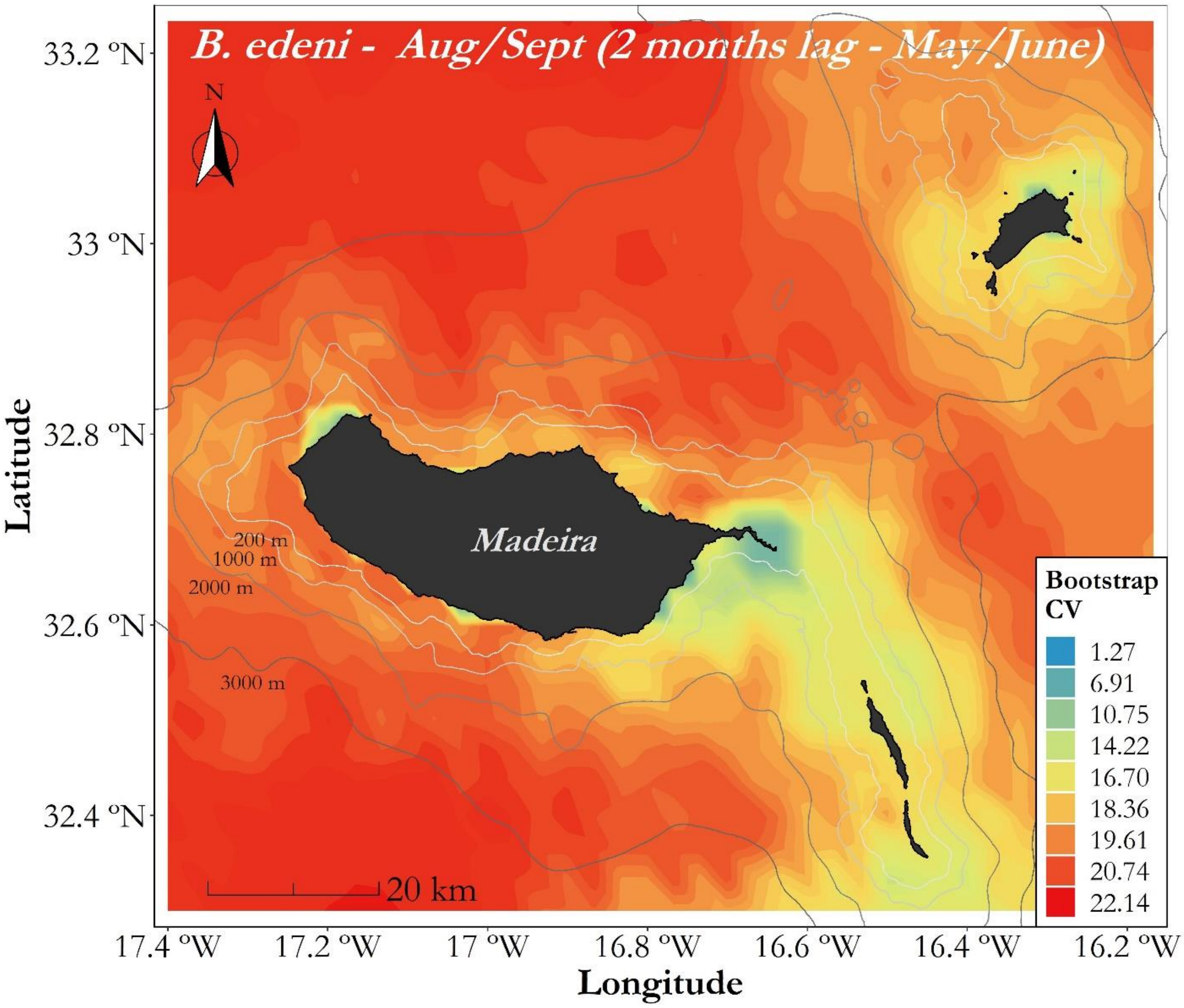


Figure V.2.1.23-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of Bryde's whales in August/September, two-months' time-lag (May/June), in the Madeira inshore waters for the period 2004 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.24. Balaenoptera edeni – October/November, no time-lag (October/November)

Model of encounter rates of groups

Table V.2.1.24-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-5.1818	0.6141	-8.438	<0.001*
Survey type SLS-RD	0.5013	0.6423	0.781	0.435
Survey type ALS	1.2036	0.7401	1.626	0.104
Survey type NSS	-0.5488	1.0601	-0.518	0.605
Survey type WWO	0.3191	0.6734	0.474	0.636
Survey type FO	-	-	-	-
*Significant at α = 0.05				

Table V.2.1.24-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Distance to 200m isobath	0.9357	9	1.150	<0.001*
Effort	4.5956	9	2.777	0.237
*Significant at α = 0.05				

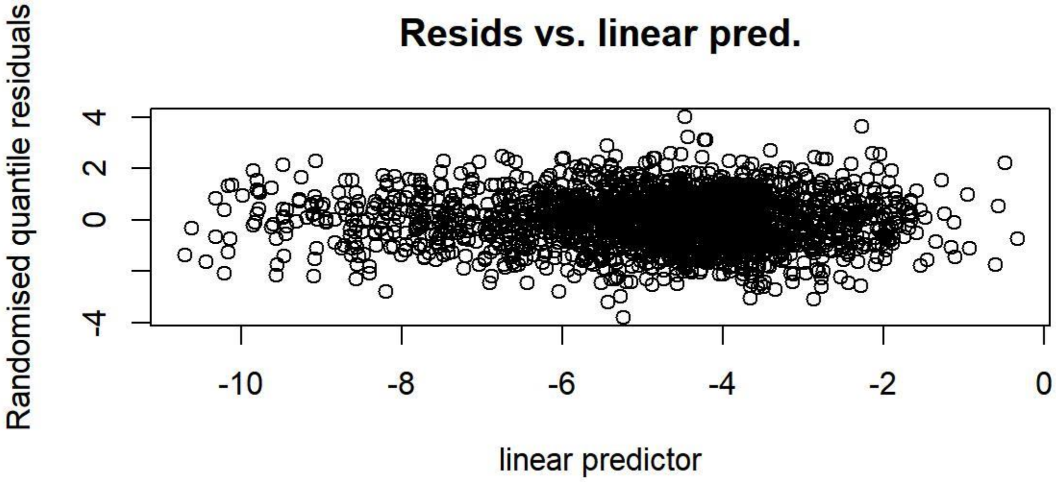


Figure V.2.1.24-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of Bryde's whale groups in October/November, no time-lag (October/November), to check heteroskedasticity.

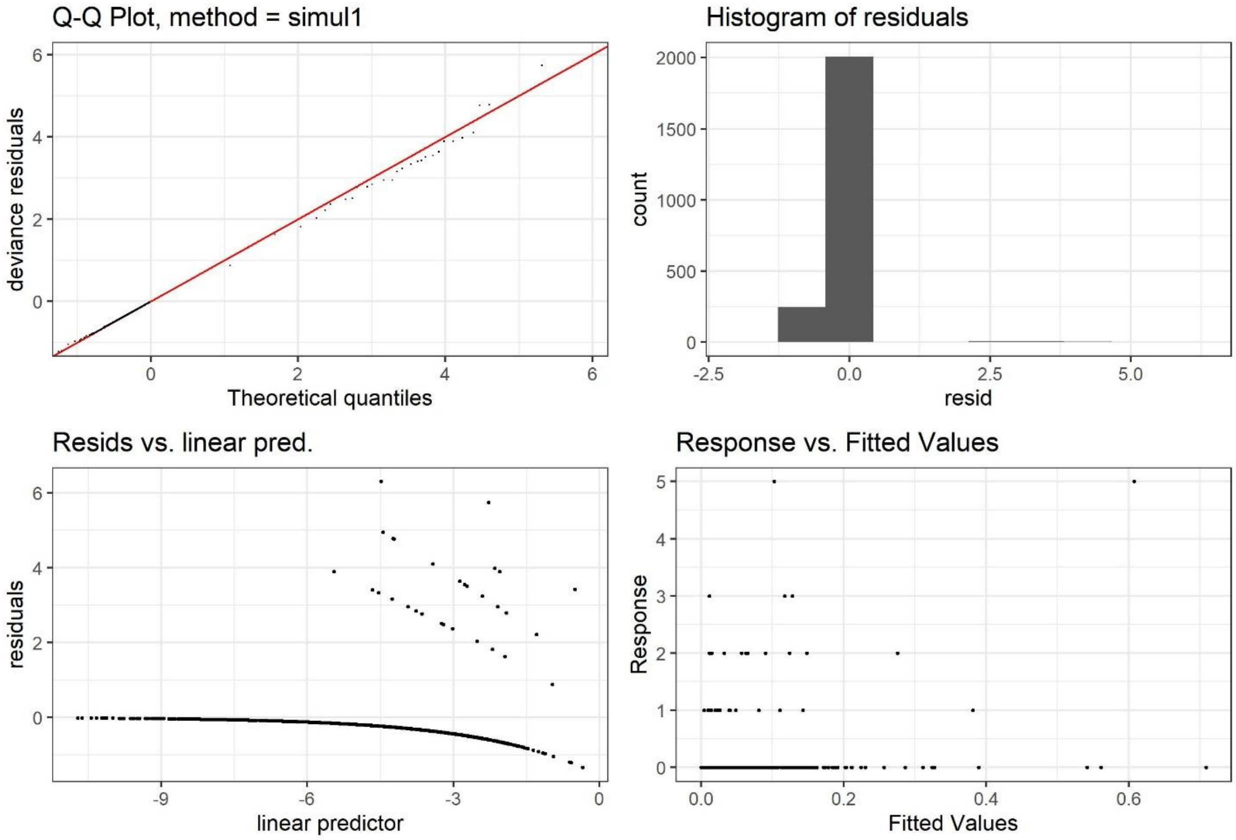


Figure V.2.1.24-2. Diagnostic plots of the selected generalised additive model of the encounter rate of Briyde's whale groups in October/November, no time-lag (October/November), for the period 2004-2017.

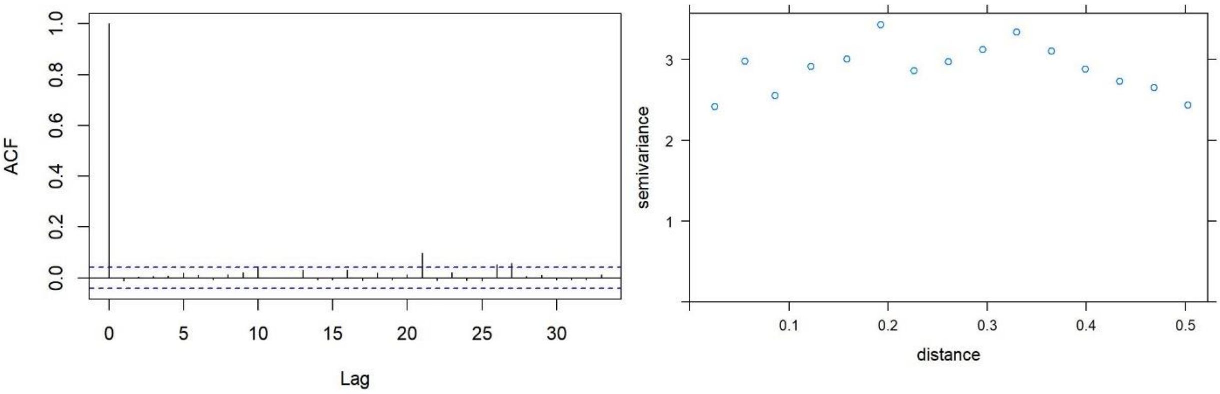


Figure V.2.1.24-3. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of Bryde's whale groups in October/November, no time-lag (October/November), for the period 2004-2017.

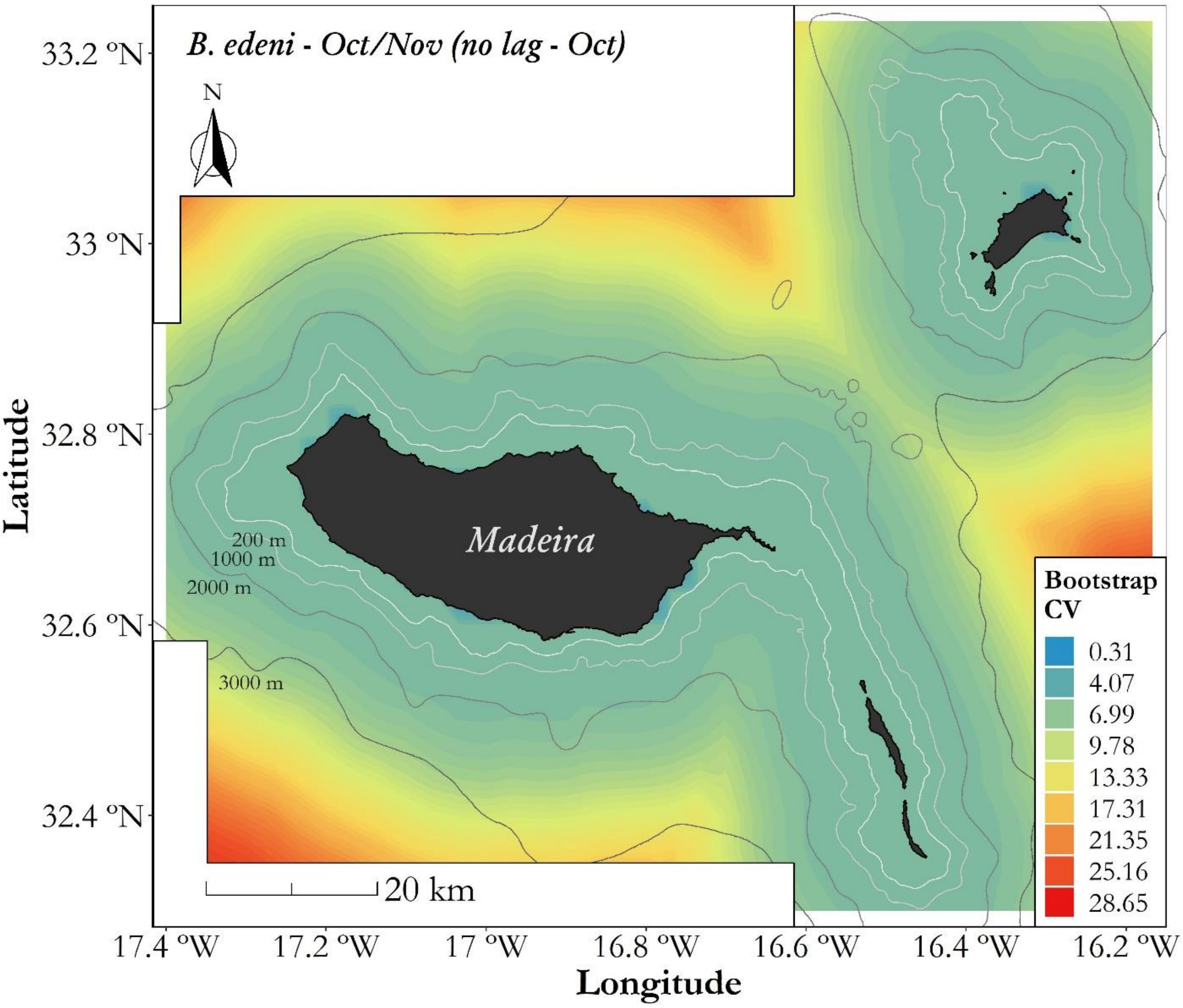


Figure V.2.1.24-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of Bryde's whales in October/November, no time-lag (October/November), in the Madeira inshore waters for the period 2004 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.25. Balaenoptera edeni – October/November, one-month time-lag (September/October)

Model of encounter rates of groups

Table V.2.1.25-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-5.1818	0.6141	-8.438	<0.001*
Survey type SLS-RD	0.5013	0.6423	0.7810	0.435
Survey type ALS	1.2036	0.7401	1.626	0.104
Survey type NSS	-0.5488	1.0601	-0.518	0.605
Survey type WWO	0.3191	0.6734	0.474	0.636
Survey type FO	-	-	-	-
*Significant at α = 0.05				

Table V.2.1.25-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Distance to 200m isobath	0.9357	9	1.150	<0.001*
Effort	4.5956	9	2.777	<0.001*
*Significant at α = 0.05				

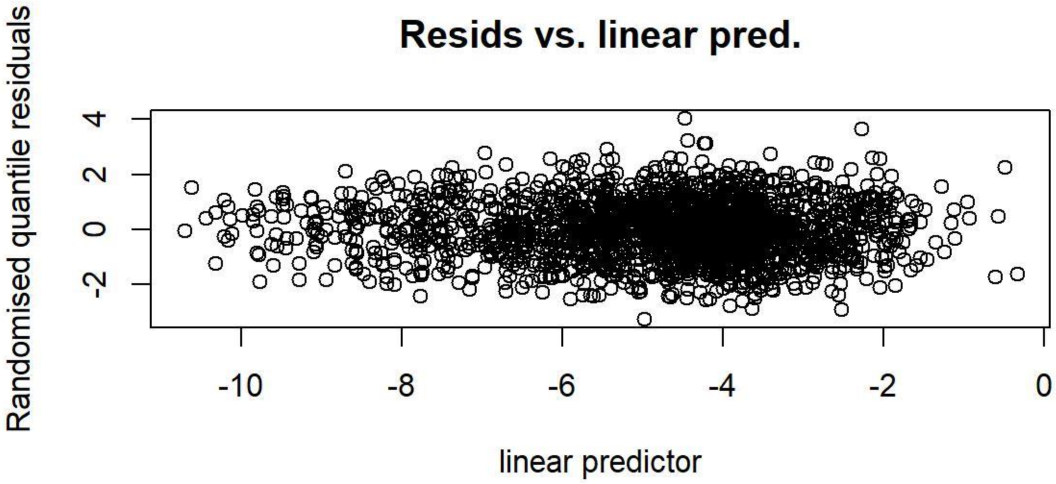


Figure V.2.1.25-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of Bryde's whale groups in October/November, one-month time-lag (September/October), to check heteroskedasticity.

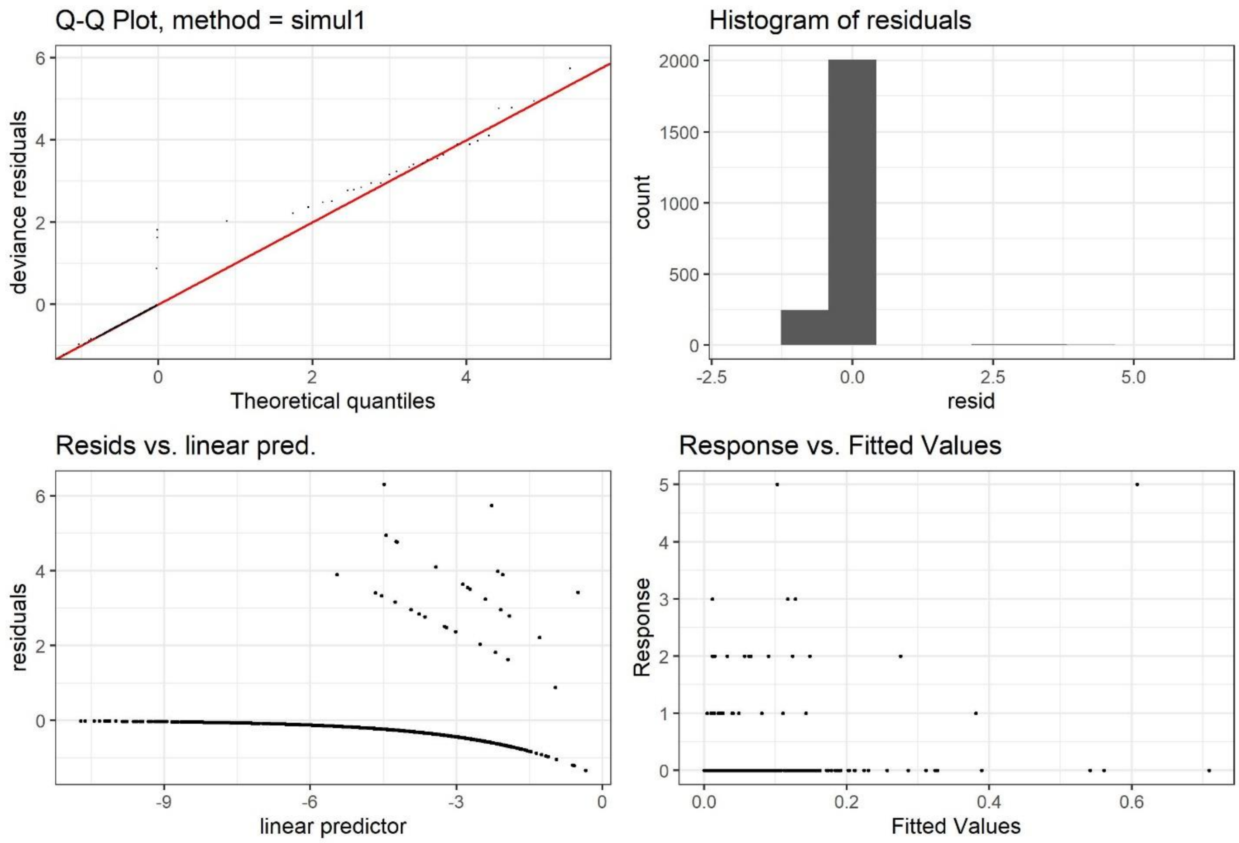


Figure V.2.1.25-2. Diagnostic plots of the selected generalised additive model of the encounter rate of Bryde's whale groups in October/November, one-month time-lag (September/October), for the period 2004-2017.

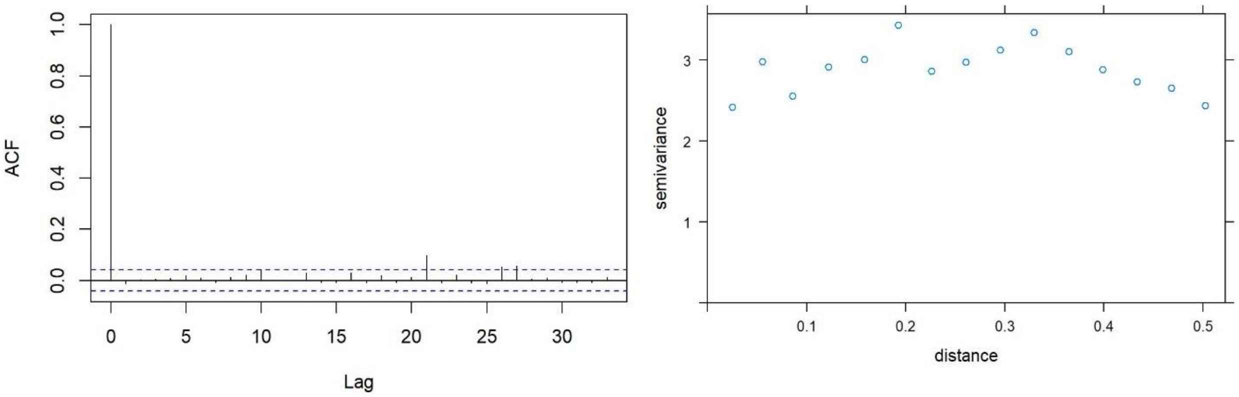


Figure V.2.1.25-3. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of Bryde's whale groups in October/November, one-month time-lag (September/October), for the period 2004-2017.

