Ecology and Conservation of Bottlenose Dolphins in Madeira Archipelago, Portugal

DOCTORAL THESIS

Ana Margarida Brites Caetano Dinis

DOCTORATE IN BIOLOGICAL SCIENCES

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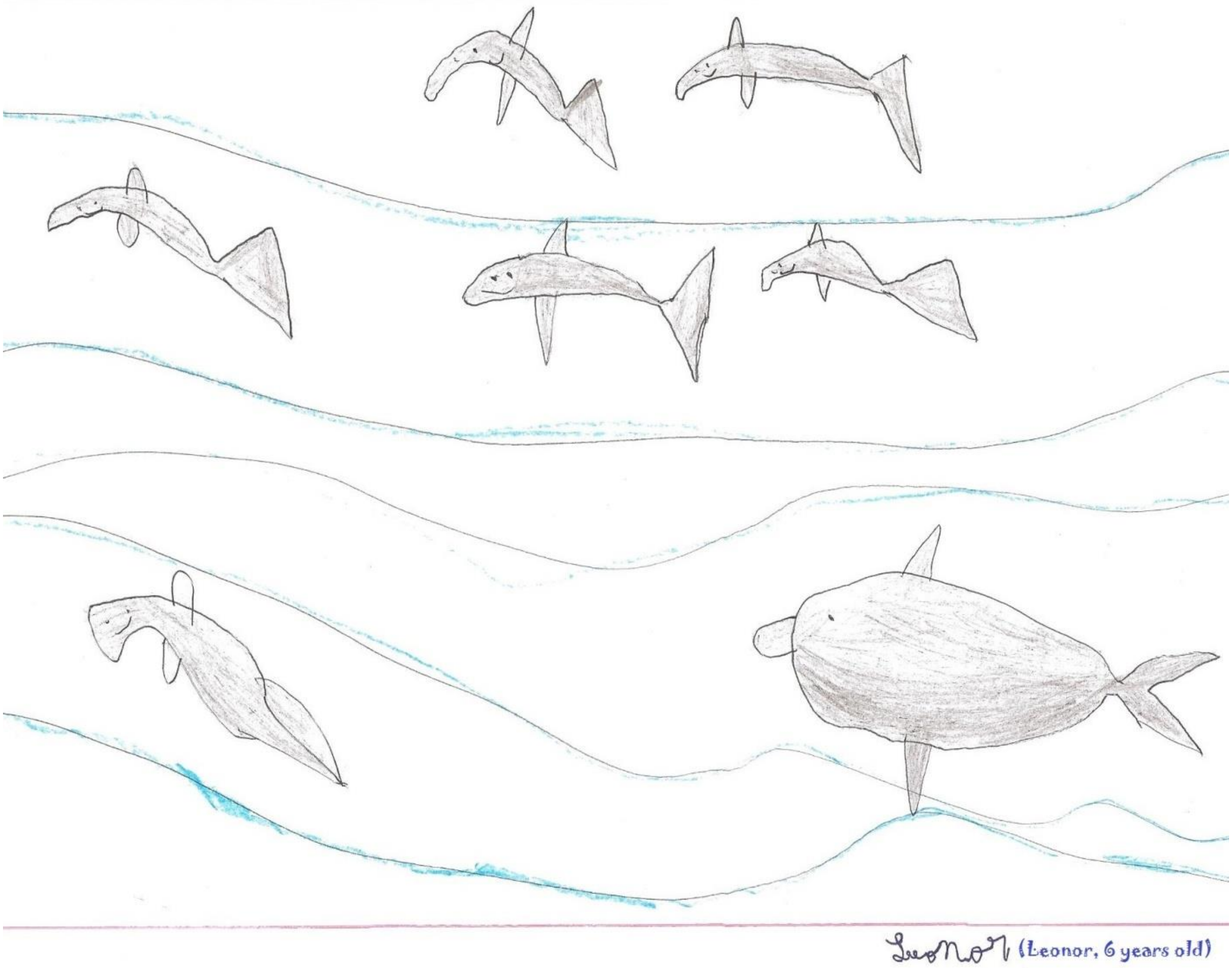

Leonor (Leonor, 6 years old)

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And finally, I dedicate this work to my father that would have been so proud.