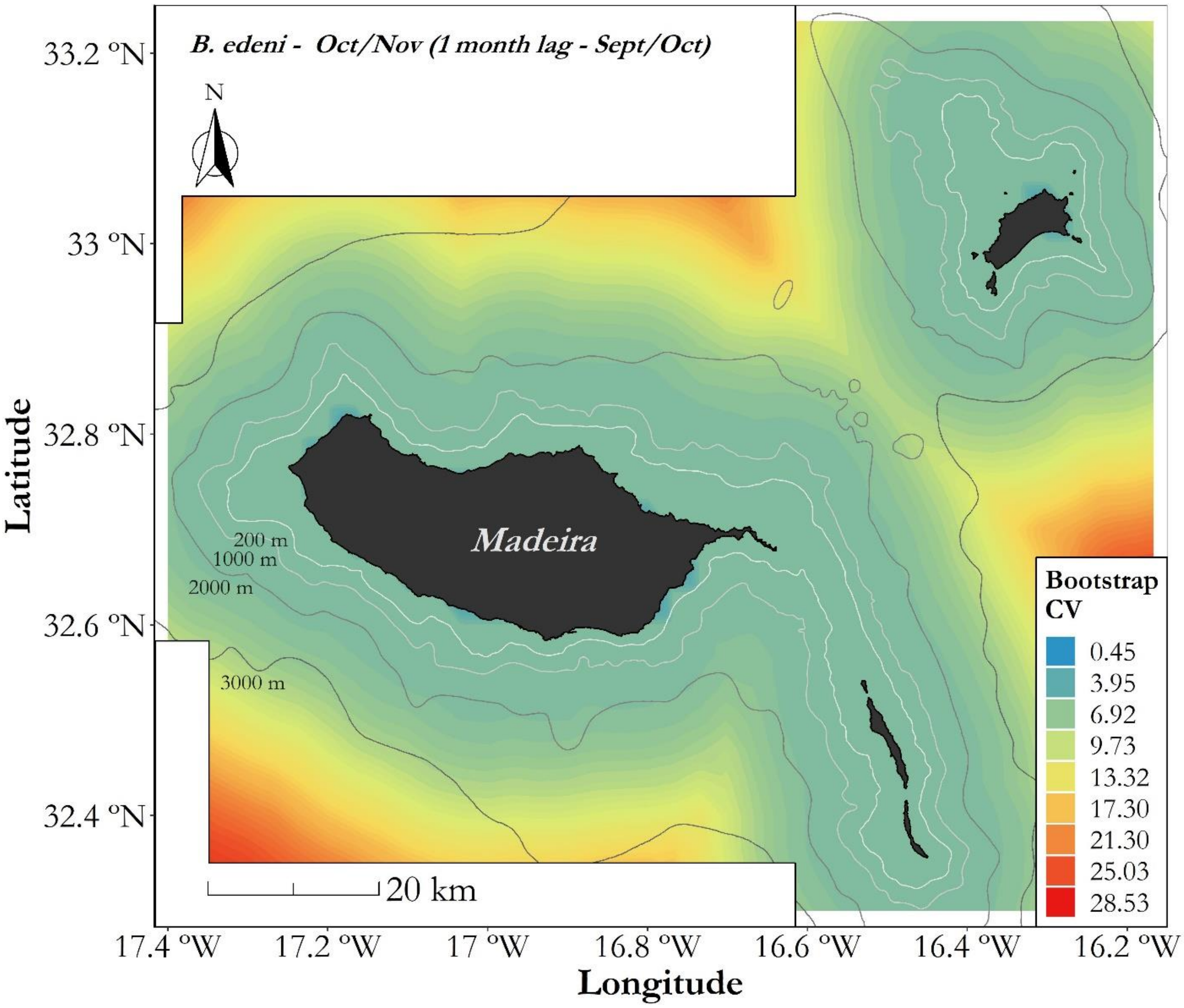


Figure V.2.1.25-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of Bryde's whales in October/November, one-month time-lag (September/October), in the Madeira inshore waters for the period 2004 – 2017, based on encounter rate (animals per km of transect line).

V.2.1.26. Balaenoptera edeni – October/November, two-months' time-lag (July/August)

Model of encounter rates of groups

Table V.2.1.26-1. Parametric coefficients in the encounter rate of groups estimation model (Std. error = Standard error; t = t distribution value).

Coefficients	Estimate	Std. error	t	p-value
Intercept	-5.1818	0.6141	-8.438	<0.001*
Survey type SLS-RD	0.5013	0.6423	0.7810	0.435
Survey type ALS	1.2036	0.7401	1.626	0.104
Survey type NSS	-0.5488	1.0601	-0.518	0.605
Survey type WWO	0.3191	0.6734	0.474	0.636
Survey type FO	-	-	-	-
*Significant at α = 0.05				

Table V.2.1.26-2. Smooth terms in the encounter rate of groups estimation model (Edf = effective degrees of freedom, Ref. df = Reference degrees of freedom, F = F distribution value).

Smooth terms	Edf	Ref. Df	F	p-value
Distance to 200m isobath	0.9357	9	1.150	<0.001*
Effort	4.5956	9	2.777	<0.001*
*Significant at α = 0.05				

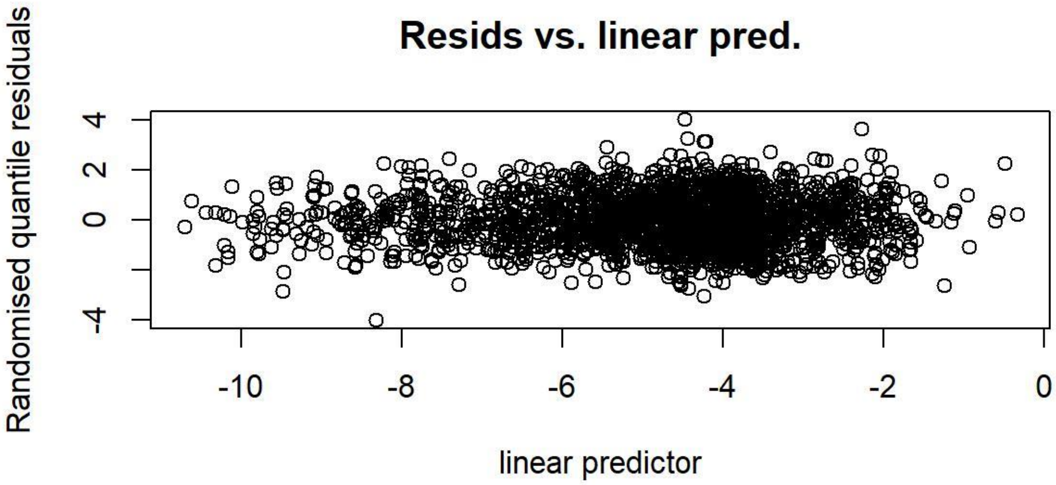


Figure V.2.1.26-1. Randomised quantile residuals plot of the selected generalised additive models of the encounter rate of Bryde's whale groups in October/November, two-months' time-lag (July/August), to check heteroskedasticity.

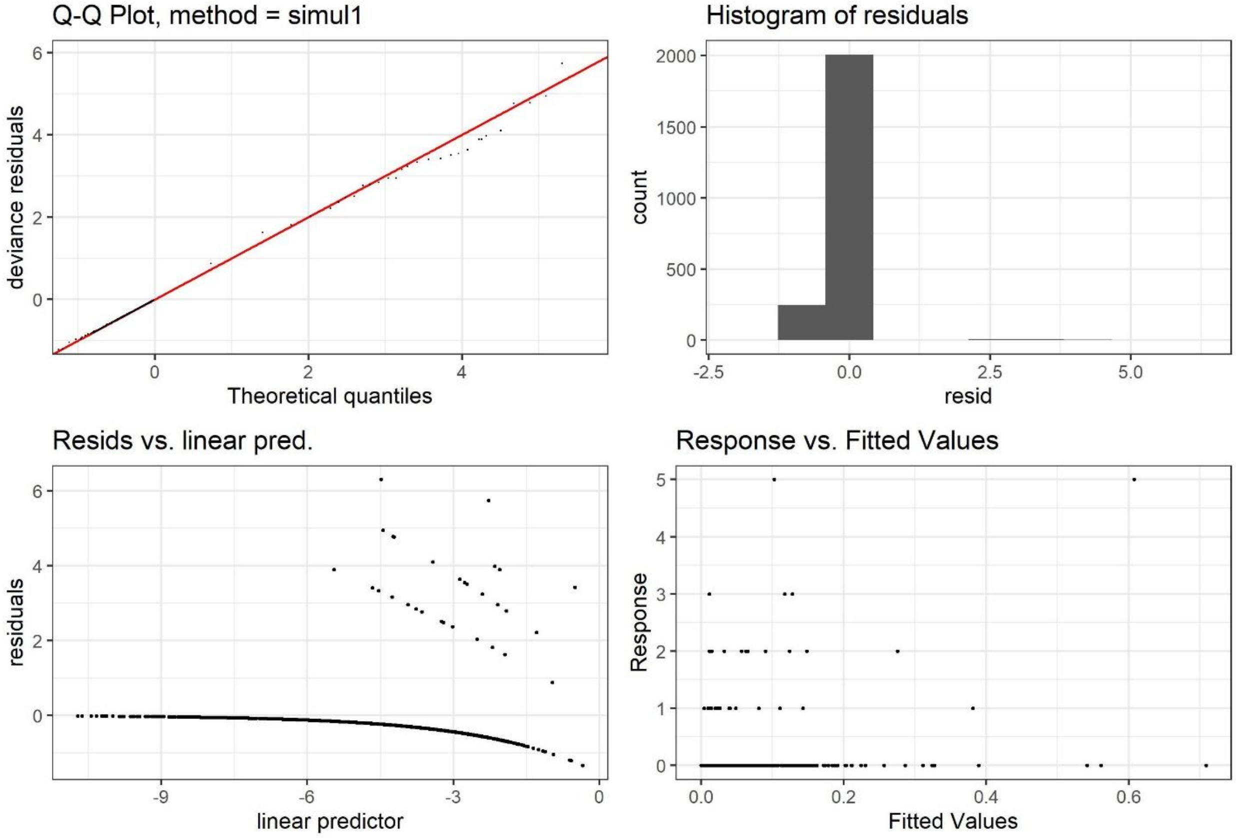


Figure V.2.1.26-2. Diagnostic plots of the selected generalised additive model of the encounter rate of Bryde's whale groups in October/November, two-months' time-lag (July/August), for the period 2004-2017.

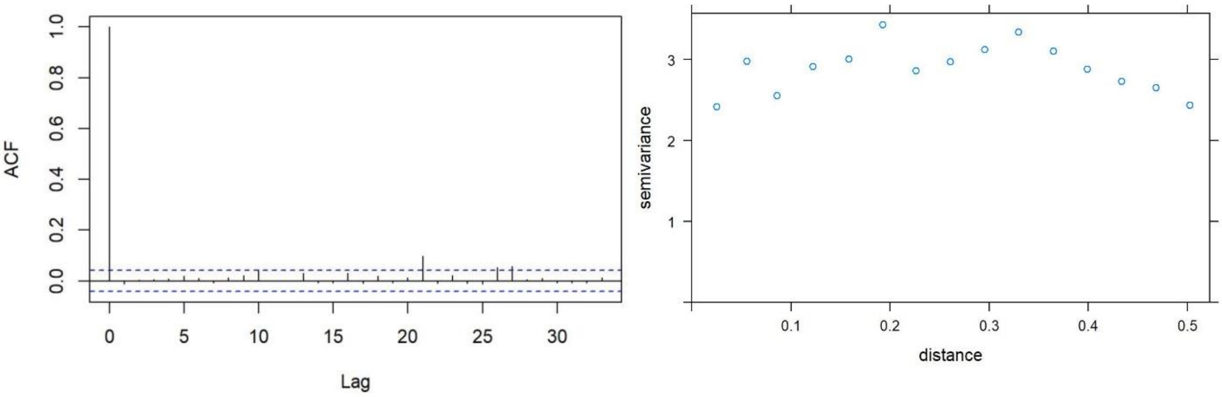


Figure V.2.1.26-3. Temporal auto-correlation regression plot from "acf" function (left) and variogram plot to assess spatial auto-correlation (right) in the selected model of Bryde's whale groups in October/November, two-months' time-lag (July/August), for the period 2004-2017.

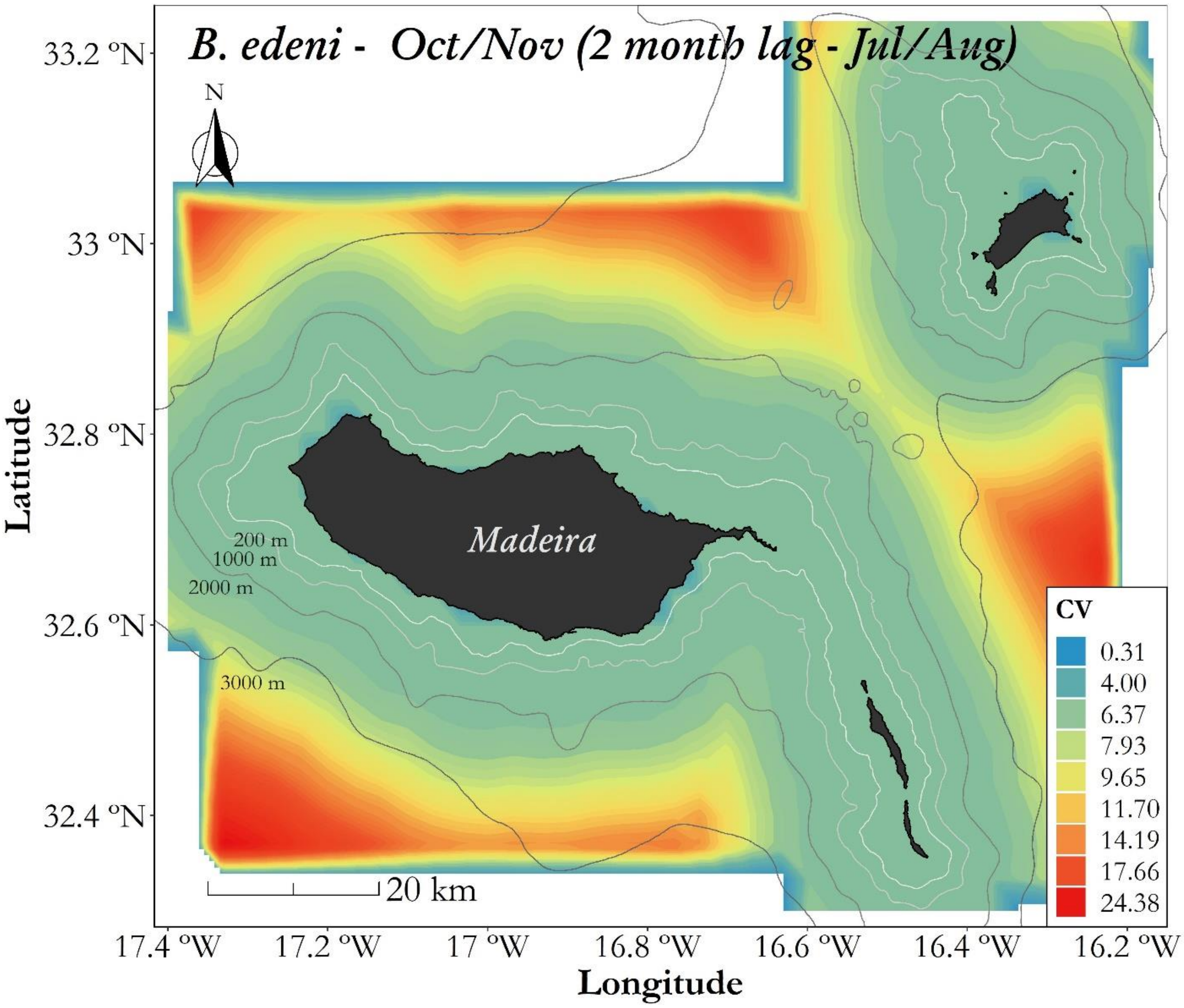


Figure V.2.1.26-4. Map of the uncertainty (coefficient of variation, CV) of the prediction of the distribution of Bryde's whales in October/November, two-months' time-lag (July/August), in the Madeira inshore waters for the period 2004 – 2017, based on encounter rate (animals per km of transect line).

APPENDIX VI

APPENDIX VI.

VI.1. Trophic niche

VI.1.1. Comparison of Comparison of isotopic signature between live and stranded animals

Table VI.1.1-1. Summary statistics of carbon and nitrogen stable isotope data and the results of the Shapiro-Wilk normality test and respective statistics. All p-values > 0.05, indicating samples cannot be excluded as coming from populations with a normal distribution of δ13C and δ15N values.

Sample	Isotope	Species	n	mean	median	min	max	var	stat	p.value
Live	δ13C	*D. Delphis*	20	-18.41	-18.36	-19.80	-15.92	1.02	0.95	0.370
Live	δ13C	*S. Frontalis*	20	-18.23	-18.11	-19.60	-17.20	0.37	0.97	0.823
Live	δ13C	*T. Truncatus*	21	-18.04	-18.22	-19.10	-16.50	0.52	0.93	0.134
Live	δ13C	Ziphiidae	4	-17.01	-17.10	-17.70	-16.14	0.52	0.93	0.568
Live	δ15N	*D. Delphis*	20	11.12	10.90	8.80	12.70	1.18	0.95	0.365
Live	δ15N	*S. Frontalis*	20	11.74	11.80	9.40	13.70	1.15	0.98	0.952
Live	δ15N	*T. Truncatus*	21	11.19	11.00	9.30	13.30	0.99	0.96	0.423
Live	δ15N	Ziphiidae	4	13.03	13.15	12.50	13.30	0.13	0.83	0.163
Stranded	δ13C	*D. Delphis*	14	-18.64	-18.58	-19.67	-17.47	0.45	0.95	0.536
Stranded	δ13C	*S. Frontalis*	4	-17.95	-18.14	-18.24	-17.30	0.20	0.77	0.054
Stranded	δ13C	*T. Truncatus*	7	-18.31	-18.60	-19.40	-16.74	1.08	0.90	0.345
Stranded	δ13C	Ziphiidae	5	-17.81	-17.80	-18.34	-17.50	0.11	0.90	0.428
Stranded	δ15N	*D. Delphis*	14	11.45	11.30	10.50	13.10	0.62	0.93	0.260
Stranded	δ15N	*S. Frontalis*	4	12.70	12.75	11.80	13.50	0.86	0.78	0.070
Stranded	δ15N	*T. Truncatus*	7	12.77	12.50	10.80	15.40	2.76	0.92	0.477
Stranded	δ15N	Ziphiidae	5	13.30	13.50	12.70	13.90	0.28	0.89	0.368

Table VI.1.1-2. Results of the Welch two sample t-test between samples of live and stranded animals by species for δ13C and δ15N, and respective statistics. The only pair wise means (live and stranded samples) significantly different ($p < 0.05$) were of *T. truncatus* for δ15N (bold).

Isotope	Species	n (live)	n (stranded)	stat	par	p-value
δ13C	*D. delphis*	20	14	0.817	31.957	0.420
δ13C	*S. frontalis*	20	4	-1.080	5.546	0.325
δ13C	*T. truncatus*	21	7	0.649	8.008	0.534
δ13C	Ziphiidae	4	5	2.066	3.979	0.108
δ15N	*D. delphis*	20	14	-1.044	31.929	0.305
δ15N	*S. frontalis*	20	4	-1.840	4.758	0.128
δ15N	*T. truncatus*	21	7	-2.389	7.488	**0.046**
δ15N	Ziphiidae	4	5	-0.931	6.903	0.383

Table VI.1.1-3. Results of the Levene's test to assess homoscedasticity of data of the species with both live and stranded animals samples.

Isotope	**Species**	**Variables**		**df**	**F value**	**Pr[>F]**
		n (live)	**n (stranded)**			
δ13C	*D. delphis*	20	14	32	1.966	0.170
δ13C	*S. frontalis*	20	4	22	0.933	0.345
δ13C	*T. truncatus*	21	7	26	1.211	0.281
δ13C	Ziphiidae	4	5	7	5.419	0.053
δ15N	*D. delphis*	20	14	32	1.660	0.207
δ15N	*S. frontalis*	20	4	22	0.003	0.953
δ15N	*T. truncatus*	21	7	26	1.962	0.173
δ15N	Ziphiidae	4	5	7	0.637	0.451

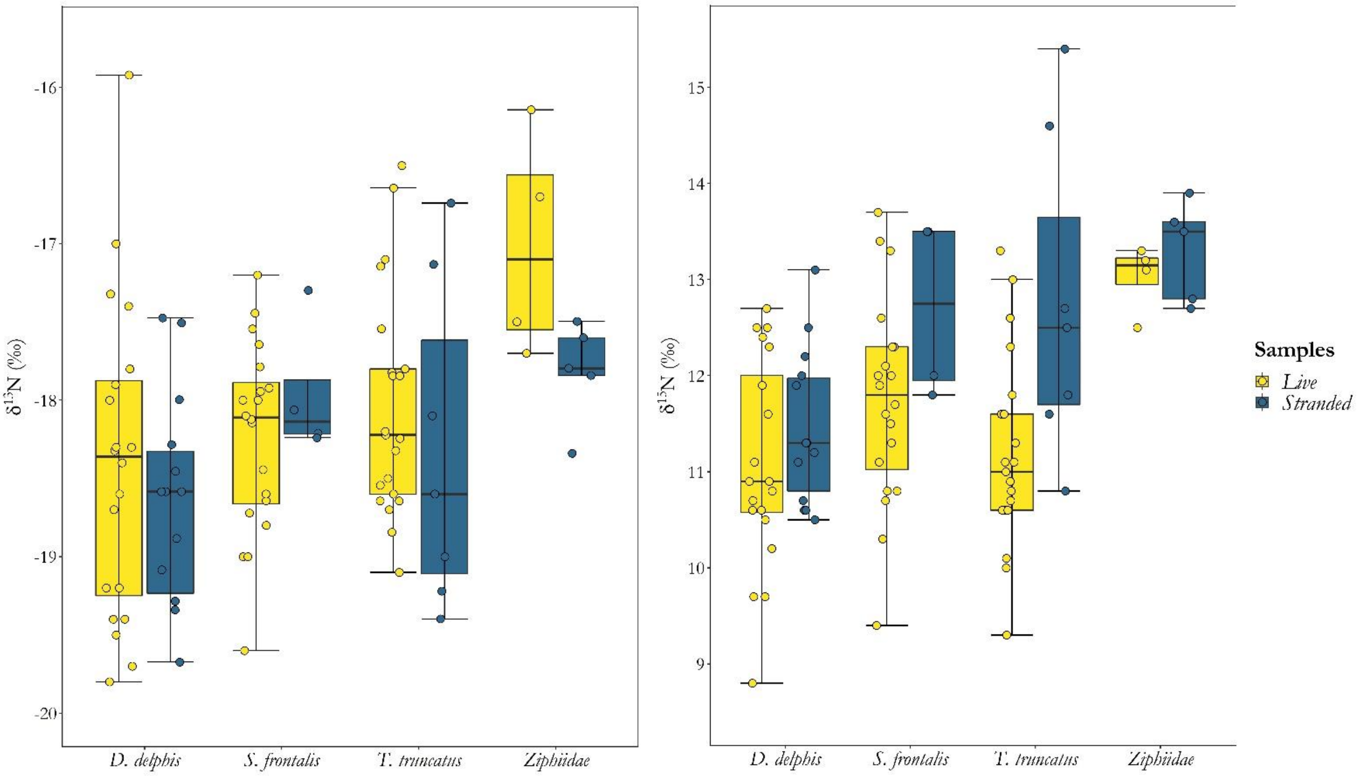


Figure VI.1.1-1. Boxplots of carbon (left) and nitrogen (right) stable isotope ratios by type of sample (live and stranded animals) of common dolphin (*D. delphis*), Atlantic spotted dolphin (*S. frontalis*), bottlenose dolphin (*T. truncatus*) and beaked whales (Ziphiidae). The raw data are plotted as dots with the colours corresponding to each type of sample.

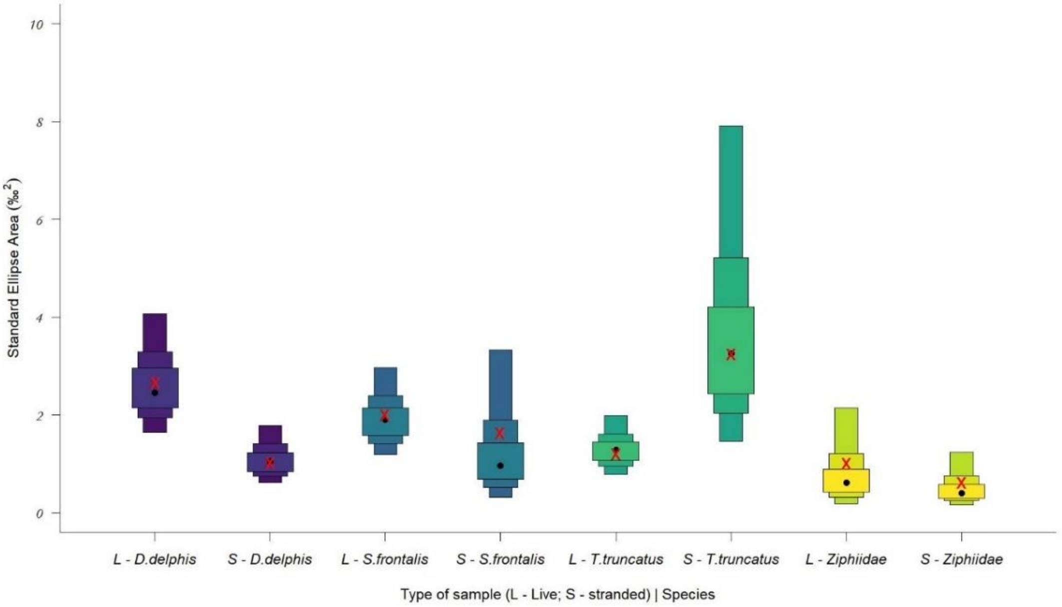


Figure VI.1.1-2. Density plot showing the SEAc (Standard Ellipse Area corrected), with for both live and stranded animals of common dolphin (*D. delphis*), Atlantic spotted dolphin (*S. frontalis*), bottlenose dolphin (*T. truncatus*) and beaked whales (Ziphiidae). The boxed areas reflect the 95, 75 and 50% credible intervals and the red x the maximum likelihood of SEAc.

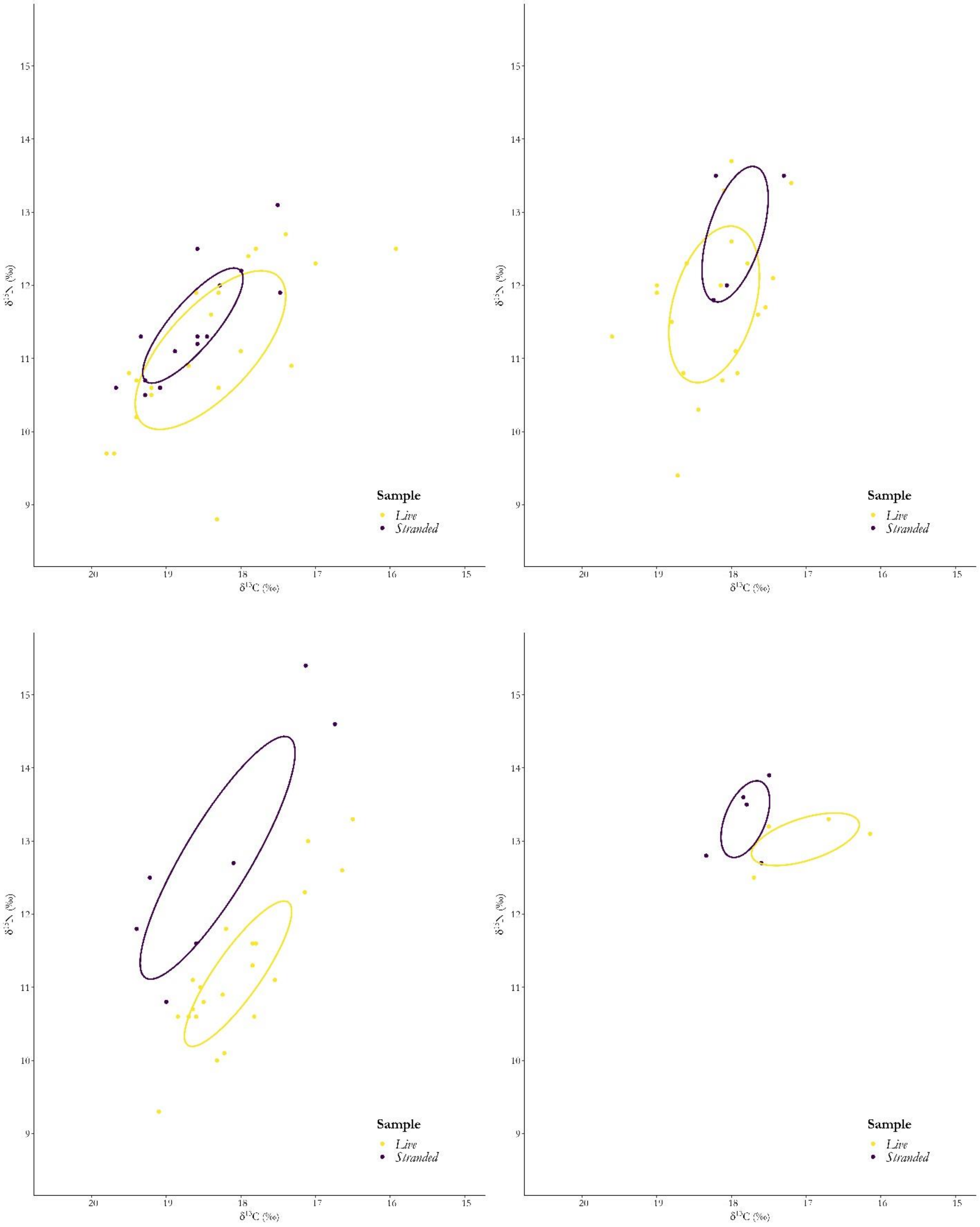


Figure VI.1.1-3. Standard ellipse area corrected (SEA$_c$) for both live and stranded animals of: top-left - common dolphin (*D. delphis*); top-right - Atlantic spotted dolphin (*S. frontalis*); bottom-left - bottlenose dolphin (*T. truncatus*); bottom-right - beaked whales (Ziphiidae).

VI.1.2. Stable isotopes analysis

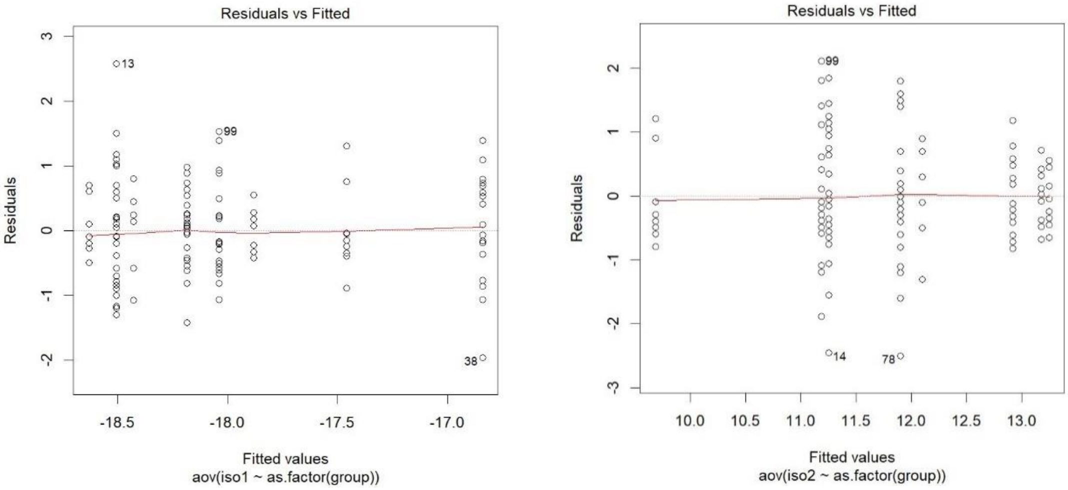


Figure VI.1.2-1. Plots (left: δ13C, right: δ15N) of the residuals versus fitted values to check the homogeneity of variances in the data (all species) used in the one-way ANOVA.

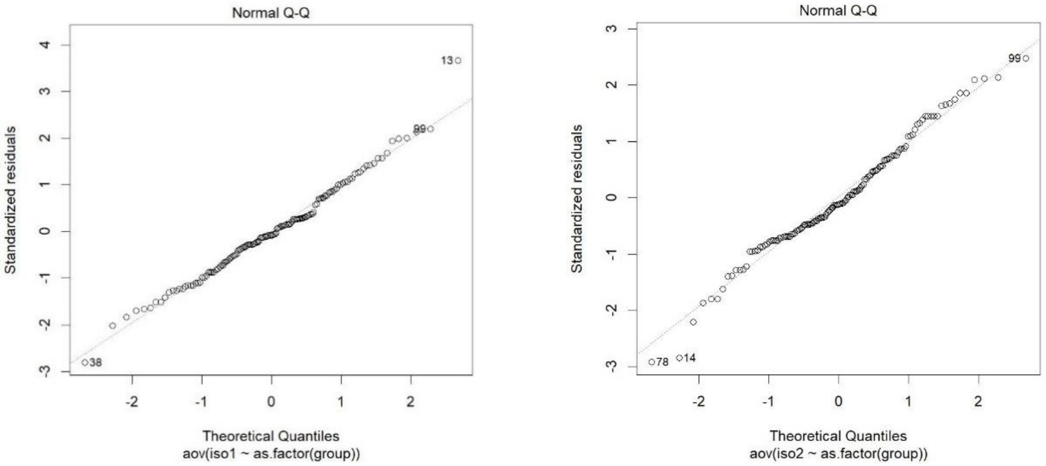


Figure VI.1.2-2. QQ plots (left: δ13C, right: δ15N) to assess the normal distribution of the residuals of the one-way ANOVA.

Table VI.1.2-1. Results of the Shapiro-Wilk test to assess the normal distribution of the residuals of the δ13C and δ15N data of seven cetacean species (*B. edeni, D. delphis, S. frontalis, S. coeruleoalba, T. truncatus, G. macrorhynchus* and *P. macrocephalus*) and one family (Ziphiidae), used in the one-way ANOVA.

SI	**Groups**	**W**	**p-value**
δ13C	8	0.987	0.250
δ15N	8	0.983	0.095

Table VI.1.2-2. Results of the Levene's test to assess homoscedasticity of the δ13C and δ15N of seven cetacean species (*B. edeni, D. delphis, S. frontalis, S. coeruleoalba, T. truncatus, G. macrorhynchus* and *P. macrocephalus*) and one family (Ziphiidae) , used in the one-way ANOVA.

SI	**Groups**	**df (group)**	**df (samples)**	**F value**	**Pr[>F]**
δ13C	8	7	126	1.910	0.073
δ15N	8	7	126	1.766	0.100

VI.1.3. Isotope niche overlap

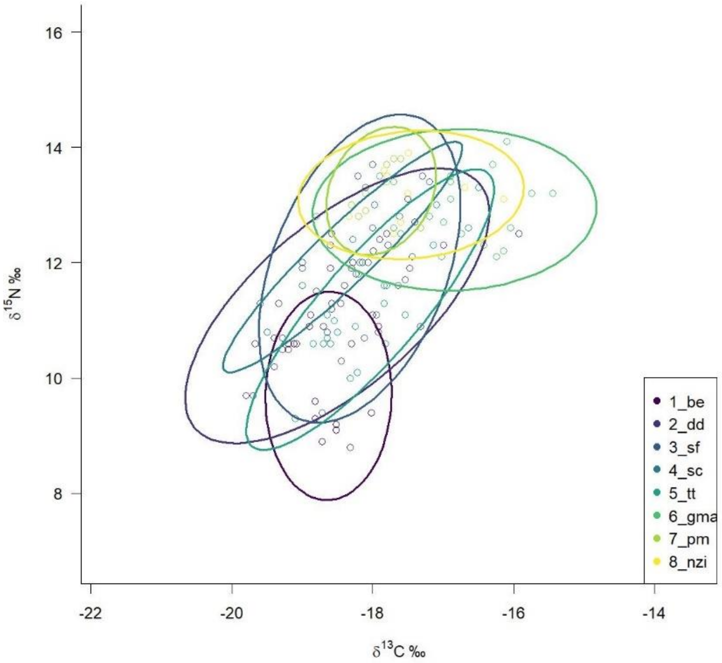


Figure VI.1.3-1. Bayesian standard ellipse Areas (SEA$_b$) calculated from 95% prediction ellipses, used to calculate the isotopic niche between species: Bryde's whale – 2_be; common dolphin – 2_dd; spotted dolphin – 3_sf; striped dolphin – 4_sc; bottlenose dolphin – 5_tt; pilot whale – 6_gma; sperm whale – 7_pm; beaked whales – 8_nzi.

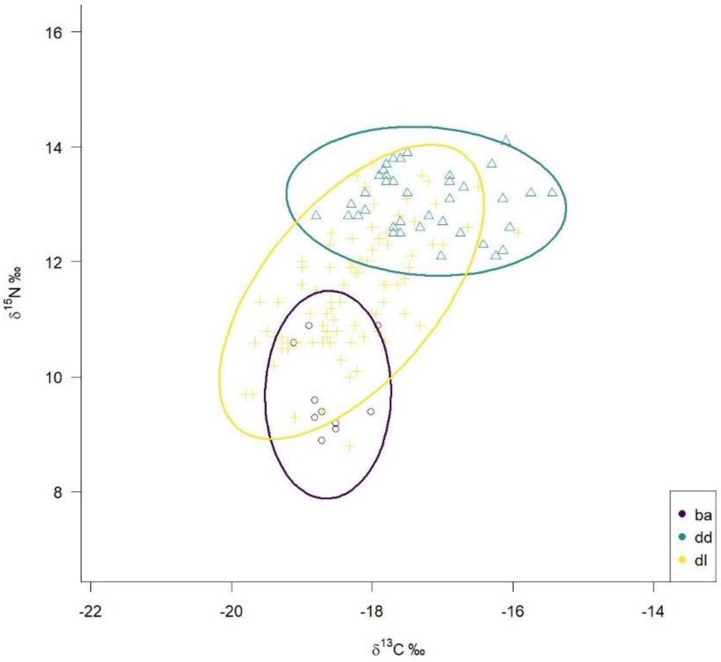


Figure VI.1.3-2. Bayesian standard ellipse Areas (SEA$_b$) calculated from 95% prediction ellipses, used to calculate the isotopic niche between groups of species: baleen whales – ba; dolphins – dl; deep divers – dd.

VI.1.4. Isotopic signatures over time

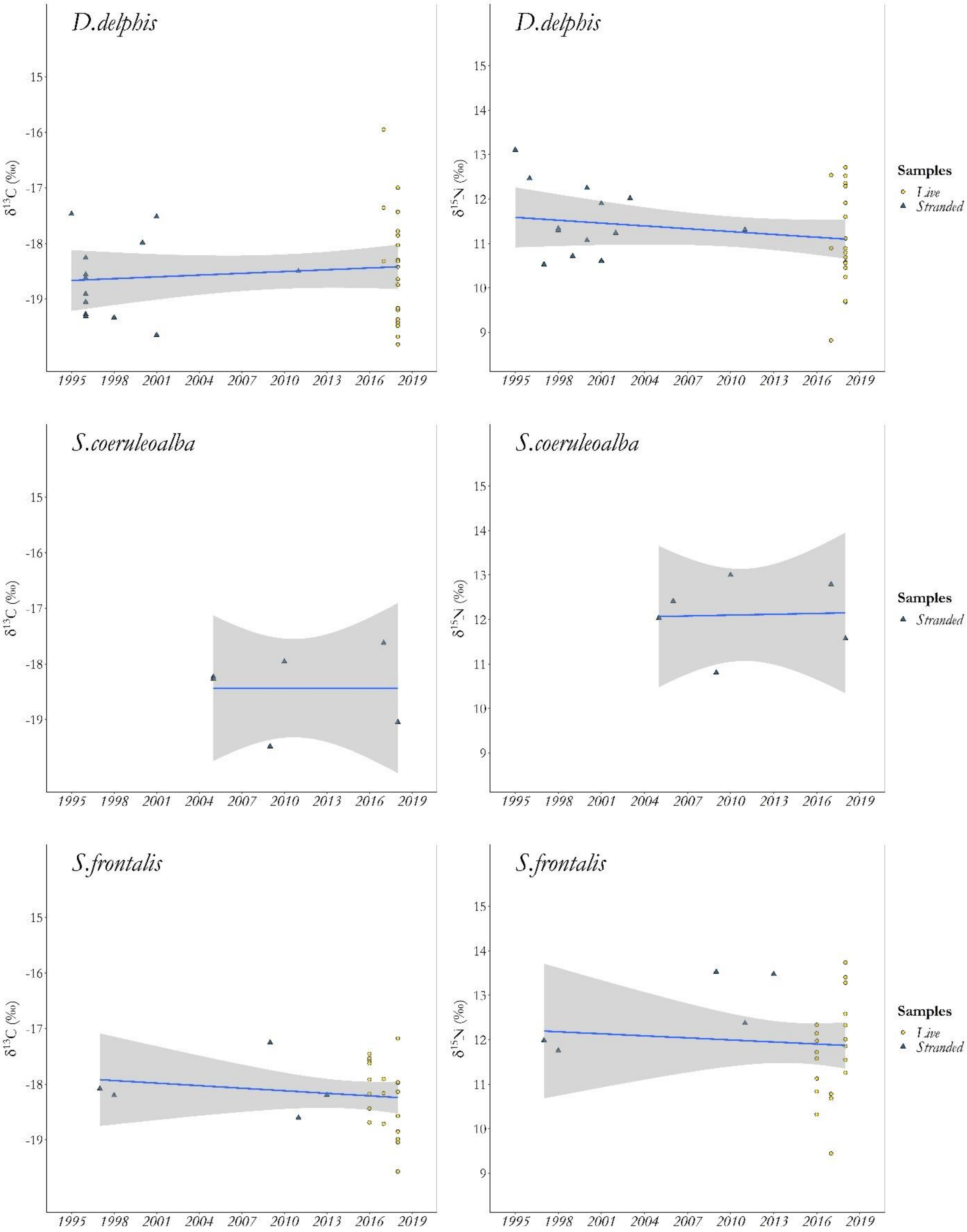


Figure VI.1.4-1. Carbon (δ13C, left) and nitrogen (δ15N, right) isotope ratio values of live and stranded animals over the study period, and respective linear regression line, including 95% confidence intervals, for common dolphin (*D. delphis*), striped dolphin (*S. coeruleoalba*) and Atlantic spotted dolphin (*S. frontalis*), for which there are historical samples from strandings.

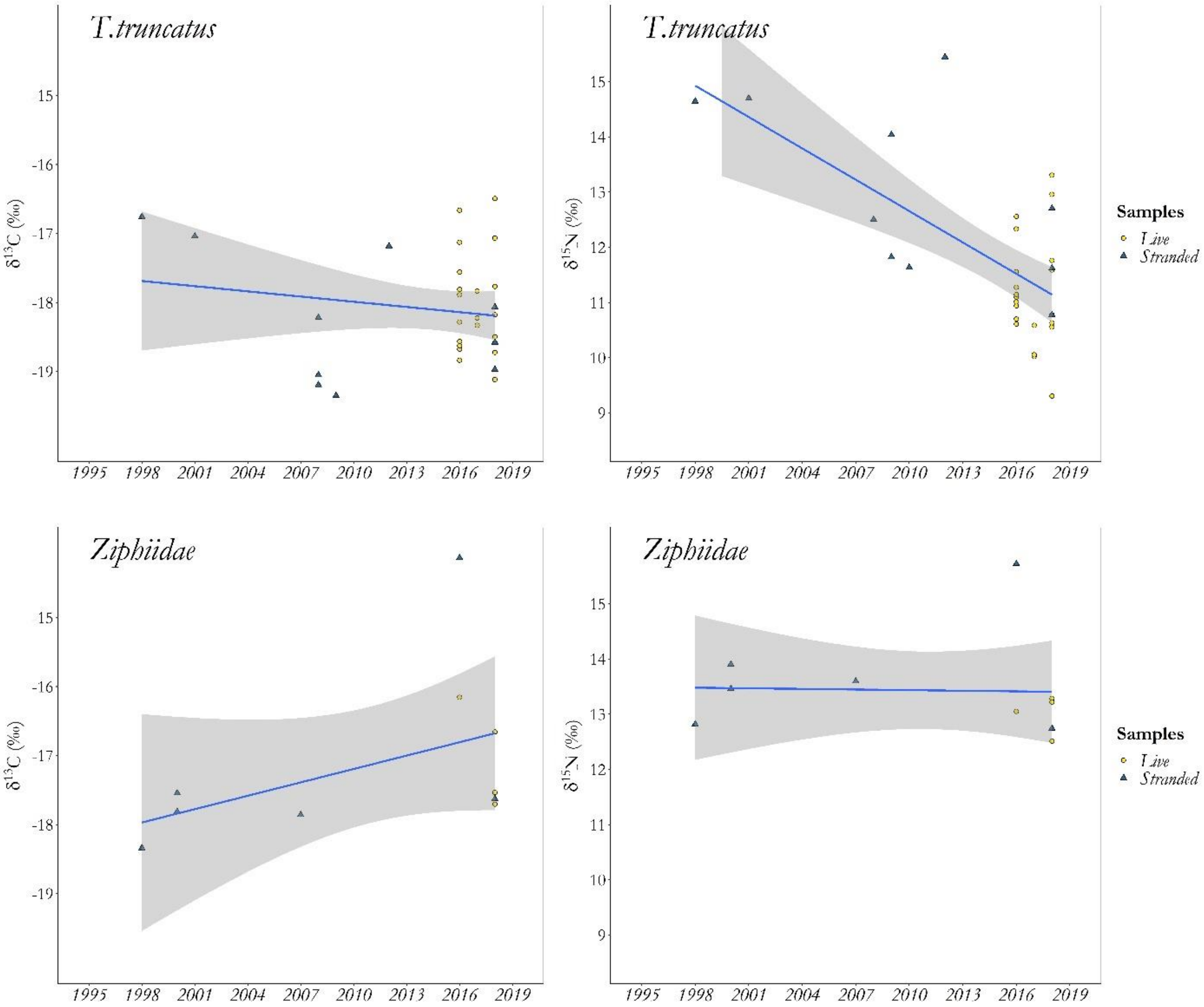


Figure VI.1.4-2. Carbon (δ13C, left) and nitrogen (δ15N, right) isotope ratio values of live and stranded animals over the study period, and respective linear regression line, including 95% confidence intervals, for bottlenose dolphin (*T. truncatus*) and beaked whales (Ziphiidae), for which there are historical samples from strandings.

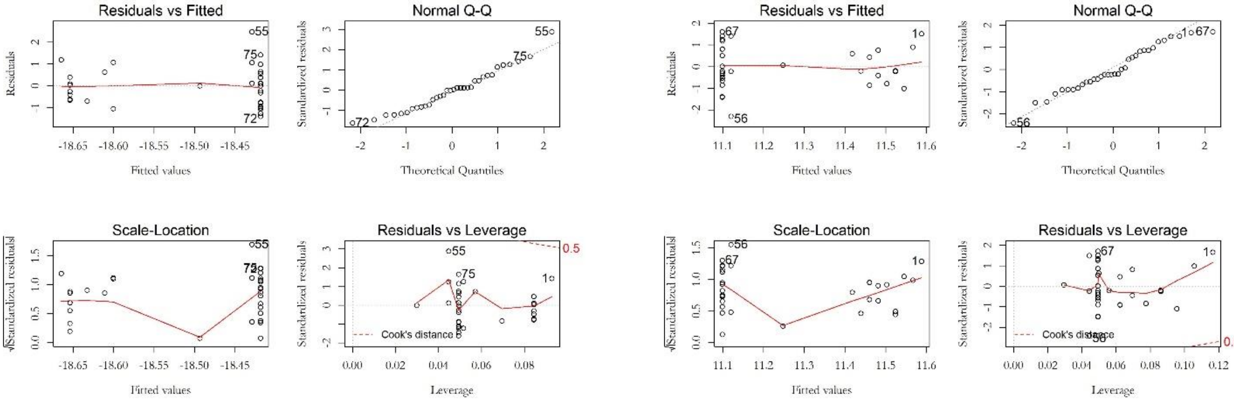
Table VI.1.4-1. Results of the linear regressions of δ13C and δ15N over the study period (years) for species with biopsy samples covering more than 3 years; $p < 0.05$ in bold.