DECLARATIONS

I hereby declare that this thesis was written by me, and that I have actively participated in the data collection. Also, I was responsible for all the analysis with the exception of the GIS work and mapping, that was done by Adalberto Carvalho. Nonetheless, this study was developed while I was a researcher in the Madeira Whale Museum, and data was collected throughout several scientific projects in which various people were involved. The scientific projects were co-funded by the Machico Town Hall and by EU and national programs, as listed below:

- 2000 to 2004; CETACEOSMADEIRA 'Projecto para a Conservação dos Cetáceos no arquipélago da Madeira' - LIFE 99NAT/P/6432;

- 2004 to 2005: MACETUS 'Estudo da estrutura populacional, distribuição, movimentos e utilização do habitat do *Physeter macrocephalus*, *Globicephala macrorhynchus*, *Tursiops truncatus* e *Stenella frontalis* na Macaronésia' - FEDER/INTERREG IIIB MAC/4.2/M10;

- 2005 to 2006: GOLFINICHO 'Utilização diferencial do nicho espacial e trófico entre o golfinho-comum (*Delphinus delphis*) e o golfinho-pintado (*Stenella frontalis*) nos Açores e Madeira' - FCT POCI/BIA-BDE/61009;

- 2006 to 2008: EMECETUS 'Estudo, Monitorização e Educação para a Conservação dos cetáceos na Macaronésia' - FEDER/INTERREG IIIB 05/MAC/4.2/M10;

- 2009 to 2013: CETACEOSMADEIRA II 'Identifying critical marine areas for bottlenose dolphin and surveillance of the cetaceans' conservation status in Madeira archipelago' - LIFE+07 NAT/P/000646.

ABSTRACT

This study aimed to provide an insight on the ecology of the bottlenose dolphin population in Madeira archipelago. To achieve this, population structure; group dynamics, site-fidelity, residency and movement patterns within and out of the study area; survival and abundance estimates and spatial and temporal distribution and habitat preferences related to physiographic parameters using data collected between 2001-2011, were investigated. Photo-identification data analysis revealed strong evidences that bottlenose dolphins seen in the archipelago of Madeira belong to an open population with regular recruitment of new animals to the area. This population exhibited a typical fission-fusion society, in which short-term acquaintances prevail, with only a few long-lasting associations. Photo-identification methods demonstrated that there is a large variability in residency pattern, with resident, transient and migrant individuals. Only a small number of dolphins were found to be resident (4.3%). Social network diagram as well as SLAR analysis supported the existence of a mixed population of residents, migrants and transients. Mark-recapture methods estimated a high survival rate, within the range of other long-lived cetacean species. The resident community is composed of app. 180 individuals. In addition, around 400 dolphins of different residency patterns were found to use the south area of Madeira Island. Spatial distribution indicated that bottlenose dolphins were regularly found in shallow and closer to shore areas, suggesting the existence of biological processes influenced by bathymetry. Moreover, temporal patterns revealed no strong seasonal fluctuation in the presence of bottlenose dolphins in Madeira archipelago waters. Bottlenose dolphins are listed under the Annex II of the EU habitats Directive that requires the designation of Special Areas of Conservation (SACs) for this species; as such, the knowledge gained through this work can be used by governmental authorities to the establishment and management of areas for the conservation of bottlenose dolphin in Madeira archipelago.

Key-words: bottlenose dolphin, ecology, photo-identification, distribution, conservation, Madeira archipelago.

RESUMO

Este trabalho teve como objectivo investigar a ecologia da população de golfinhos roazes no Arquipélago da Madeira. Foram utilizados dados de 2001-2012 para investigar a estrutura populacional; estrutura e composição dos grupos, residência, movimentos na área de estudo; taxas de sobrevivência e o tamanho da população e, finalmente a distribuição espacial e temporal. A análise dos dados de foto-identificação indicaram que os animais avistados no arquipélago pertencem a uma população aberta com recrutamento regular de novos indivíduos. Esta população revelou ter uma estrutura dinâmica, na qual prevalecem as associações rápidas e de curta duração. Através da foto-identificação verificou-se a existência de três padrões diferentes de residência: residentes, migrantes e transeuntes. Apenas um pequeno número de golfinhos demonstrou ser residente (4.3%).O diagrama social e as associações temporais revelaram que os golfinhos dos três padrões de residência se misturam. Através de métodos de captura e recaptura foi possível estimar uma taxa de sobrevivência elevada. Cerca de 180 golfinhos são residentes. Também foi possível determinar que cerca de 400 animais de diferentes padrões de residência, utilizaram as águas do sul da Ilha da Madeira, no período de estudo. A distribuição espacial revelou que a maioria dos golfinhos foi avistada em águas menos profundas e mais próximo da costa, sugerindo a existência de processos biológicos influenciados pela batimetria. A distribuição temporal não revelou marcadas flutuações sazonais na presença de golfinhos no arquipélago. Os golfinhos roazes são uma das espécies presentes no Anexo II da Directiva Habitats da União Europeia. Como tal, é requerido aos países membros a criação de Zonas Especiais de Conservação para esta espécie; assim, espera-se que o conhecimento adquirido através deste estudo possa ser utilizado pelas entidades governamentais para a implementação e gestão de áreas de protecção para o golfinho roaz no arquipélago da Madeira.