Isotope	Species	Parameter	Estimate	Std error	t value	p value	df	R^2	R^2 adj	F statistics
δ13C	*Delphinus delphis*	Intercept	-40.007	30.268	-1.322	0.196	32	0.016	-0.015	0.505
		slope	0.011	0.015	0.710	0.483				
	Stenella coeruleoalba	Intercept	-18.503	123.394	-0.150	0.888	4	0.000	-0.250	0.000
		slope	0.000	0.061	0.001	1.000				
	Stenella frontalis	Intercept	12.612	43.569	0.289	0.775	23	0.021	-0.021	0.500
		slope	-0.015	0.022	-0.707	0.487				
	Tursiops truncatus	Intercept	32.422	57.088	0.568	0.574	29	0.026	-0.007	0.783
		slope	-0.025	0.028	-0.885	0.383				
	Ziphiidae	Intercept	-147.084	89.620	-1.641	0.139	8	0.208	0.109	2.103
		slope	0.065	0.045	1.450	0.185				
δ15N	*Delphinus delphis*	Intercept	54.005	37.054	1.457	0.155	32	0.040	0.010	1.331
		slope	-0.021	0.018	-1.154	0.257				
	Stenella coeruleoalba	Intercept	-0.664	149.519	-0.004	0.997	4	0.002	-0.248	0.007
		slope	0.006	0.074	0.085	0.936				
	Stenella frontalis	Intercept	42.780	79.188	0.540	0.594	23	0.007	-0.037	0.152
		slope	-0.015	0.039	-0.390	0.700				
	Tursiops truncatus	Intercept	393.069	83.323	4.717	0.000	29	0.419	0.399	20.942
		slope	-0.189	0.041	-4.576	**0.000**				
	Ziphiidae	Intercept	20.821	74.550	0.279	0.787	8	0.001	-0.124	0.010
		slope	-0.004	0.037	-0.099	0.923				

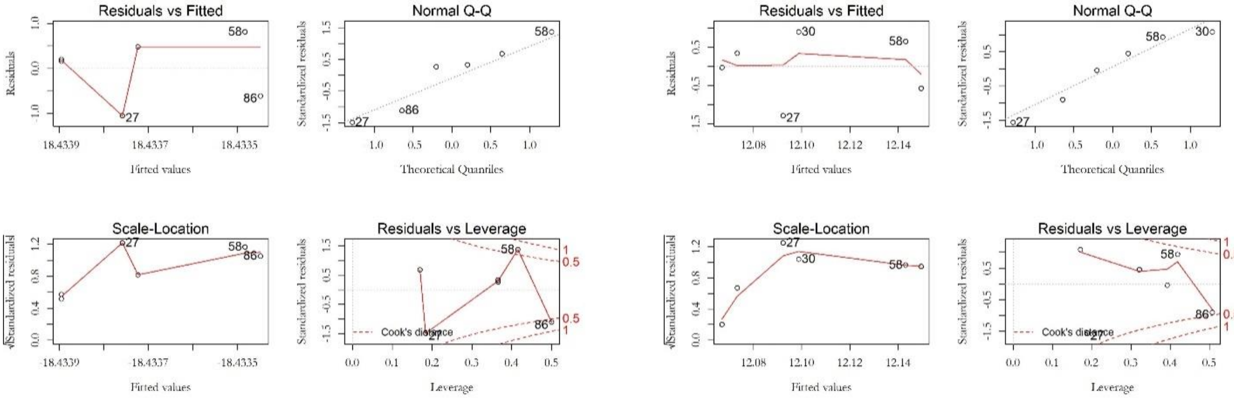
Table VI.1.4-2. Results of the linear regressions of δ13C and δ15N within-year (months) for all species sampled, including both samples from live and stranded animals; $p < 0.05$ in bold.

Isotope	Species	Parameter	Estimate	Std error	t value	p value	df	R^2	R^2 adj	F statistics
δ13C	*Balaenoptera edeni*	Intercept	-18.985	1.049	-18.103	0.000	9	0.012	-0.098	0.111
		slope	0.039	0.118	0.333	0.747				
	Delphinus delphis	Intercept	-19.319	0.280	-69.121	0.000	32	0.268	0.245	11.723
		slope	0.227	0.066	3.424	**0.002**				
	Stenella coeruleoalba	Intercept	-18.678	1.017	-18.366	0.000	4	0.016	-0.230	0.064
		slope	0.049	0.193	0.252	0.813				
	Stenella frontalis	Intercept	-18.108	0.365	-49.596	0.000	23	0.002	-0.041	0.055
		slope	-0.012	0.050	-0.235	0.816				
	Tursiops truncatus	Intercept	-18.288	0.308	-59.374	0.000	29	0.015	-0.018	0.455
		slope	0.035	0.052	0.675	0.505				
	Globicephala macrorhynchus	Intercept	-17.673	0.281	-62.803	0.000	18	0.399	0.366	11.973
		slope	0.173	0.050	3.460	**0.003**				
	Physeter macrocephalus	Intercept	-18.717	0.888	-21.077	0.000	7	0.114	-0.012	0.904
		slope	0.094	0.099	0.951	0.373				
	Ziphiidae	Intercept	-18.057	0.894	-20.194	0.000	8	0.140	0.032	1.298
		slope	0.162	0.142	1.139	0.288				
δ15N	*Balaenoptera edeni*	Intercept	13.055	1.638	7.968	0.000	9	0.322	0.246	4.269
		slope	-0.381	0.185	-2.066	0.069				
	Delphinus delphis	Intercept	11.180	0.359	31.162	0.000	32	0.002	-0.029	0.060
		slope	0.021	0.085	0.245	0.808				
	Stenella coeruleoalba	Intercept	11.961	1.200	9.971	0.001	4	0.004	-0.245	0.016
		slope	0.029	0.228	0.126	0.906				
	Stenella frontalis	Intercept	13.238	0.592	22.360	0.000	23	0.194	0.159	5.537
		slope	-0.190	0.081	-2.353	**0.028**				
	Tursiops truncatus	Intercept	12.533	0.550	22.772	0.000	29	0.079	0.048	2.497
		slope	-0.147	0.093	-1.580	0.125				
	Globicephala macrorhynchus	Intercept	13.454	0.204	65.821	0.000	18	0.336	0.299	9.088
		slope	-0.110	0.036	-3.015	**0.007**				
	Physeter macrocephalus	Intercept	11.619	1.185	9.806	0.000	7	0.213	0.101	1.898
		slope	0.182	0.132	1.378	0.211				
	Ziphiidae	Intercept	13.229	0.710	18.643	0.000	8	0.012	-0.111	0.101
		slope	0.036	0.113	0.318	0.759				

Common dolphin



Striped dolphin



Atlantic Spotted dolphin

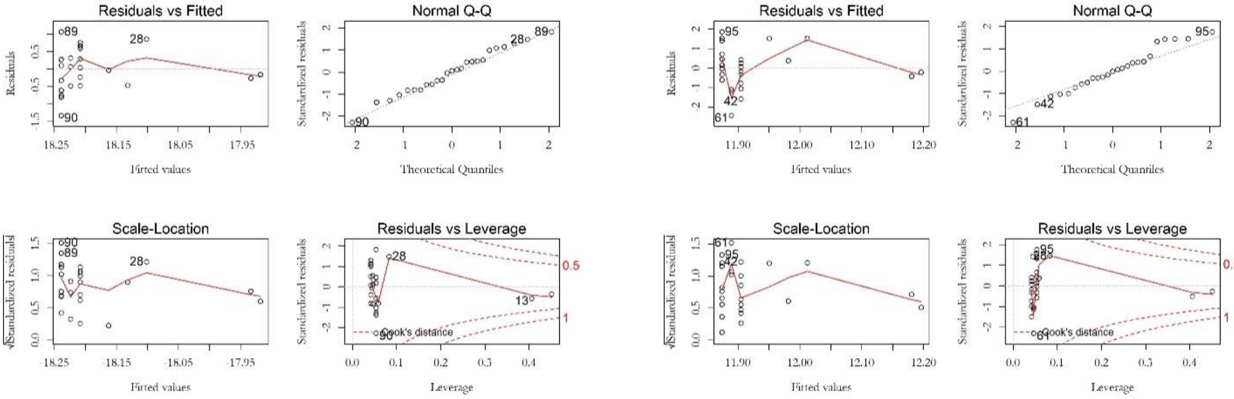
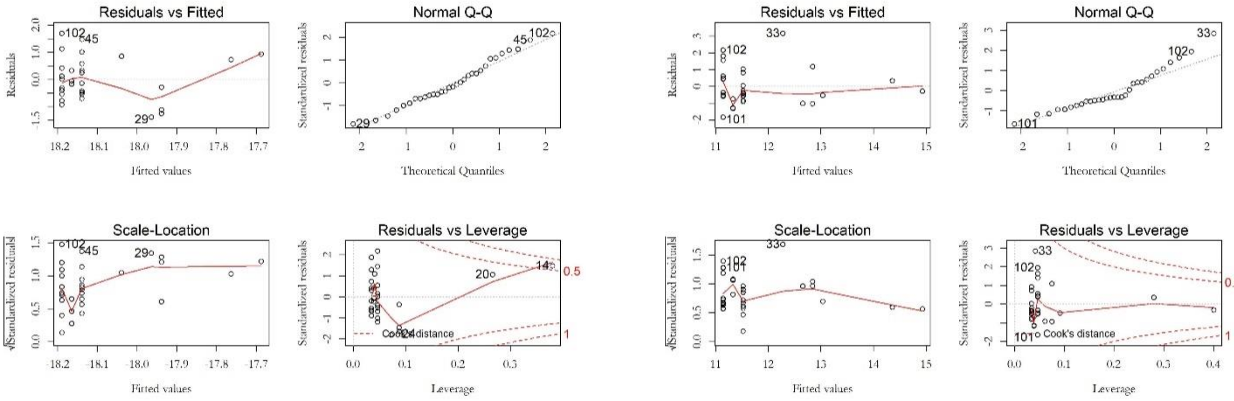


Figure VI.1.4-3. Diagnostic plots of the linear regression of carbon (δ13C, left) and nitrogen (δ15N, right) isotope ratio values over the study period (1995-2018), for common dolphin (*D. delphis*), striped dolphin (*S. coeruleoalba*) and Atlantic spotted dolphin (*S. frontalis*), for which there are historical samples from strandings.

Bottlenose dolphin



Beaked whales

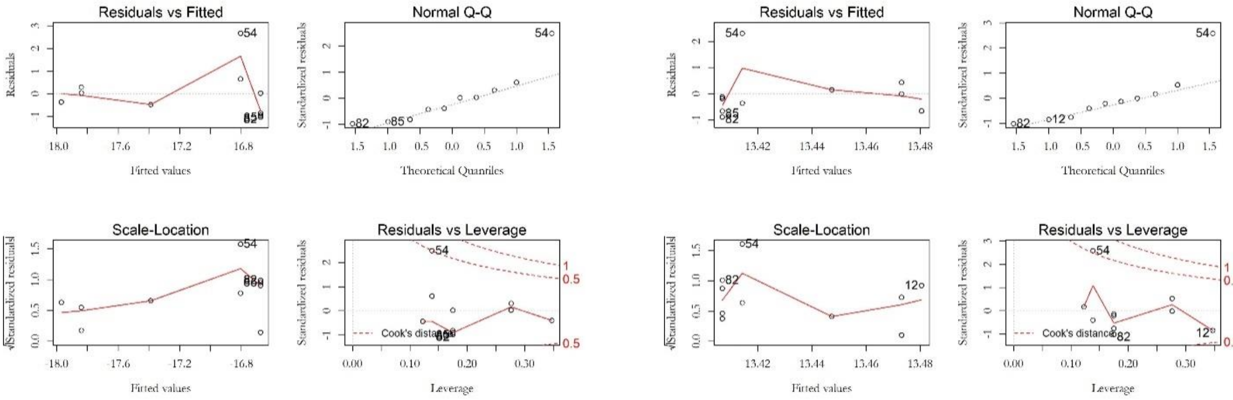
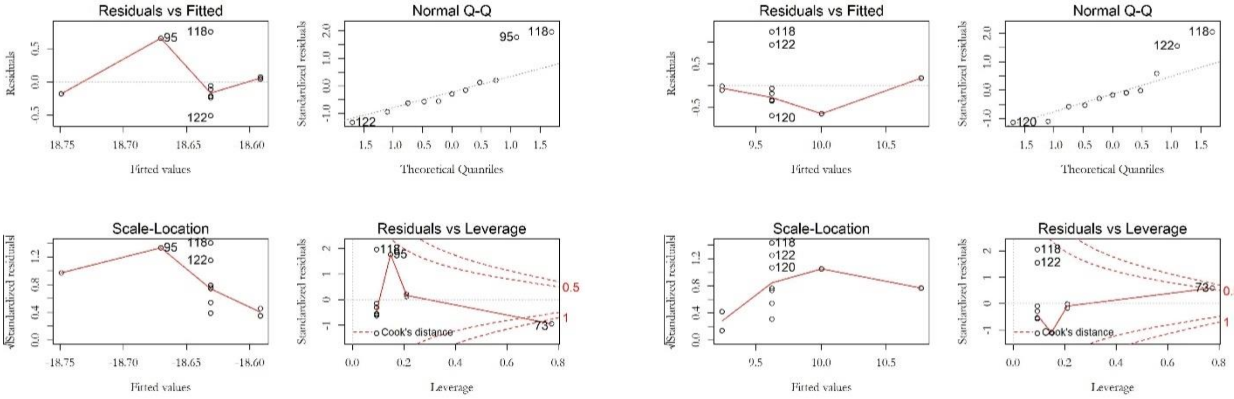
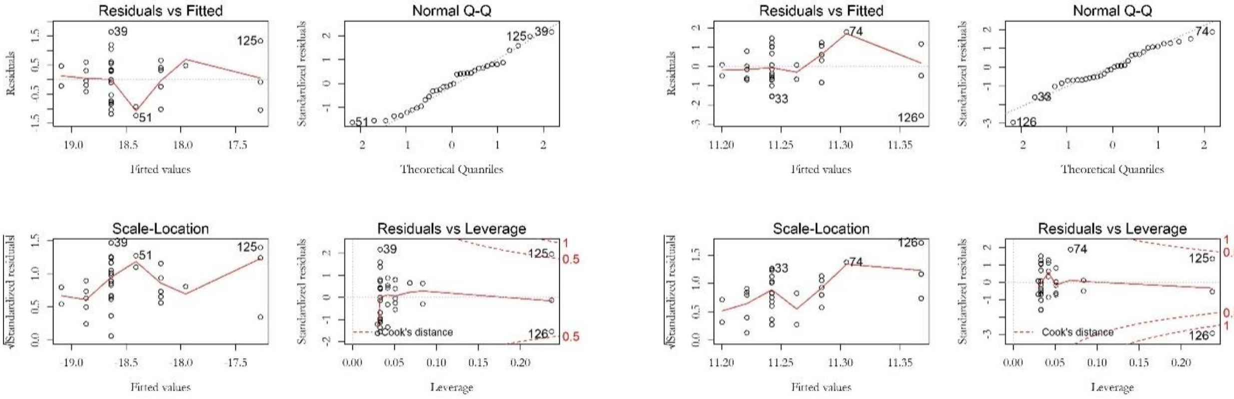


Figure VI.1.4-4. Diagnostic plots of the linear regression of carbon (δ13C, left) and nitrogen (δ15N, right) isotope ratio values over the study period (1995-2018), for bottlenose dolphin (*T. truncatus*) and beaked whales (Ziphiidae), for which there are historical samples from strandings.

Bryde's whale



Common dolphin



Striped dolphin

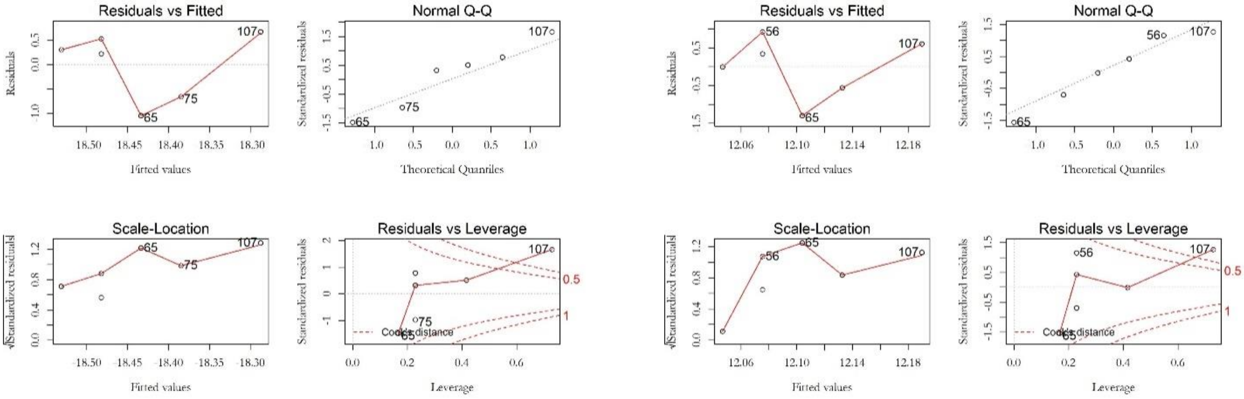
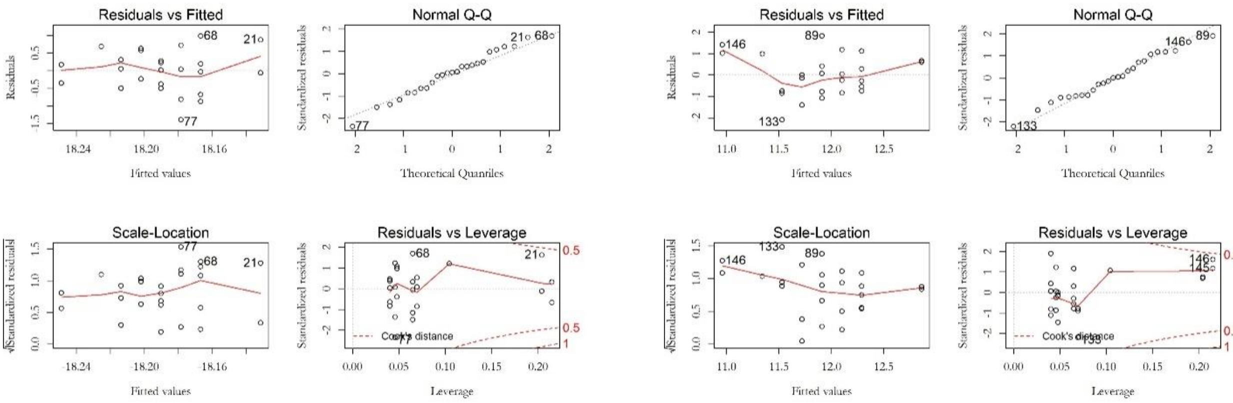


Figure VI.1.4-5. Diagnostic plots of the linear regression of carbon (δ13C, left) and nitrogen (δ15N, right) isotope ratio values over the year, for Bryde's whale (*B. edeni*), common dolphin (*D. delphis*) and striped dolphin (*S. coeruleoalba*).

Atlantic spotted dolphin



Bottlenose dolphin

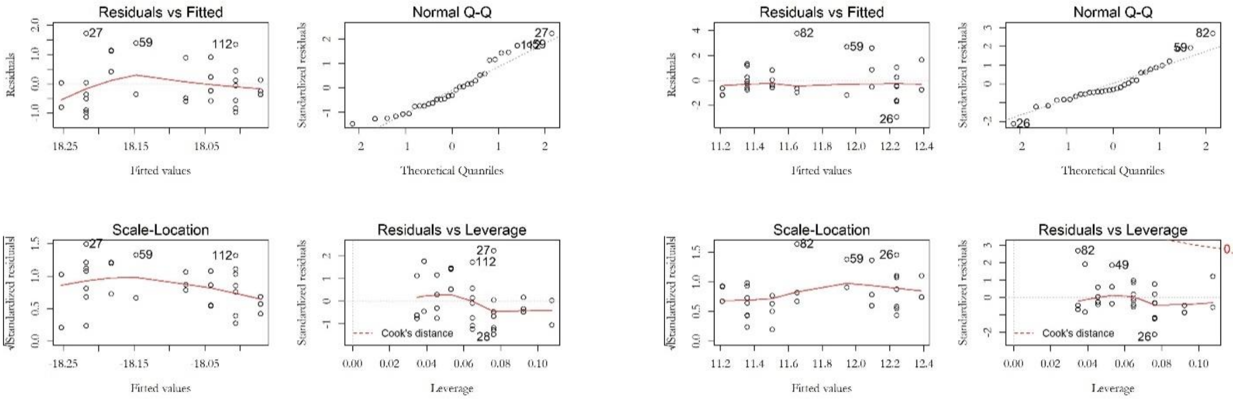
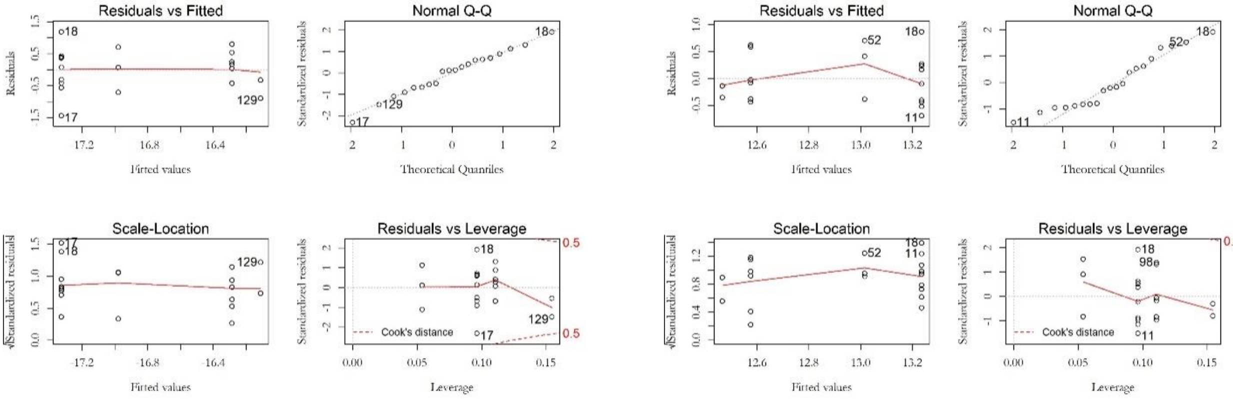
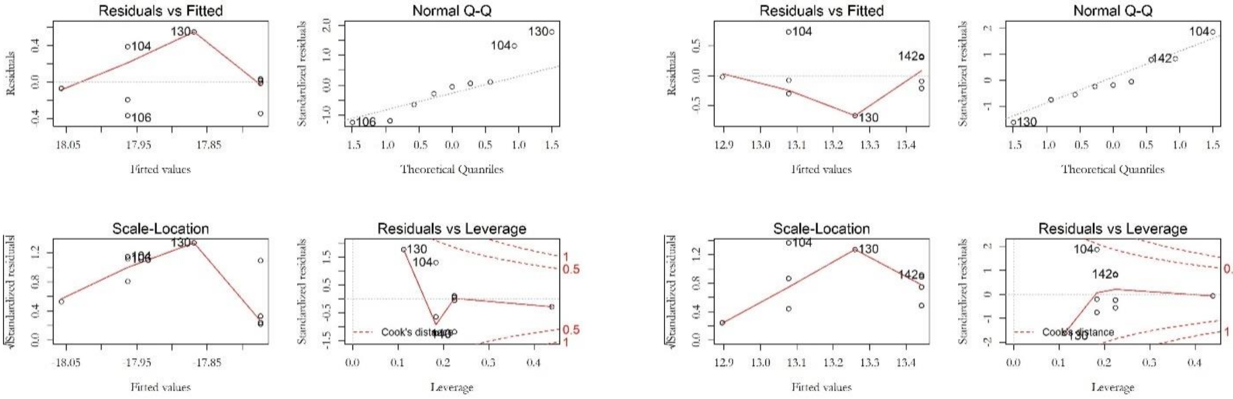


Figure VI.1.4-6. Diagnostic plots of the linear regression of carbon (δ13C, left) and nitrogen (δ15N, right) isotope ratio values over the year, for Atlantic spotted dolphin (*S. frontalis*) and bottlenose dolphin (*T. truncatus*).

Short-finned pilot whale



Sperm whale



Ziphiidae

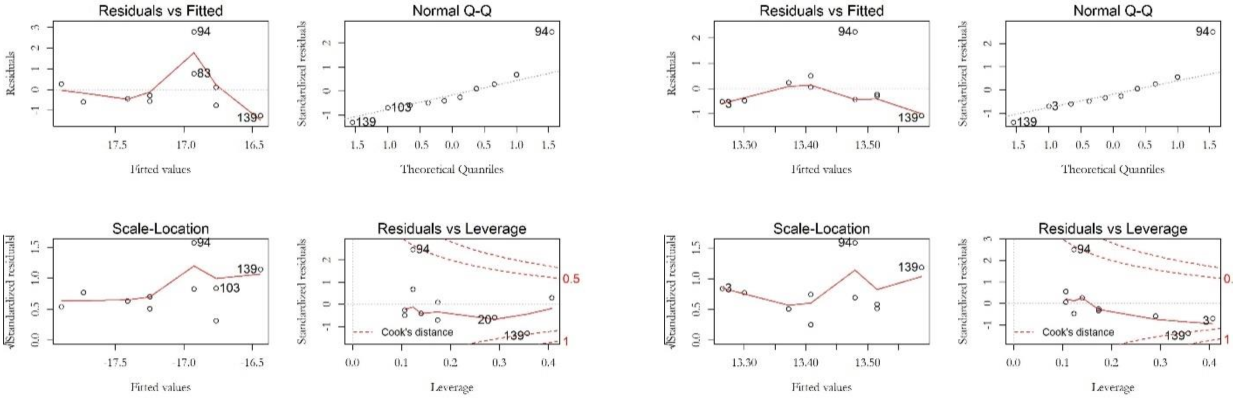


Figure VI.1.4-7. Diagnostic plots of the linear regression of carbon (δ13C, left) and nitrogen (δ15N, right) isotope ratio values over the year, for short-finned pilot whale (*Globicephala macrorhynchus*), sperm whale (*P. macrocephalus*) and beaked whales (Ziphiidae).

VI.2. Within-year temporal niche overlap

VI.2.1 Within-year temporal overlap plots

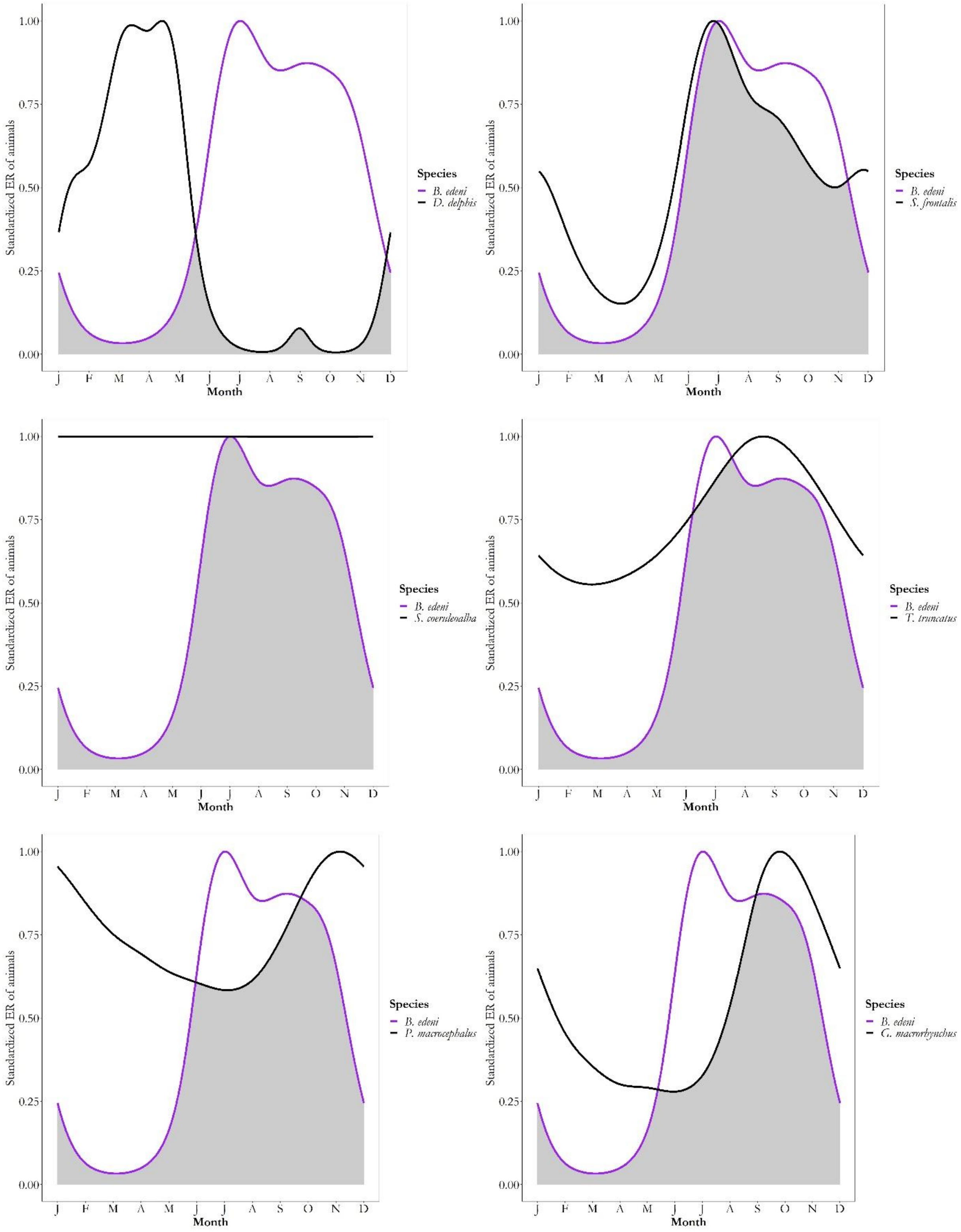


Figure VI.2.1-1. Standardized within-year temporal distribution, and respective proportion of temporal overlap, of the cetacean species with an isotopic niche overlap < 0.3. The temporal overlap of the species is represented by the grey area under the curve.

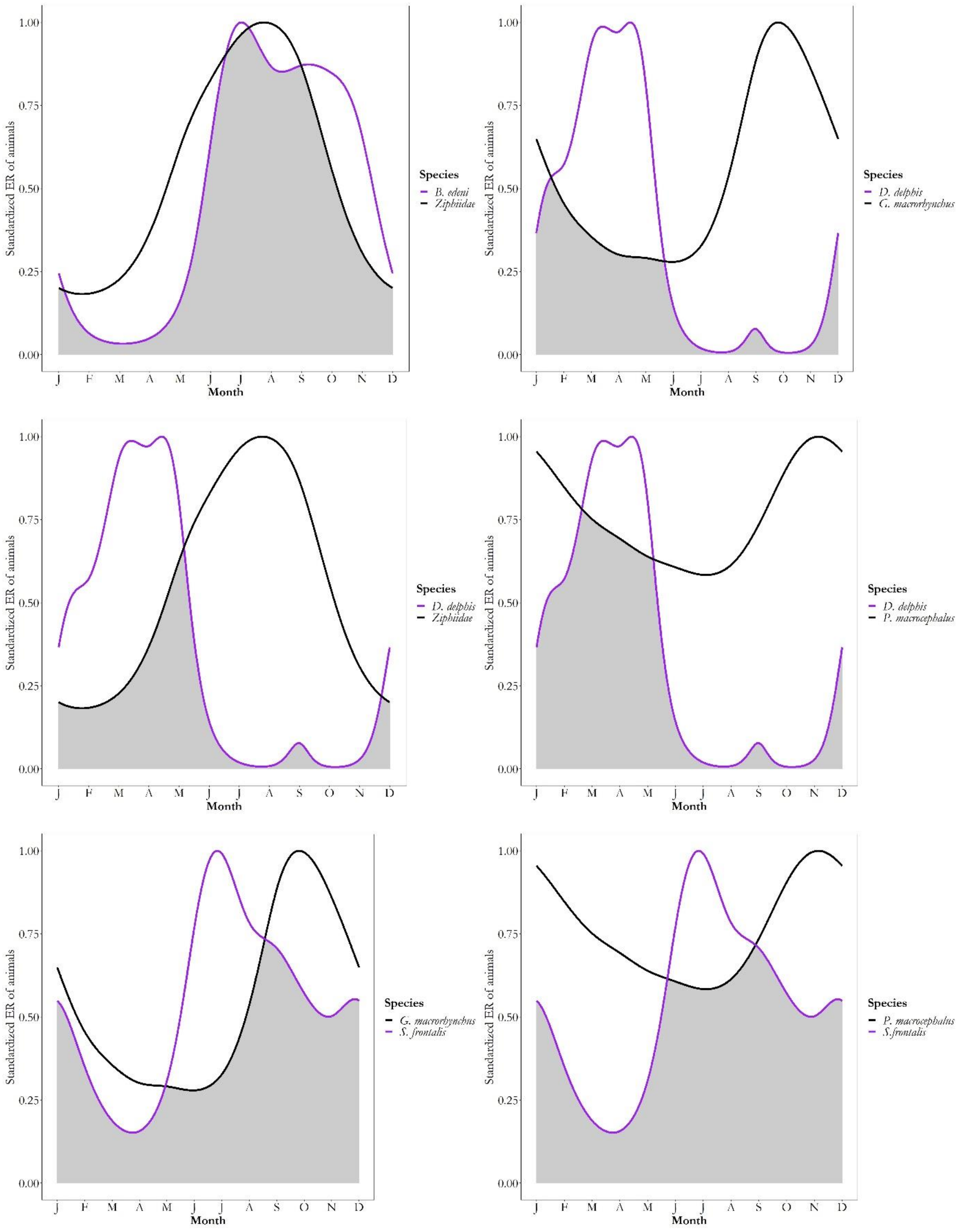


Figure VI.2.1-2. Standardized within-year temporal distribution, and respective proportion of temporal overlap, of the cetacean species with an isotopic niche overlap < 0.3 (continuation). The temporal overlap of the species is represented by the grey area under the curve.

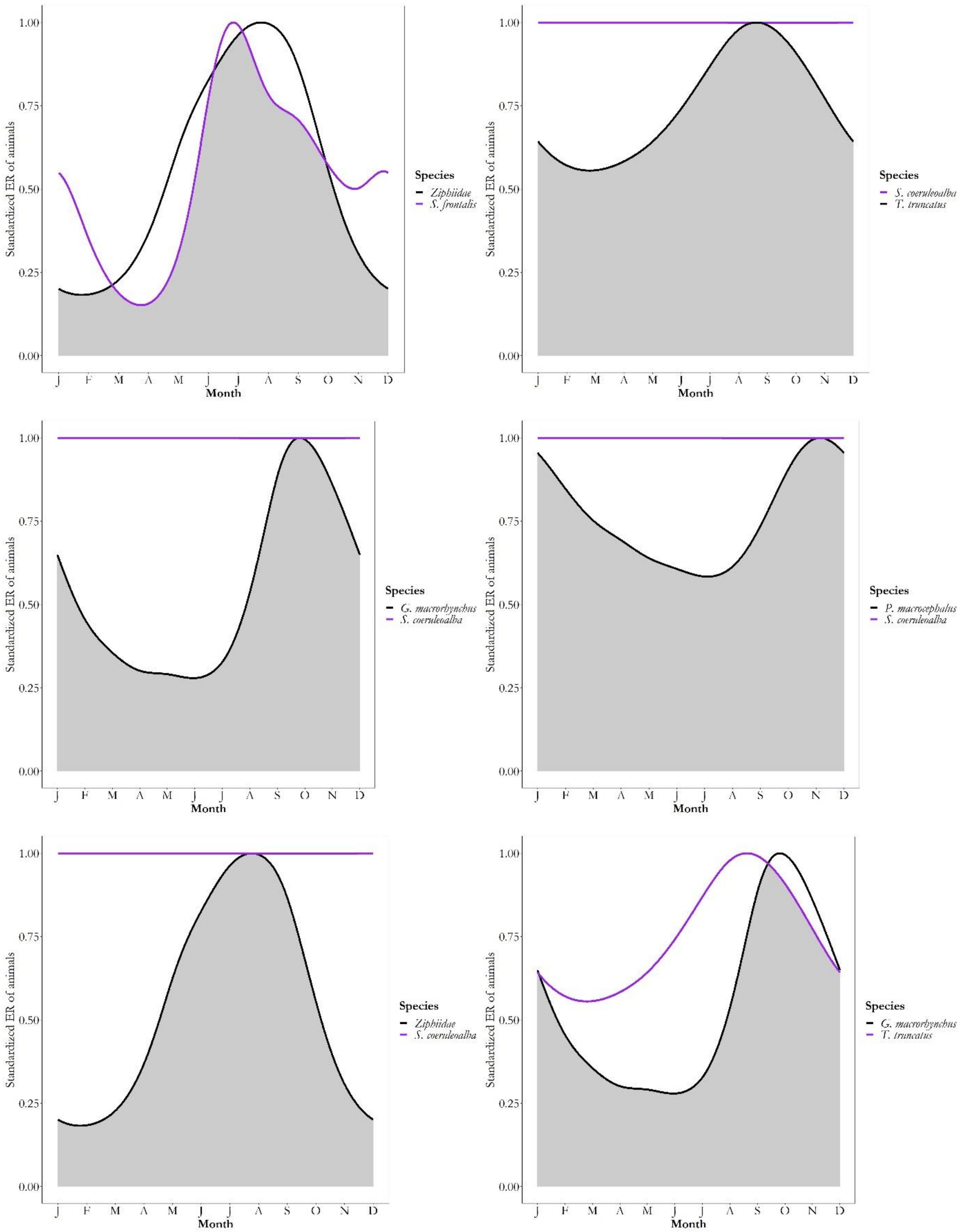


Figure VI.2.1-3. Standardized within-year temporal distribution, and respective proportion of temporal overlap, of the cetacean species with an isotopic niche overlap < 0.3 (continuation). The temporal overlap of the species is represented by the grey area under the curve.

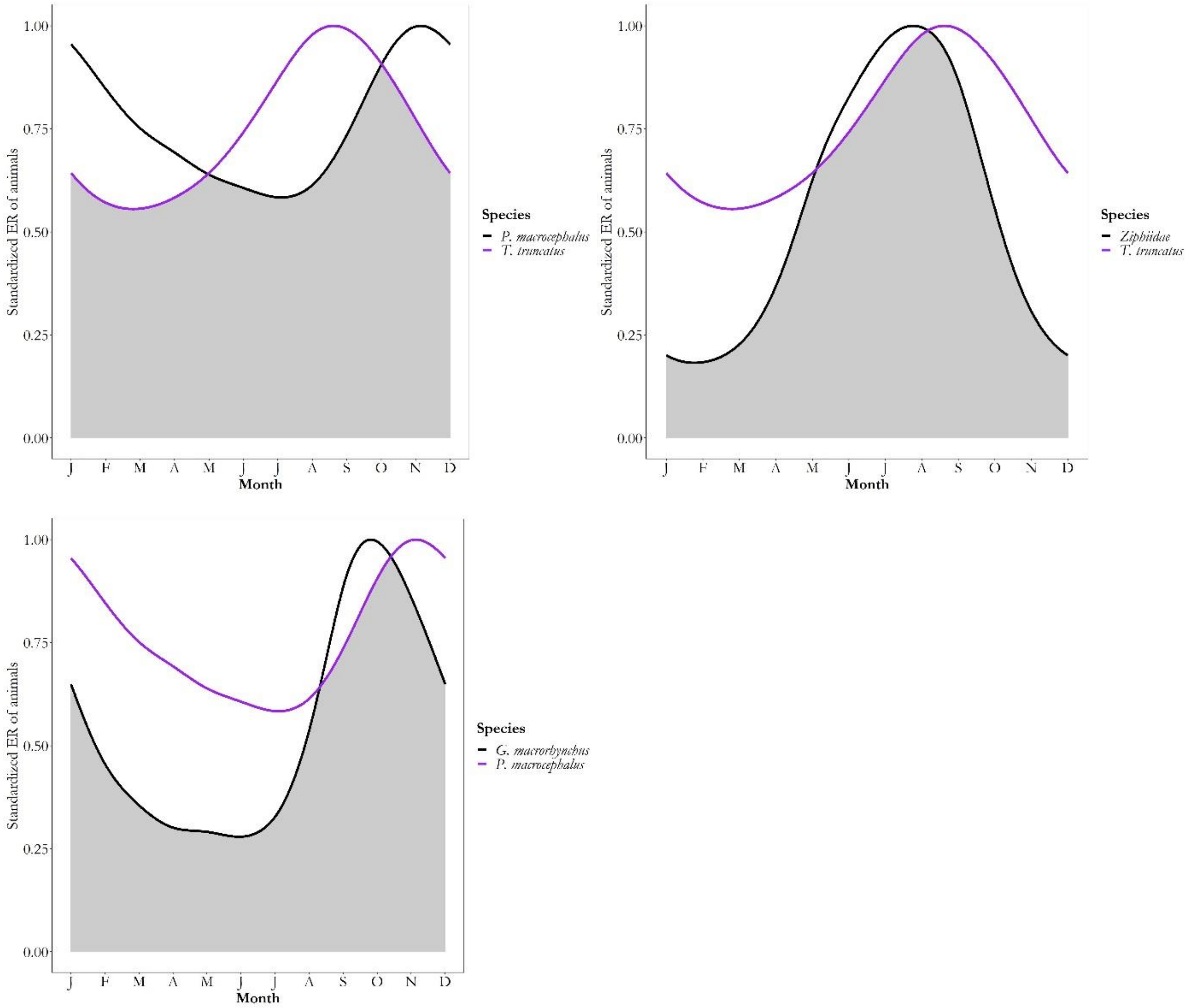


Figure VI.2.1-4. Standardized within-year temporal distribution, and respective proportion of temporal overlap, of the cetacean species with an isotopic niche overlap < 0.3 (continuation). The temporal overlap of the species is represented by the grey area under the curve.

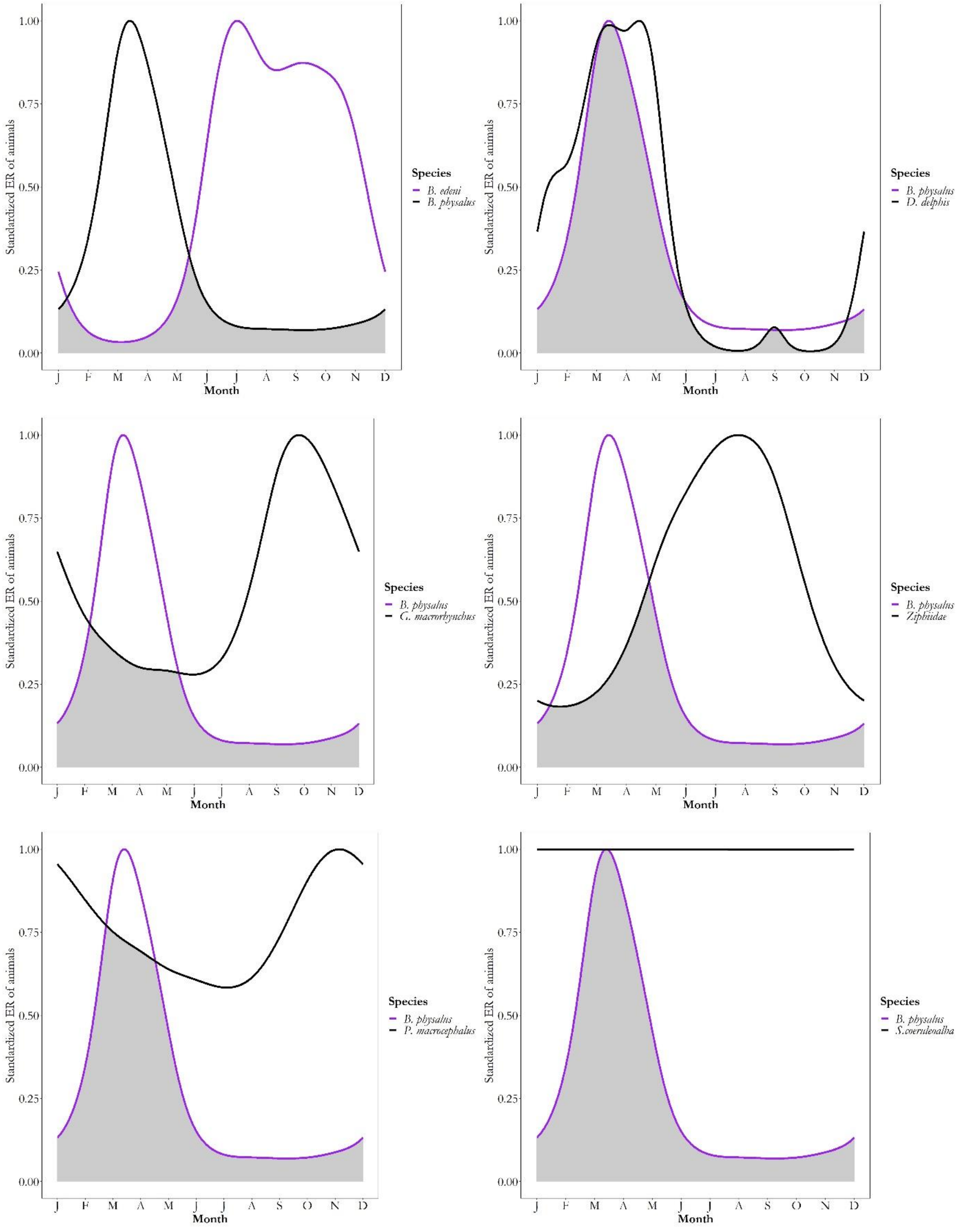


Figure VI.2.1-5. Standardized within-year temporal distribution, and respective proportion of temporal overlap, of the fin whale (*Balaenoptera physalus*) with the remaining cetacean species. The temporal overlap of the species is represented by the grey area under the curve.

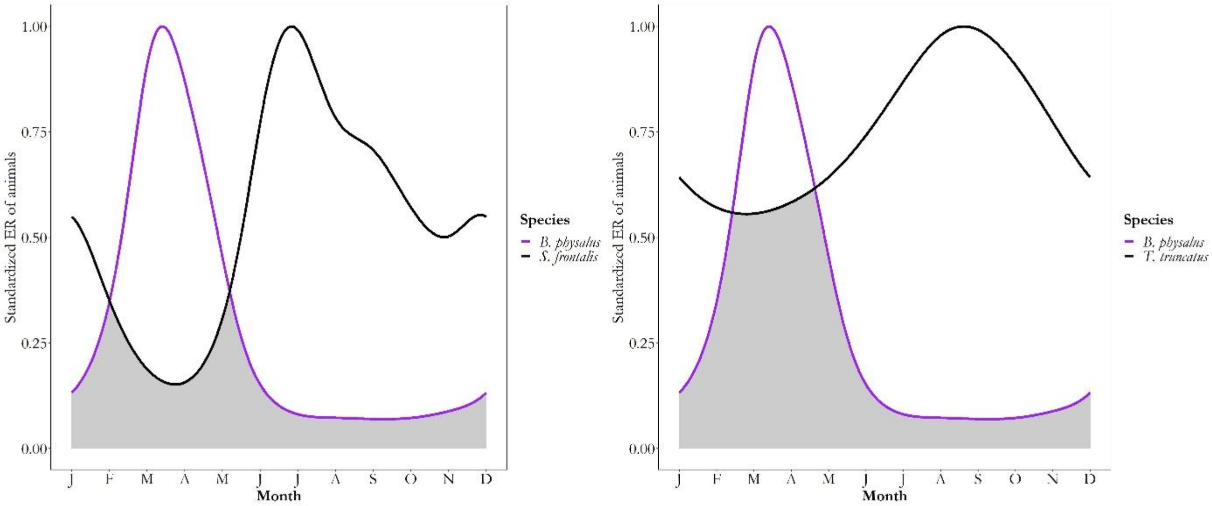


Figure VI.2.1-6. Standardized within-year temporal distribution, and respective proportion of temporal overlap, of the fin whale (*Balaenoptera physalus*) with the remaining cetacean species (continuation). The temporal overlap of the species is represented by the grey area under the curve.