Palavras-chave: golfinho-roaz, ecologia, foto-identificação, distribuição, conservação, Arquipélago da Madeira.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Conservation of the marine environment

Conservation and protection of marine life is becoming more important as we better understand the importance of the oceans and our impacts on them. Both direct and indirect anthropogenic impacts can influence species in the marine environment. However, direct impacts such as boat disturbance, over fishing, by-catch and ship strikes often cause immediate declines among various marine species (Mann *et al.* 2000). Moreover, in the last 50 years land and sea surface temperatures have increased globally as a result of climate change (IPCC 2001). Global and regional impacts from increased temperatures include changes in weather patterns, ocean currents, salinity, pH, sea-ice cover and rises in sea levels. As a result, many governments are now establishing plans and taking actions to reduce and monitor the effects of global warming (Skilling 2007). Marine habitat conservation is lagged behind land conservation (Hoyt 2011), and establishing measures to prevent human activities from impacting too negatively marine ecosystems, is vital for conservation of biodiversity (Cañadas 2006).
The designation of especially marine protected areas (MPAs) is one of the most common approaches to marine conservation, and a declared MPA signifies a positive intention towards a portion of habitat (Hoyt 2001). Within the context of the European Union, the Habitats Directive (97/62/CEE of the Council), in its Natura 2000 programme, imputes the responsibility to the countries of establishing a network of marine and land-based protected areas (Hoyt 2011). The first step in becoming a 'special area of conservation' (SAC) is to be named a 'site of community importance' (SCI). A site of community importance is defined as 'a site

that contributes significantly to the maintenance or restoration at a favourable conservation status of a natural habitat type in Annex I or of a species in Annex II'.

A special area of conservation (SAC) is defined as 'a site of community importance where necessary measures are applied to maintain, or restore, to favourable conservation status, the habitats or populations of the species for which the site is designated' (European Union Habitats Directive, 1992).

In order to be accepted as part of the European Natura 2000 Network of protected areas, a proposed SAC should demonstrate being of particular importance for the conservation of the species (Cañadas 2006).

1.2 Cetacean Biology and Ecology

Cetaceans include 87 species of whales, dolphins and porpoises (Hoyt 2011) and they are key components of marine ecosystems (Croll *et al.* 1998). The role of cetaceans in ecosystem functioning and dynamics is still poorly understood, as they spend most of their lives hidden below the water's surface (Connor *et al.* 2000). Despite their diversity of form, behaviour and habitat, these aquatic mammals share some common characteristics, such as being air-breathing and live-bearing homeotherms, like their terrestrial ancestors (Ballance 2009). They are long-lived, reproduce slow, yet they have invaded a large proportion of the ocean's habitats (Connor *et al.* 2000). They inhabit coastal waters up to the top zone, neritic waters over continental shelves and the more oceanic and pelagic systems (Ballance 2009) Marine habitat types are not static in space or time, they change with the water masses and surface currents that define them (Ballance 2009). Topographic features such as sea floor slope and depth (Ingram & Rogan 2002) and prey abundance have also been found to influence habitat use among marine mammals. Cetacean ecology is described as the relationships between cetaceans and their physical environment (Ballance 2009), however determining the cause of habitat selection and examining the behavioural ecology of cetaceans is often a difficult task, particularly in the dynamic marine environment (Connor *et al.* 2000).

Understanding the ecological mechanisms that make some species more prone to population decline, range contraction, and extinction than others has been always one of the main goals of marine mammal researchers. Information on the abundance, status, distribution, behaviour and movement patterns of wild populations contributes to establishing appropriate conservation and management initiatives (Lettink & Armstrong 2003).