VI.3. Spatial niches overlap

VI.3.1. Maps of relative abundance distribution and respective overlap

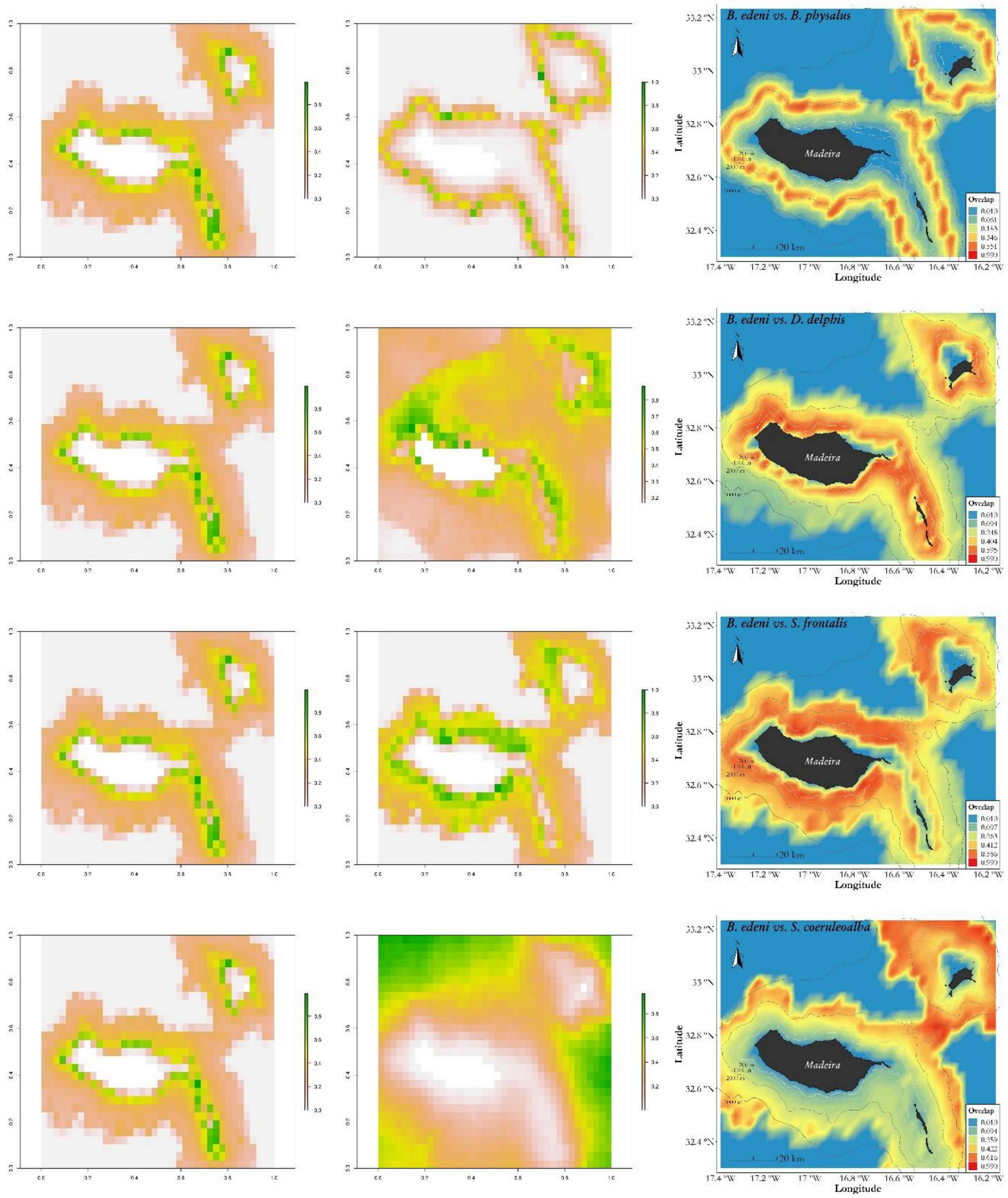


Figure VI.3.1-1. Standardized relative abundance prediction maps of Bryde's whale (*B. edeni*; left) and other cetacean taxa (centre), and the respective overlap map (right). The taxa identifications are given on the top of the corresponding overlap map.

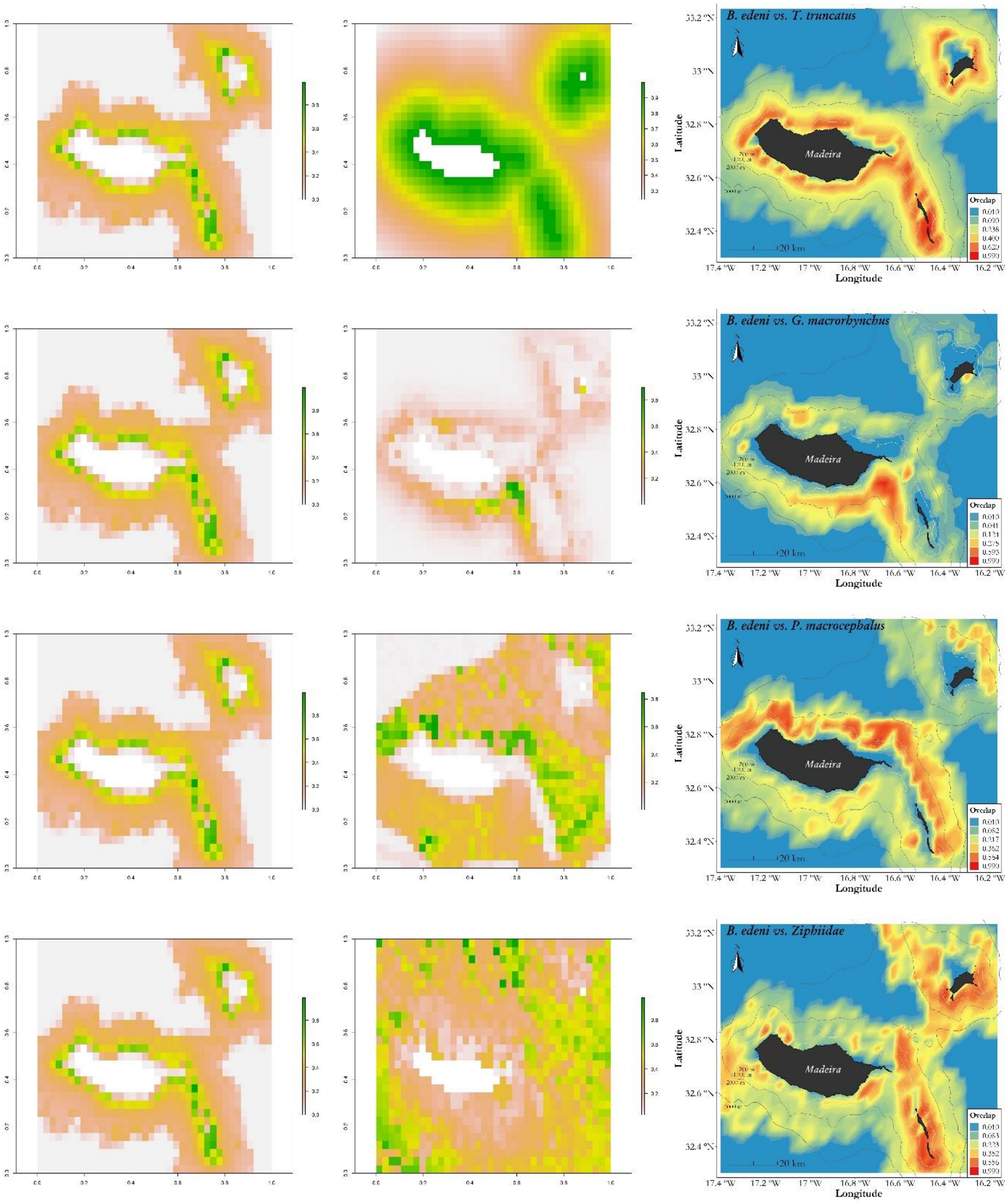


Figure VI.3.1-2. Standardized relative abundance prediction maps of Bryde's whale (*B. edeni*; left) and other cetacean taxa (centre), and the respective overlap map (right). The taxa identifications are given on the top of the corresponding overlap map (continuation).

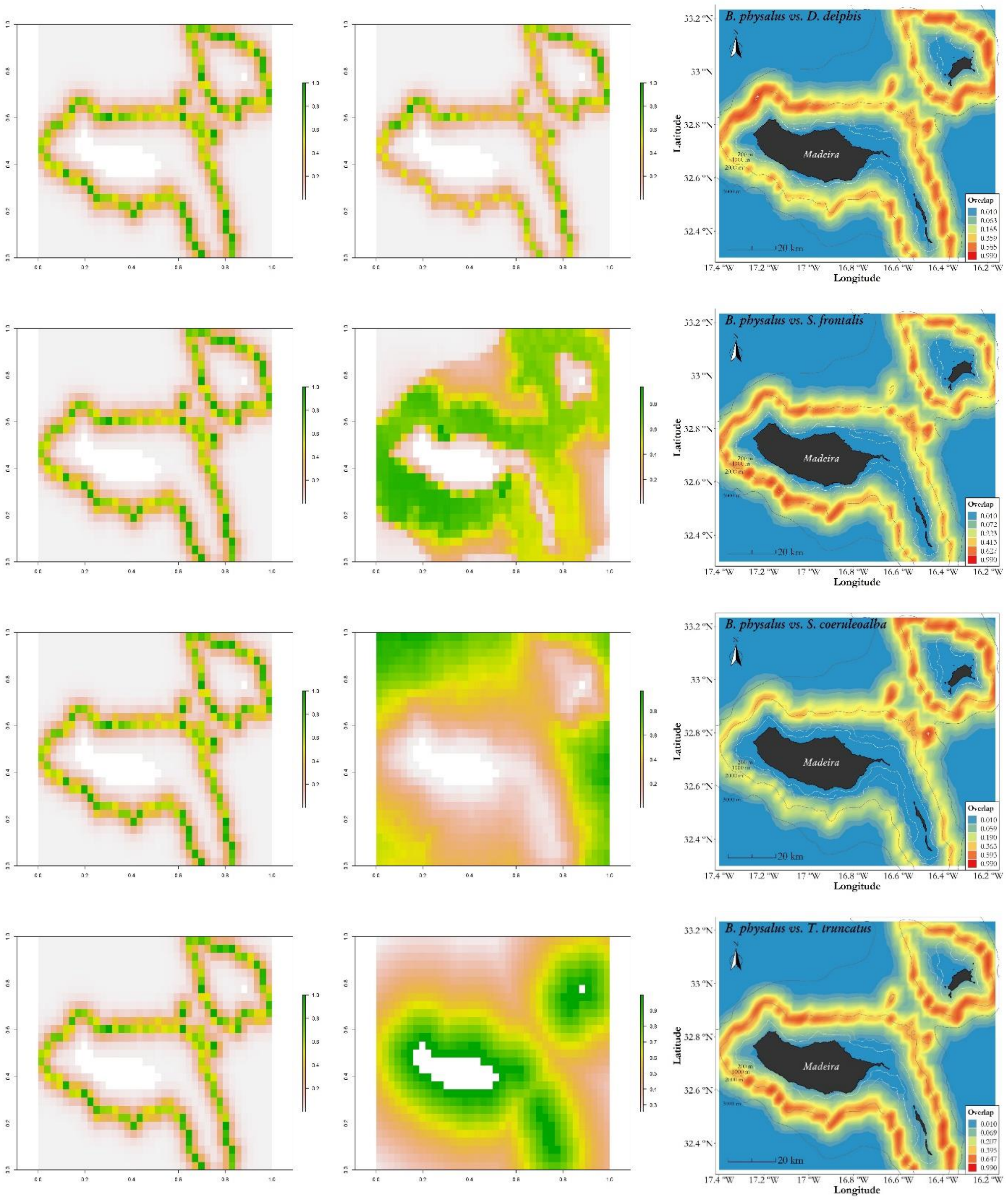


Figure VI.3.1-3. Standardized relative abundance prediction maps of fin whale (*B. physalus*; left) and other cetacean taxa (centre), and the respective overlap map (right). The taxa identifications are given on the top of the corresponding overlap map.

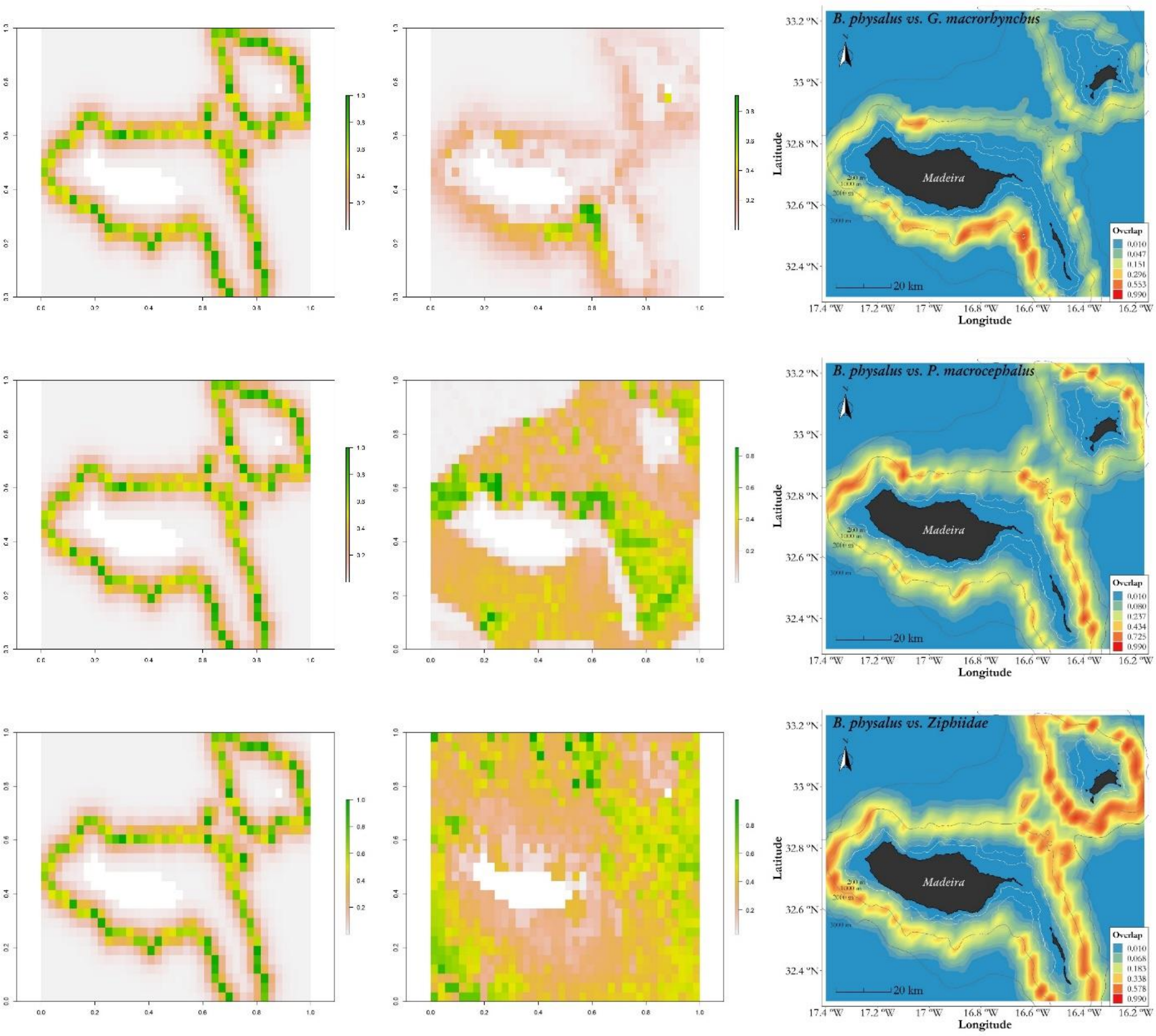


Figure VI.3.1-4. Standardized relative abundance prediction maps of fin whale (*B. physalus*; left) and other cetacean taxa (centre), and the respective overlap map (right). The taxa identifications are given on the top of the corresponding overlap map (continuation).

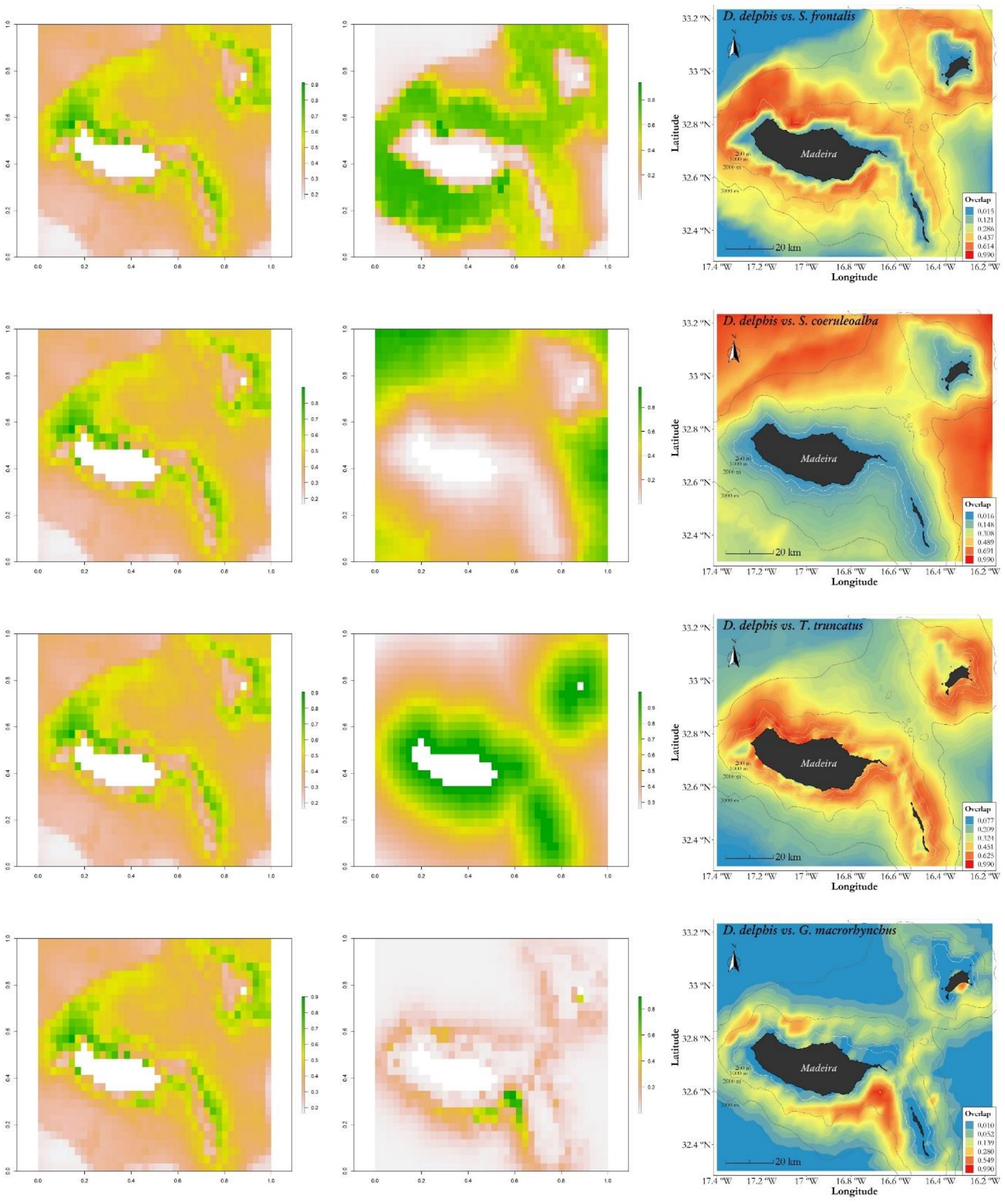


Figure VI.3.1-5. Standardized relative abundance prediction maps of common dolphin (*D. delphis*; left) and other cetacean taxa (centre), and the respective overlap map (right). The taxa identifications are given on the top of the corresponding overlap map.

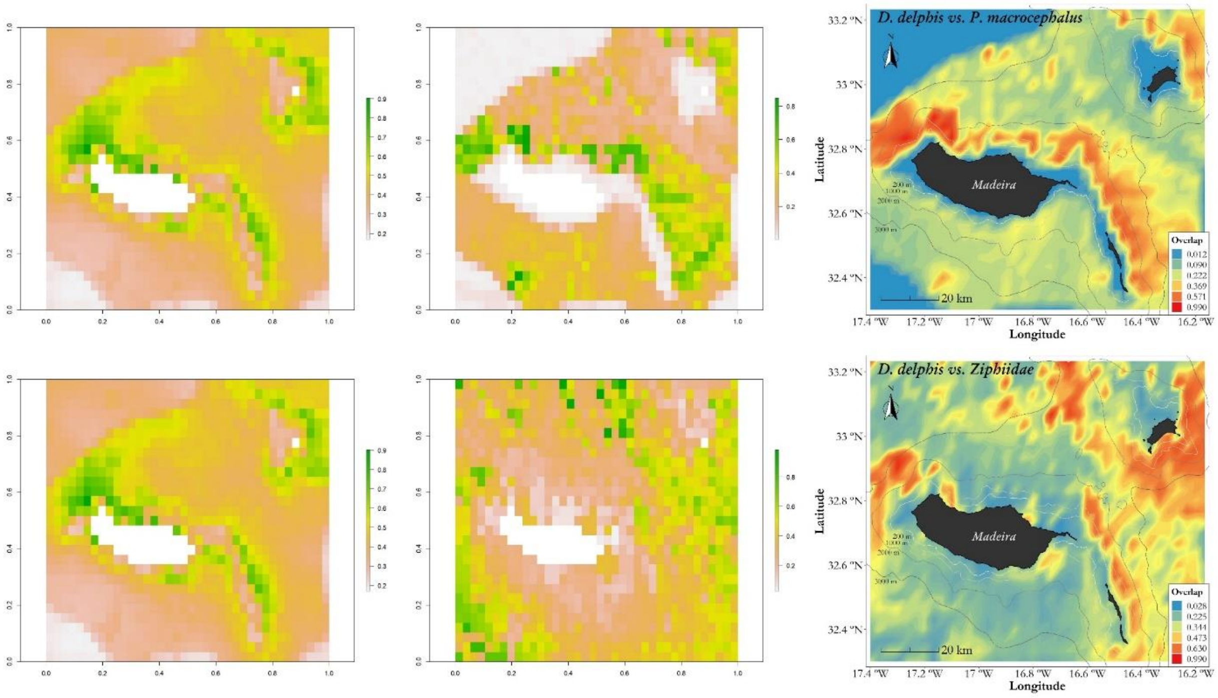
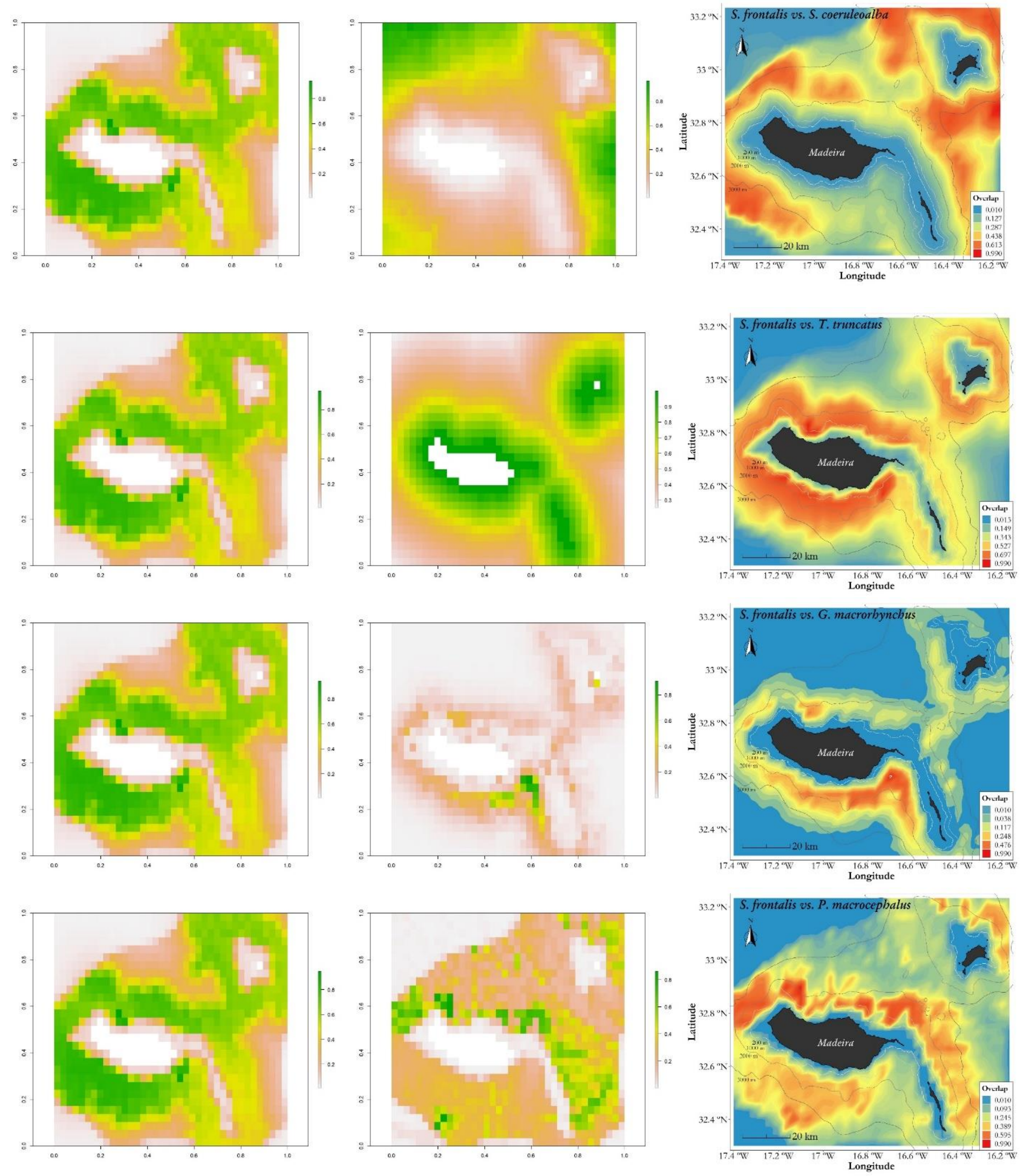


Figure VI.3.1-6. Standardized relative abundance prediction maps of common dolphin (*D. delphis*; left) and other cetacean taxa (centre), and the respective overlap map (right). The taxa identifications are given on the top of the corresponding overlap map (continuation).



S. frontalis vs. S. coeruleoalba

S. frontalis vs. T. truncatus

S. frontalis vs. G. macrorhynchus

S. frontalis vs. P. macrocephalus

Figure VI.3.1-7. Standardized relative abundance prediction maps of Atlantic spotted dolphin (*S. frontalis*; left) and other cetacean taxa (centre), and the respective overlap map (right). The taxa identifications are given on the top of the corresponding overlap map.

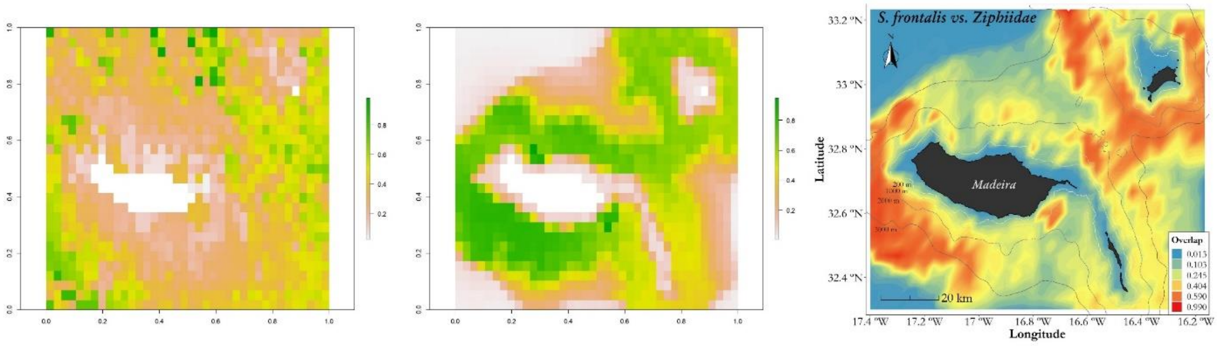


Figure VI.3.1-8. Standardized relative abundance prediction maps of Atlantic spotted dolphin (*S. frontalis*; left) and other cetacean taxa (centre), and the respective overlap map (right). The taxa identifications are given on the top of the corresponding overlap map (continuation).

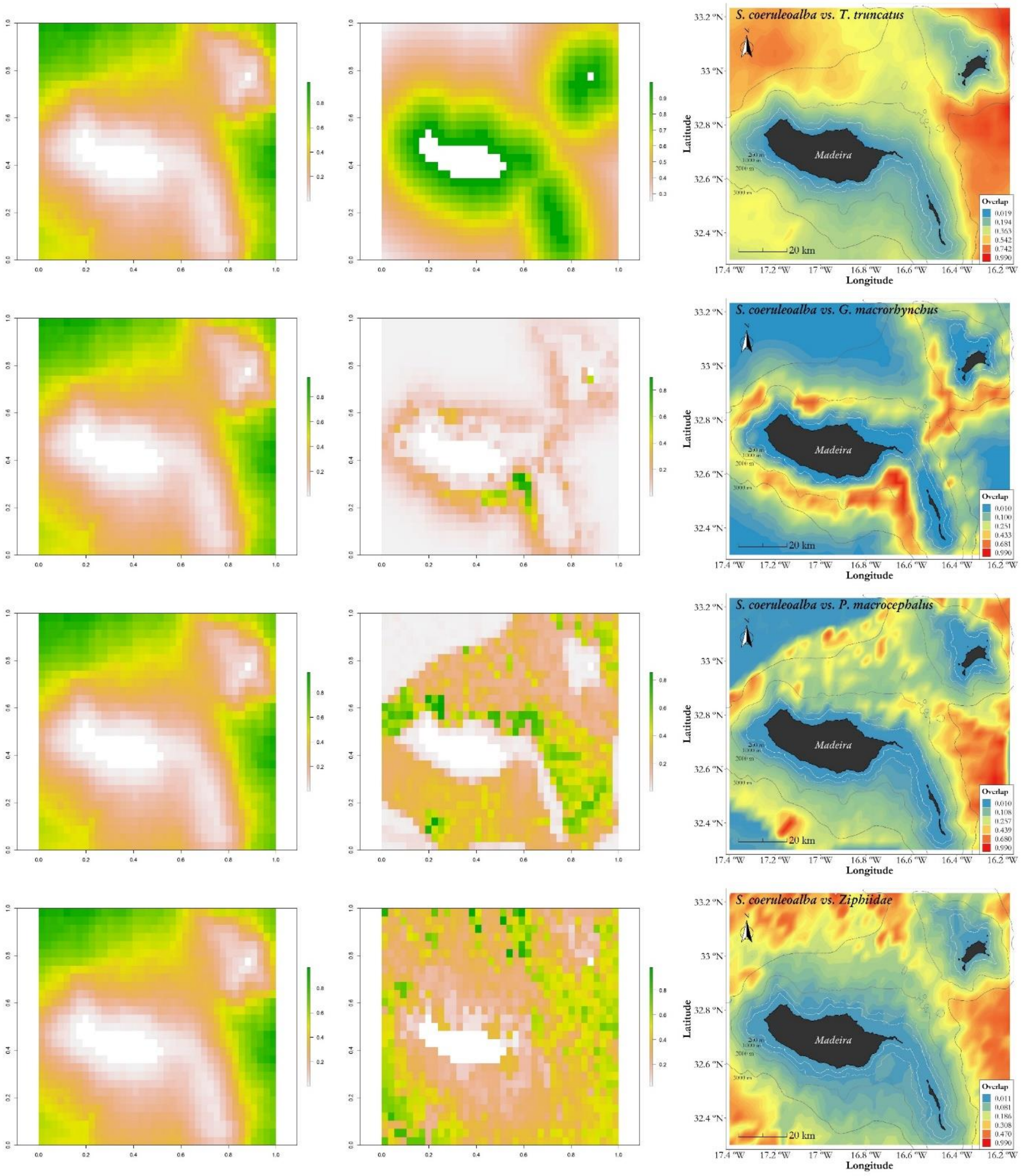


Figure VI.3.1-9. Standardized relative abundance prediction maps of striped dolphin (*S. coruleoalba*; left) and other cetacean taxa (centre), and the respective overlap map (right). The taxa identifications are given on the top of the corresponding overlap map.

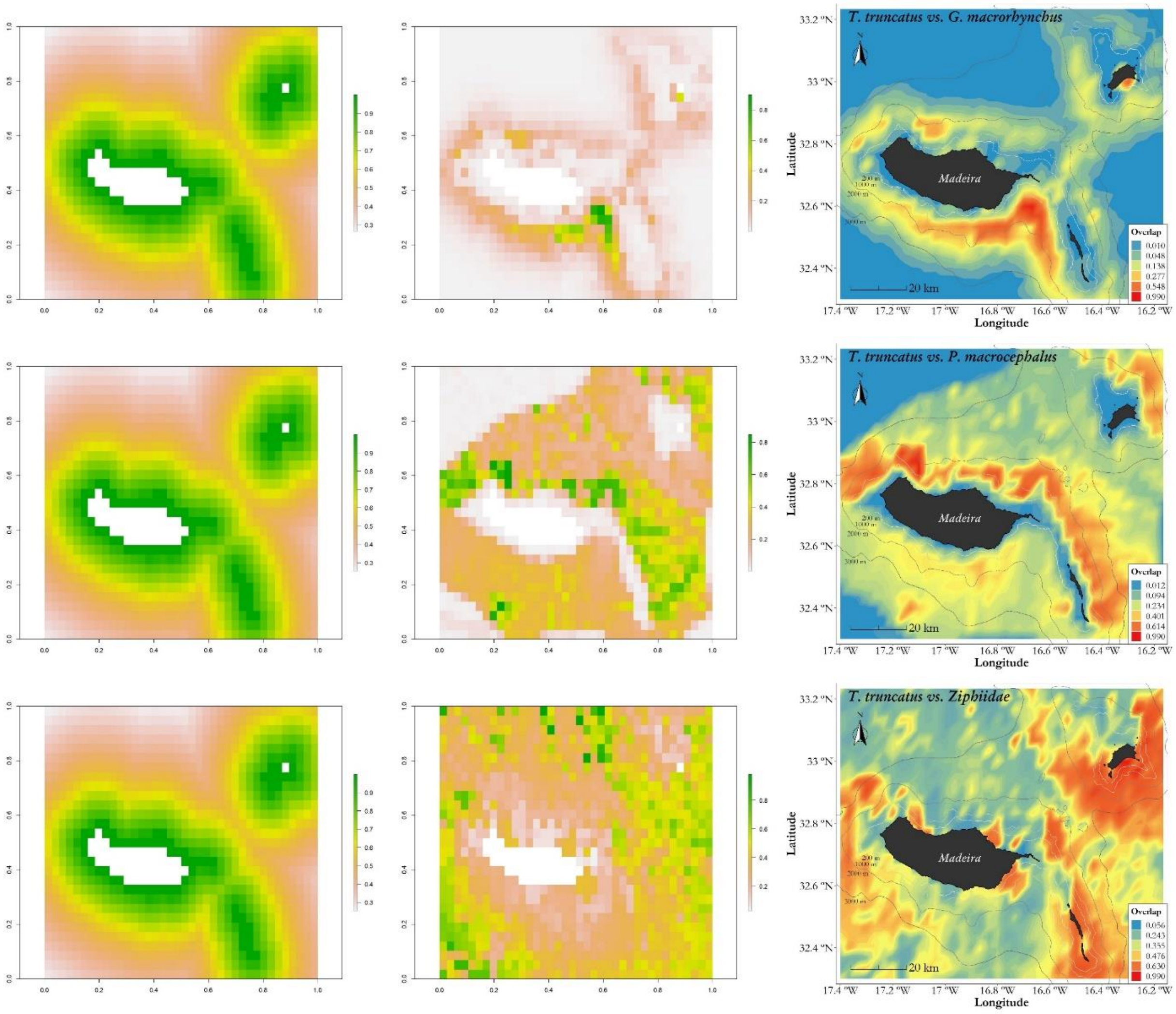


Figure VI.3.1-10. Standardized relative abundance prediction maps of bottlenose dolphin (*T. truncatus*; left) and other cetacean taxa (centre), and the respective overlap map (right). The taxa identifications are given on the top of the corresponding overlap map.

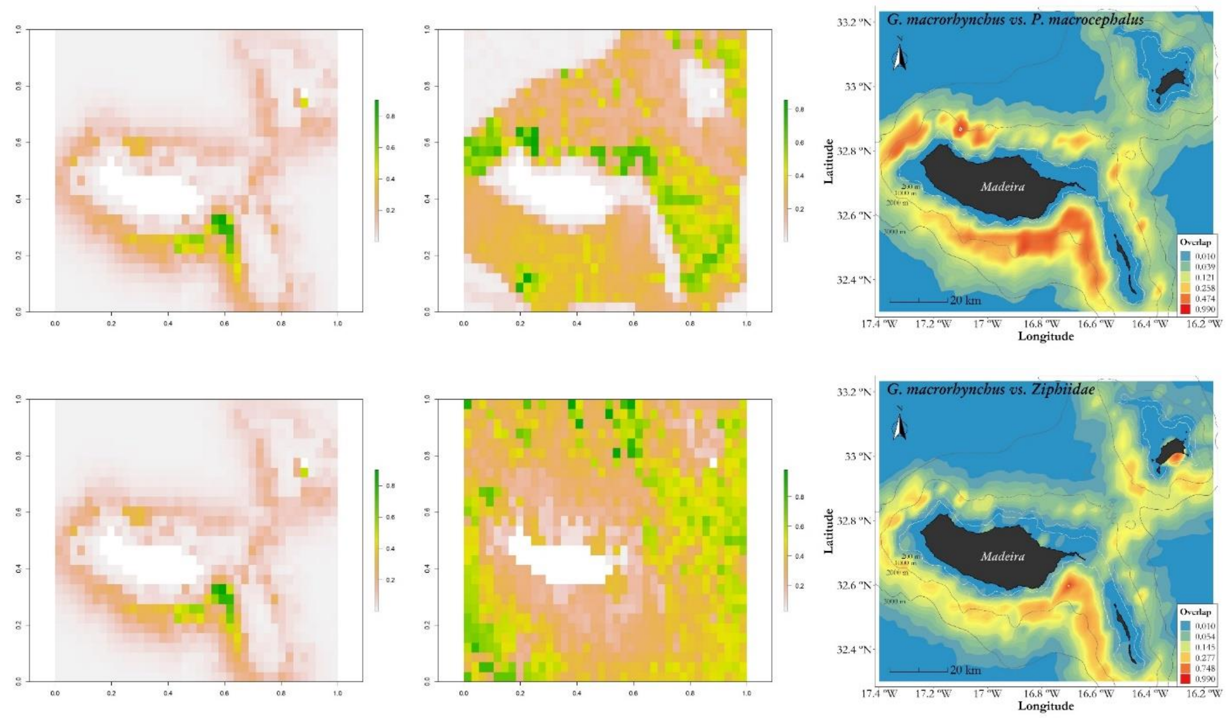


Figure VI.3.1-11. Standardized relative abundance prediction maps of short-finned pilot whale (*G. macrorhynchus*; left) and other cetacean taxa (centre), and the respective overlap map (right). The taxa identifications are given on the top of the corresponding overlap map.

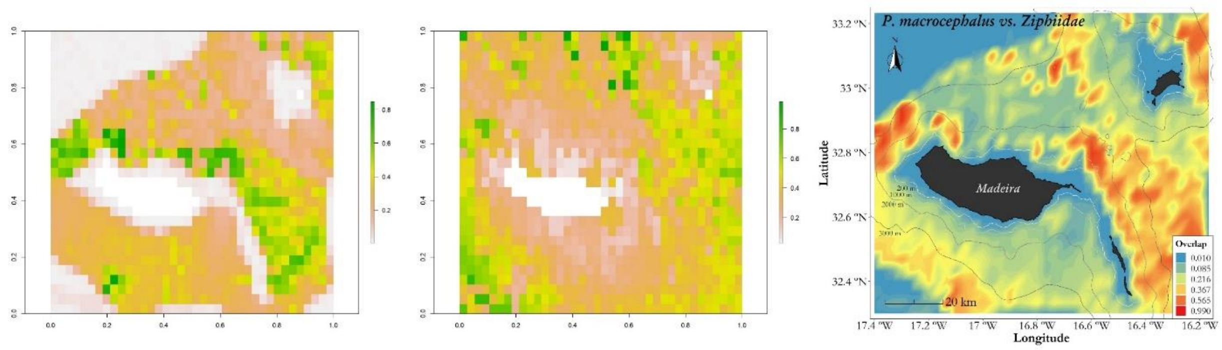


Figure VI.3.1-12. Standardized relative abundance prediction maps of sperm whale (*P. macrocephalus*; left) and Ziphiidae (centre), and the respective overlap map (right). The taxa identifications are given on the top of the corresponding overlap map.

VI.4. Ecological niches

VI.4.1. Overlapped niche dimensions threshold

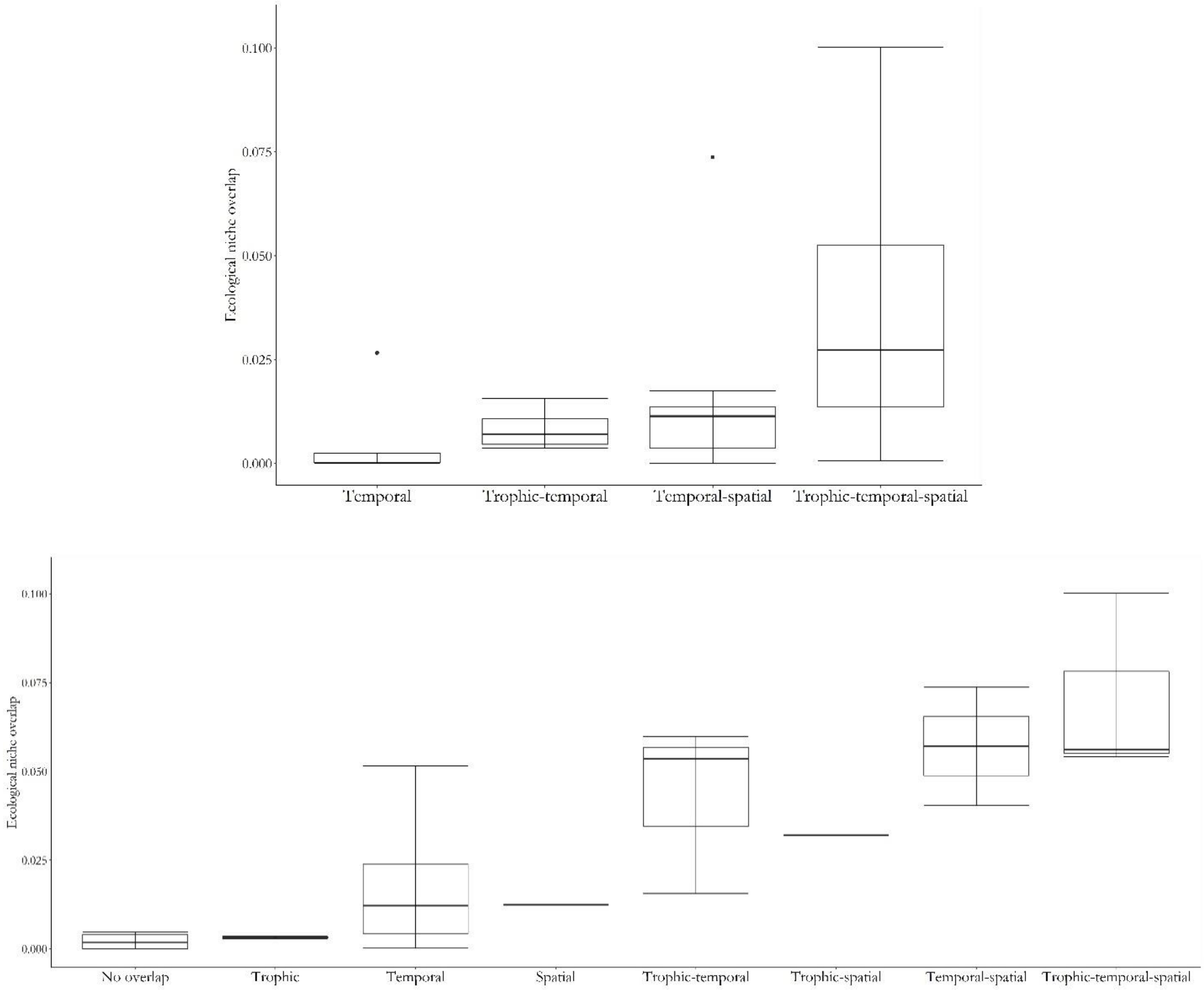


Figure VI.4.1-1. Boxplots of ecological niche overlap values of pairs of cetacean species versus the combined overlap classes those pairs of species were allocated to when the overlap threshold was ≥0.1 (top plot) and ≥0.3 (bottom plot) in each of the dimensions (trophic, temporal and spatial). The whiskers, the box and the central line represent the minimum and maximum, the 25th and 75th percentile, and the median, respectively. The dots are outliers.

VI.4.2. Clustering of overlapped niche dimensions

Table VI.4.2-1. Within cluster sum of squares (the smaller the value the more closely related objects are within the cluster) and average silhouette width (a value closer to 1 suggests the data is better clustered) used to selected the most adequate method to cluster the pairs of cetacean species according to their ecological niche overlap (ENO).

	Kmeans	**DHC**	**AHC**
Within cluster sum of squares	1.24	0.90	1.00
Average silhouette width	0.41	0.40	0.39

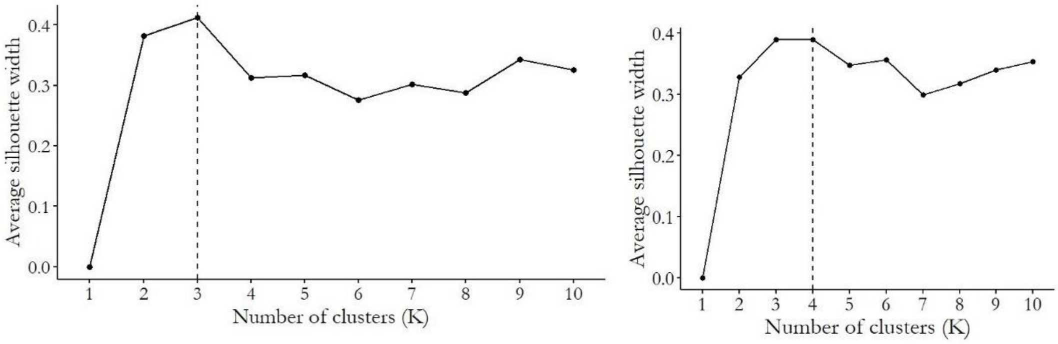


Figure VI.4.2-1. The optimal number of clusters, chosen with the average Silhouette method, to group the pairs of species with the K-means method (left) and define the cutting point for the DHC and AHC methods (right).

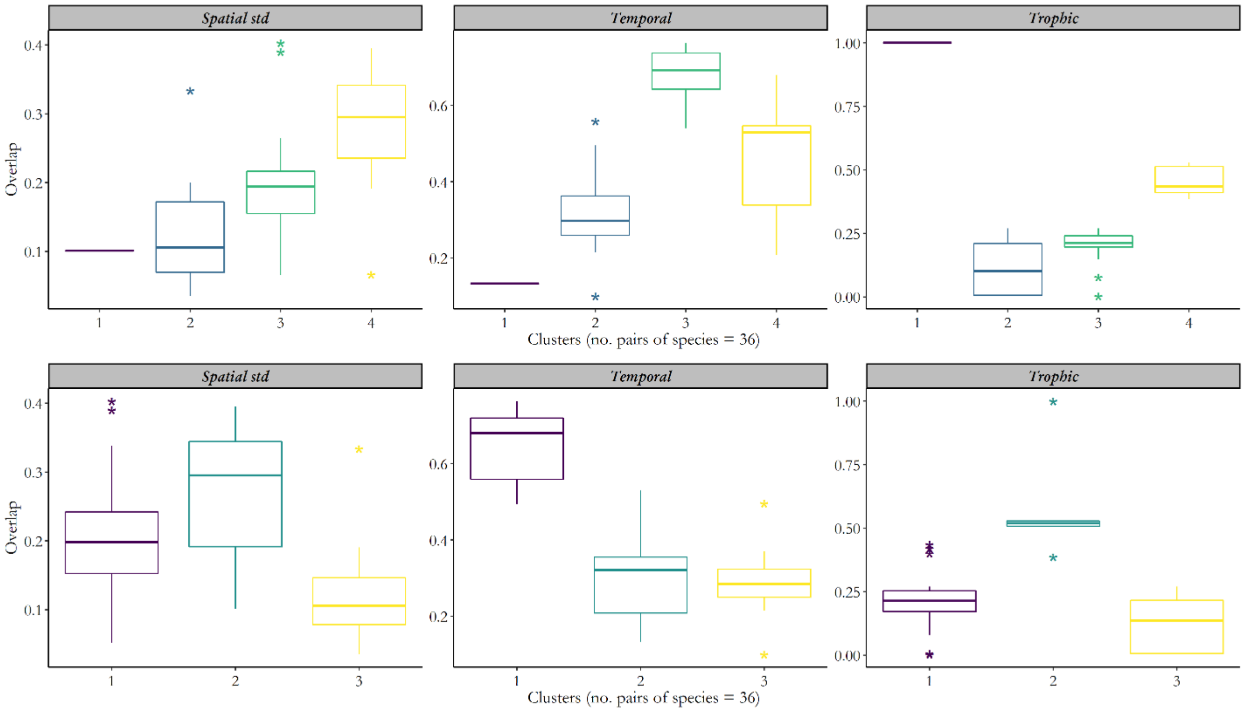


Figure VI.4.2-2. Boxplots of the overlap values between pairs of cetacean species clustered by K-means (top) and AHC (bottom), in the spatial, temporal and trophic dimensions. The whiskers, the box and the central line represent the minimum and maximum, the 25th and 75th percentile, and the median, respectively. The dots are outliers.

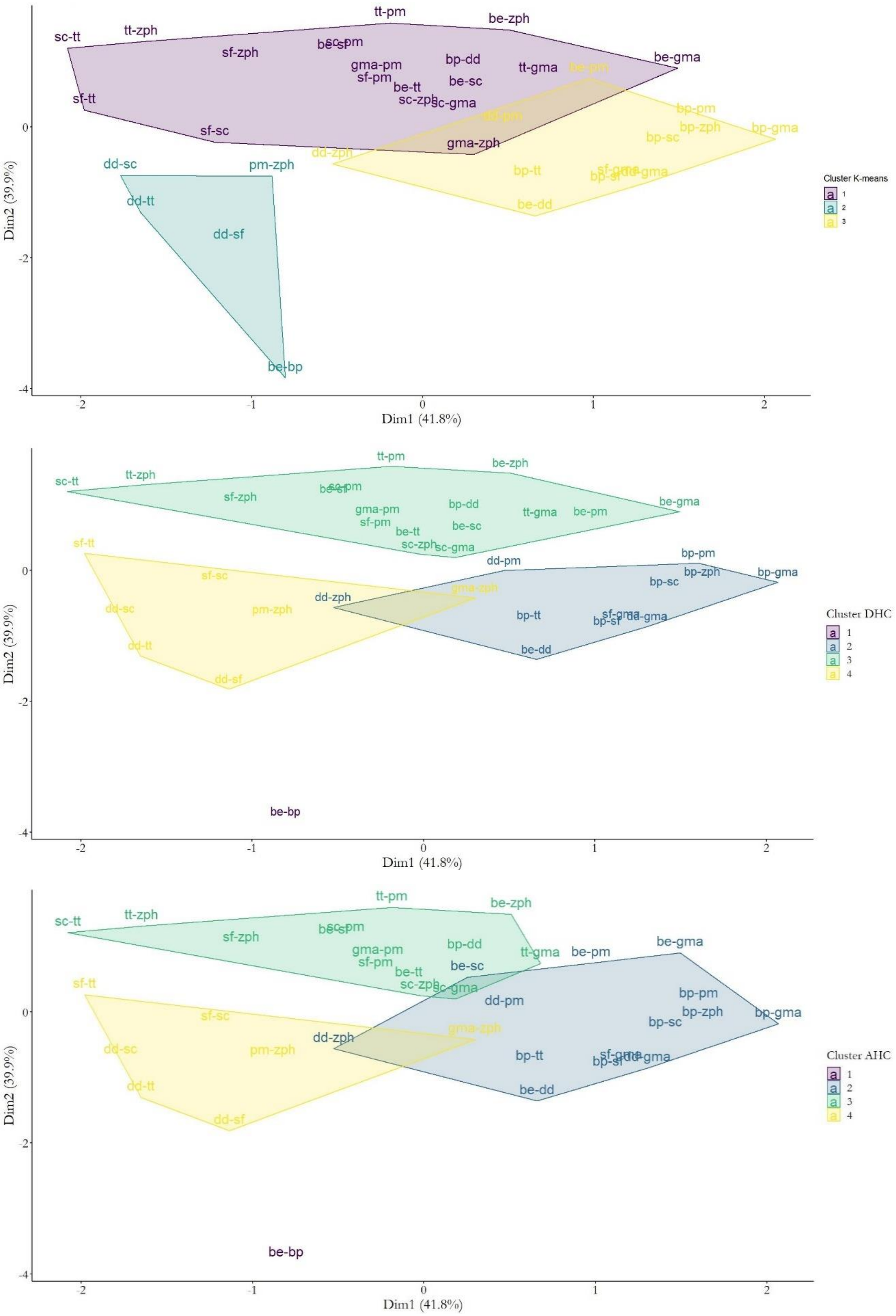
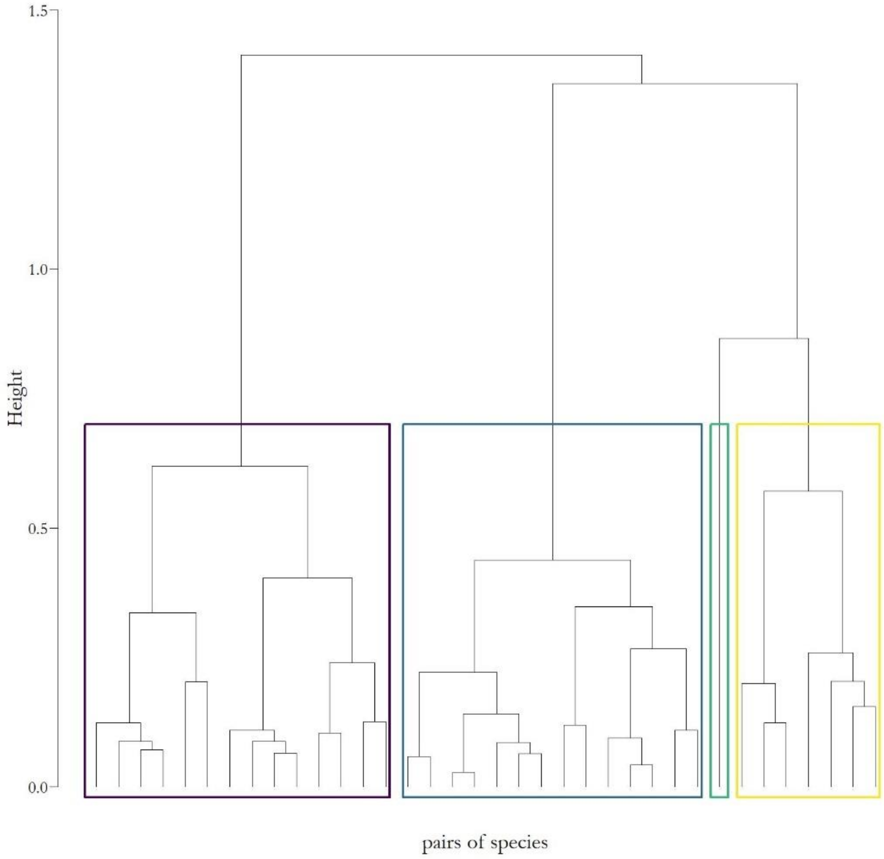


Figure VI.4.2-3. The optimal number of clusters, chosen with the average Silhouette method, to group the pairs of species with the K-means method (left) and define the cutting point for the DHC and AHC methods (right).



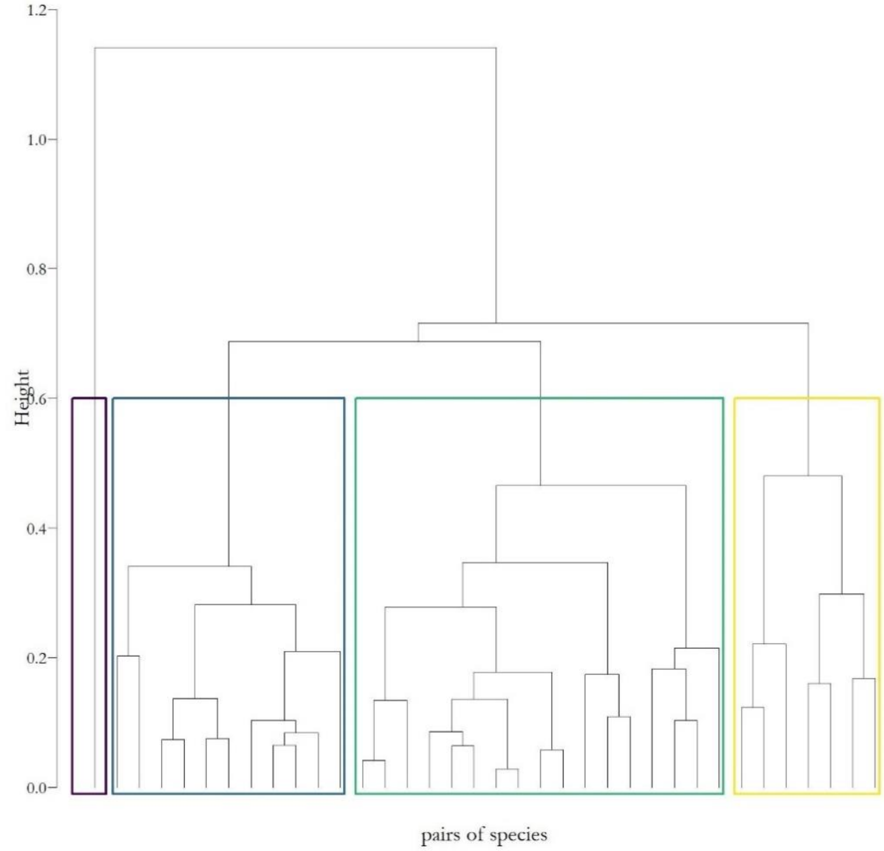
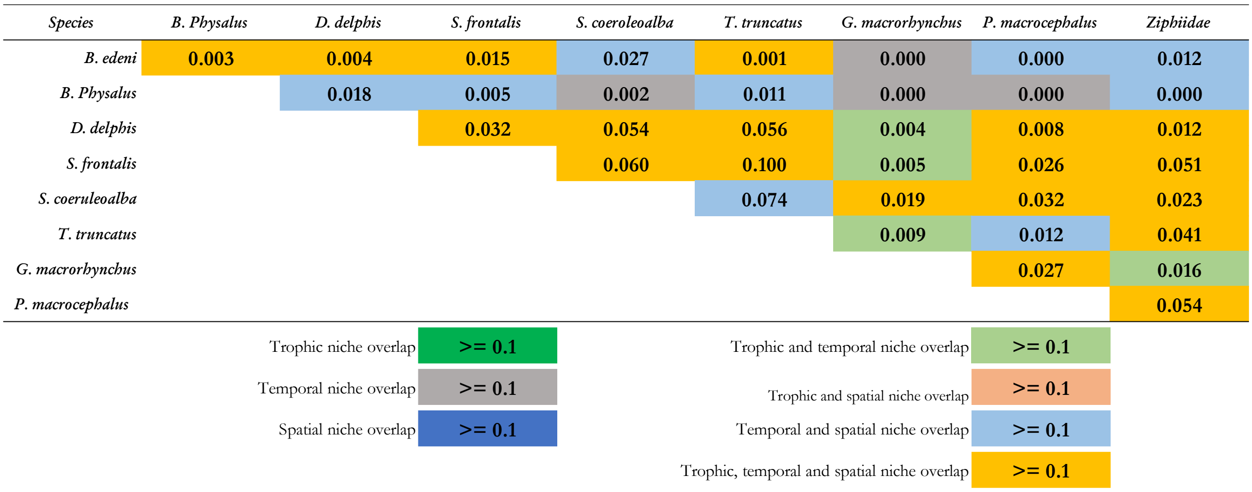


Figure VI.4.2-4. Dendrograms representing the clustering results from the divisive hierarchical clustering (DHC; top) and the agglomerative hierarchical clustering (AHC; bottom).

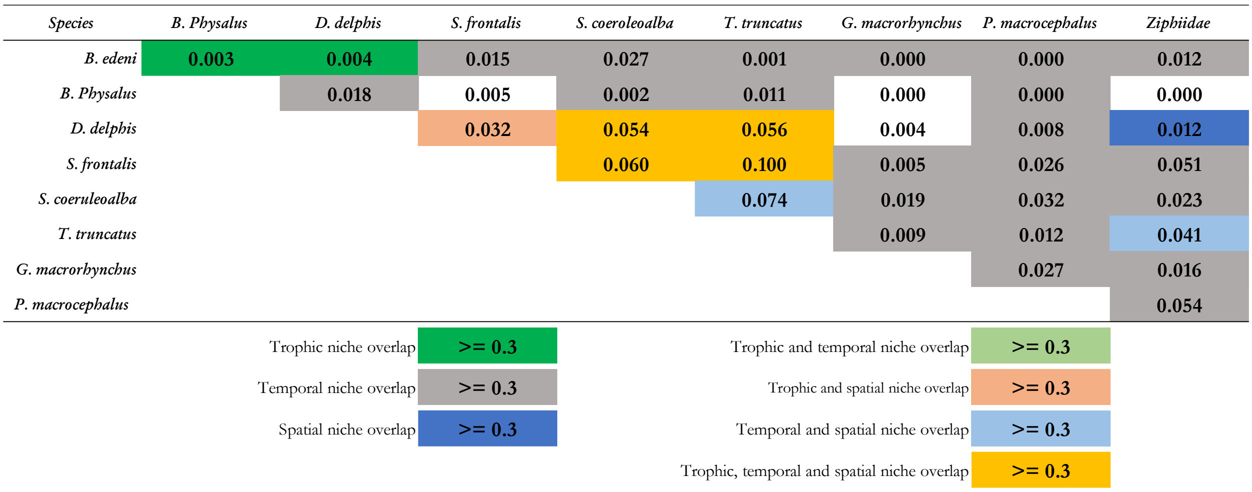
Table VI.4.2-1. The ecological niche overlap (ENO) between pairs of cetacean taxa. The colour code identifies the pairs of species allocated to each group defined by the threshold approach with a value of 0.1.



Species	*B. Physalus*	*D. delphis*	*S. frontalis*	*S. coeroleoalba*	*T. truncatus*	*G. macrorhynchus*	*P. macrocephalus*	*Ziphiidae*
B. edeni	0.003	0.004	0.015	0.027	0.001	0.000	0.000	0.012
B. Physalus		0.018	0.005	0.002	0.011	0.000	0.000	0.000
D. delphis			0.032	0.054	0.056	0.004	0.008	0.012
S. frontalis				0.060	0.100	0.005	0.026	0.051
S. coeruleoalba					0.074	0.019	0.032	0.023
T. truncatus						0.009	0.012	0.041
G. macrorhynchus							0.027	0.016
P. macrocephalus								0.054

Trophic niche overlap	>= 0.1	Trophic and temporal niche overlap	>= 0.1
Temporal niche overlap	>= 0.1	Trophic and spatial niche overlap	>= 0.1
Spatial niche overlap	>= 0.1	Temporal and spatial niche overlap	>= 0.1
		Trophic, temporal and spatial niche overlap	>= 0.1

Table VI.4.2-2. The ecological niche overlap (ENO) between pairs of cetacean taxa. The colour code identifies the pairs of species allocated to each group defined by the threshold approach with a value of 0.3.



Species	*B. Physalus*	*D. delphis*	*S. frontalis*	*S. coeroleoalba*	*T. truncatus*	*G. macrorhynchus*	*P. macrocephalus*	*Ziphiidae*
B. edeni	0.003	0.004	0.015	0.027	0.001	0.000	0.000	0.012
B. Physalus		0.018	0.005	0.002	0.011	0.000	0.000	0.000
D. delphis			0.032	0.054	0.056	0.004	0.008	0.012
S. frontalis				0.060	0.100	0.005	0.026	0.051
S. coeruleoalba					0.074	0.019	0.032	0.023
T. truncatus						0.009	0.012	0.041
G. macrorhynchus							0.027	0.016
P. macrocephalus								0.054

Trophic niche overlap	>= 0.3	Trophic and temporal niche overlap	>= 0.3
Temporal niche overlap	>= 0.3	Trophic and spatial niche overlap	>= 0.3
Spatial niche overlap	>= 0.3	Temporal and spatial niche overlap	>= 0.3
		Trophic, temporal and spatial niche overlap	>= 0.3

VI.5. Estimation of biomass and daily prey of biomass consumption

VI.5.1. Methodology

The biomass of each cetacean taxon, except the baleen whales, was estimated as:

$$B^z = A^z * P_a^z * {W_i}_a^z + A^z * P_{(j)}^z * {W_i}_{(j)}^z + A^z * P_{(c)}^z * {W_i}_{(c)}^z \qquad \text{(Equation 6.9)}$$

where B^z is the species z overall estimate of biomass; $A^z$is the abundance of that species estimated for the period 2007 – 2012 (Freitas *et al* in prep.) or 2017 – 2018 (Freitas, Cañadas, Esteban *et al* in prep.; Esteban, Cañadas, Freitas *et al* in prep.); P_a^z, $P_{(j)}^z$ and $P_{(c)}^z$ are the average proportion of adults, juveniles and calves from sightings of MBM surveys in 2017 – 2019, the latter two used in the calculations whenever there were available individual weight estimates of juveniles (${W_i}_{(j)}^z$) and calves (${W_i}_{(c)}^z$); and ${W_i}_a^z$ the average individual weights of adults. All individual weights were obtained from animals of these species stranded in Madeira and the Canary Islands over the last decades (RACAM – MBM data and ULPG-IUSA data), or in the case of the sperm whale from its weight:length relationship (Lockyer 1976), considering 5 m as the average size of the calves, 8 m as the average size of juveniles and 11 m as the average size of adults.

The biomass of baleen whales was estimated together as:

$$B = \sum_{s=1}^{n} \left(A * P_a^s * {W_i}_a^s + A * P_{(j)}^s * {W_i}_{(j)}^s \; A * P_{(c)}^s * {W_i}_{(c)}^s \right) * P^s \qquad \text{(Equation 6.10)}$$

where B is the baleen whales' overall estimate of biomass; A is the abundance of the family Balaenoteridae estimated for the period 2007 – 2012 (Freitas *et al* in prep.); P_a^s, $P_{(j)}^s$ and $P_{(c)}^s$ are the average proportion of adults, juveniles and calves from sightings of MBM surveys in 2017 – 2019, the latter two used in the calculations whenever there were available individual weight estimates of juveniles (${W_i}_{(j)}^z$) and calves (${W_i}_{(c)}^z$); ${W_i}_a^z$ the average individual weights of adults, obtained in the case of the Bryde's whale from its weight:length relationship (Lockyer 1976), considering 5 m as the average size of the calves, 8 m as the average size of juveniles and 11 m as the average size of adults, and in the case of fin whales the average size of adults (45 000 kg) from the literature (Aguilar and García-Vernet, 2018); and P^s is the proportion of sightings of species s.

Biomass is a function of species abundance and energetic requirements, considering each species' average individual body mass, while the daily prey biomass consumption takes into consideration the energetic needs of species and gives an indication of how much prey these species might be consuming in Madeira archipelago. The biomass estimates are an approximation of the unknown true biomasses of these taxa in the study area. Furthermore, they should be interpreted in relative terms because the abundance estimates are not corrected for either perception bias or avialiability bias, and thus are likely negatively biased, some taxa more than others.

The values of the parameters of each taxon used to estimate biomass for the periods 2007 – 2012 and 2017 – 2018 are presented in Table VI.5.2-1 and Table VI.5.2-2, respectively.

VI.5.2. Biomass estimates and calculation parameters

Table VI.5.2-1. Values of the parameters of each taxon used to estimate biomass for the period 2007 – 2012, according to the formulas presented above.

Group	**Species**	**Proportion age classes**				**Average individual weights (kg)**				**Proportion species**			**Abundance**		**Biomass**	
		Adults	**Juveniles**	**Calves**	**Sources**	**Adults**	**Juveniles**	**Calves**	**Sources**	***B. edeni***	***B. physalus***	**Sources**	**Estimates**	**Sources**	**Kg**	**Metric tons**
Baleen whales	*B. edeni*	0.82	0.13	0.04	MBM (NSS 2017-2019)	8705	3638	1004	Weight estimated from length:weight relationship (Lockyer 1976), considering the average size: calves - 5 m; juvenile - 8 m; adults - 11 m	0.81	-	MBM; multiple surveys 2001-2017	20	Estimate of baleen whales, SLS MBM 2007-12 (Freitas *et al* in prep)	125415	125
	B. physalus	1.00			-	45000			Aguilar, A. and García-Vernet, R., 2018	-	0.19	MBM; multiple surveys 2001-2017	20	Estimate of baleen whales, SLS MBM 2007-12 (Freitas *et al* in prep)	168000	168
Dolphins	*D. delphis*	0.80	0.08	0.12	MBM (NSS 2017-2019)	80.2	30	21	MBM and IUSA (Stranding data)	-	-	-	521	Estimate of the species, SLS MBM 2007-12 (Freitas *et al* in prep)	35946	36
	T. truncatus	0.79	0.07	0.14	MBM (NSS 2017-2019)	214.0	133	43	MBM and IUSA (Stranding data)	-	-	-	561	Estimate of the species, SLS MBM 2007-12 (Freitas *et al* in prep)	103256	103
	S. frontalis	0.66	0.08	0.26	MBM (NSS 2017-2019)	67.7	34	16	MBM and IUSA (Stranding data)	-	-	-	1081	Estimate of the species, SLS MBM 2007-12 (Freitas *et al* in prep)	55641	56
Deep divers	*G. macrorhynchus*	0.71	0.16	0.14	MBM (NSS 2017-2019)	674.50	219	80	MBM and IUSA (Stranding data)	-	-	-	103	Estimate of the species, SLS MBM 2007-12 (Freitas *et al* in prep)	53716	54
	zhipiidae	0.90	0.05	0.05	MBM (NSS 2017-2019)	1425.67	837	0	MBM and IUSA (Stranding data)	-	-	-	23	Estimate of the family, SLS MBM 2007-12 (Freitas *et al* in prep)	30529	31

Table VI.5.2-2. Values of the parameters of each taxon used to estimate biomass for the period 2017 – 2018, according to the formulas presented above.

Group	**Species**	**Proportion age classes**				**Average individual weights (kg)**				**Abundance**		**Biomass**	
		Adults	**Juveniles**	**Calves**	**Sources**	**Adults**	**Juveniles**	**Calves**	**Sources**	**Estimates**	**Sources**	**Kg**	**Metric tons**
Baleen whales	*B. edeni*	0.82	0.13	0.04	MBM (Kogia 2017-2019)	8705	3638	1004	Weight estimated from length:weight relationship (Lockyer 1976), considering the average size: calves - 5 m; juvenile - 8 m; adults - 11 m	94	SLS MSII 2017-18 (Freitas, Cañadas, Esteban et al in prep.)	724736	725
Dolphins	*D. delphis*	0.80	0.08	0.12	MBM (Kogia 2017-2019)	80	30	21	MBM and IUSA (Stranding data)	262	SLS MSII 2017-18 (Freitas, Cañadas, Esteban et al in prep.)	18077	18
	T. truncatus	0.79	0.07	0.14	MBM (Kogia 2017-2019)	214	133	43	MBM and IUSA (Stranding data)	765	SLS MSII 2017-18; (Freitas, Cañadas, Esteban et al in prep.)	140804	141
	S. frontalis	0.66	0.08	0.26	MBM (Kogia 2017-2019)	68	34	16	MBM and IUSA (Stranding data)	2641	SLS MSII 2017-18; (Freitas, Cañadas, Esteban et al in prep.)	135938	136
	S. coeruleoalba	0.71	0.00	0.29	MBM (Kogia 2017-2019)	88.4	58	15	MBM and IUSA (Stranding data)	76	SLS MSII 2017-18; (Freitas, Cañadas, Esteban et al in prep.)	5107	5
Deep divers	*G. macrorhynchus*	0.71	0.16	0.14	MBM (Kogia 2017-2019)	675	219	80	MBM and IUSA (Stranding data)	271	SLS MSII 2017-18 (Esteban, Cañadas, Freitas et al in prep.)	141331	141
	P. macrocephalus	0.73	0.09	0.18	MBM (Kogia 2017-2019)	18044	4949	1612	Weight estimated from length:weight relationship (Lockyer 1976), considering the average size: calves - 5 m; juvenile - 8 m; adults - 11 m	28	SLS MSII 2017-18 (Esteban, Cañadas, Freitas et al in prep.)	399511	400
	zhipiidae	0.90	0.05	0.05	MBM (Kogia 2017-2019)	1426	837	-	MBM and IUSA (Stranding data)	17	SLS MSII 2017-18 (Esteban, Cañadas, Freitas et al in prep.)	22565	23