1.3 The Bottlenose Dolphin, *Tursiops truncatus*, (Montagu, 1821)

The common bottlenose dolphin, *Tursiops truncatus*, (Cetacea: Delphinidae) (hereafter referred as bottlenose dolphin) is, without any doubt, the best known of all cetaceans (Wells & Scott 2009). For most people the word 'dolphin' invokes an image of a bottlenose dolphin (Connor *et al.* 2000), as they are one of the most displayed cetacean in public performances in aquaria (Corketon 2009). Also, their proximity to human activity exposes them to numerous threats. Although not endangered at genus level, specific populations of bottlenose dolphins might be considered threatened (Connor *et al.* 2000). Ultimately, they are apex predators, and determining the status of a bottlenose dolphin population may prove to be a useful indicator of the health and stability of the surrounding environment.

1.3.1 Characteristics and Systematics

Bottlenose dolphins are cosmopolitan in distribution, and demonstrate a great deal of geographic variation in morphology. They are recognizable by their medium-size, robust body, a moderate falcate dorsal fin, and dark coloration (Well & Scott 2009). The genus *Tursiops* exhibits striking regional variations in body size (Connor *et al.* 2000), and it appears to vary inversely with water temperature in many parts of the world (Well & Scott 2009).

Phylogenetic variation along with geographic location, body size, tooth count and coloration indicate the presence of two species *T. truncatus* and *T. aduncus* within the genus (Ross 1977, Curry 1997, LeDuc *et al.* 1999). The systematics of the genus *Tursiops* is presently unclear as recent genetic, morphologic, and physiologic studies suggest that revision of the genus may be necessary to acknowledge significant differences between forms from different oceans, as well as differences between forms in inshore *versus* offshore habitats within ocean basins (Le Duc *et al.* 1999; Rice 1998; Mead & Potter 1995; Hersh & Duffield 1990). Differences between inshore and offshore ecotypes have been interpreted with respect to habitat differences: higher haemoglobin concentration, hematocrits, and red blood cell counts of offshore animals suggest an adaptation for greater oxygen-carrying capacity to facilitate deeper and longer dives (Duffield *et al.* 1983); smaller body sizes and larger size of flippers of coastal animals may be an adaptation to shallow habitats where manoeuvrability is important (Hersh & Duffield 1990); and differences in skull dimensions between the two forms seem to be related to distinct feeding habits and foraging strategies (Hersh & Duffield 1990).

Although information on the distribution of the two ecotypes is scarce in most geographic areas, in the western North Atlantic there is some evidence of habitat partitioning. The coastal population occupy very shallow waters, coastal to shore, while offshore bottlenose dolphins usually occur along the shelf break (Kenney 1990; Torres *et al.* 2003).

1.3.2 Distribution and Ecology

Bottlenose dolphins are found in temperate and tropical marine waters worldwide (Well & Scott 2009). They have adapted to a variety of marine and estuarine habitats, even ranging into rivers (Well & Scott 2009). This versatility is also reflected in bottlenose dolphin feeding and foraging. They feed on a variety of fish, cephalopods, occasionally shrimp (Gunter 1951), and even small rays and sharks (Mead & Potter 1990). Bottlenose dolphins pursue both schooling and solitary prey throughout the water column as well into the air above, into the sand below, and even into shore (Connor *et al.* 2000). Resuming, bottlenose dolphins are described as opportunistic feeders that take advantage of locally available prey (Barros & Odell 1990).

1.3.3. Life history

Bottlenose dolphins, like all cetaceans are long-lived mammals. Females can live more than 50 years and reach sexual maturity between five and thirteen years, whereas males may live more than 40 years and become sexually mature from eight to thirteen years (reviewed in Connor *et al.* 2000). Bottlenose dolphins show diffuse seasonal reproduction, with usually one or two peaks in the timing of births around spring/early summer and fall (Mann *et al.* 2000). Females give birth to a single calf after a twelve-month gestation period (Schroeder 1990, Schroeder & Keller 1990). Calves are reported to stay with their mothers for several years (Wells *et al.* 1987, Smolker *et al.* 1992). Maternal investment is high, with some calves observed nursing up to three years of age (Mann *et al.* 2000), although longer dependencies are not uncommon (Connor *et al.* 2000).

1.3.4 Home range and Migration

Bottlenose dolphins show a full spectrum of movements, from seasonal migrations, year-round home ranges, periodic residency, and a combination of occasional long-range movements and repeated local residency (Shane *et al.* 1986; Wells & Scott 1999). At many sites worldwide, long-term residency has been reported. In one of the longest-term study of its kind, the year-round residents of dolphin communities along the west coast of Florida have maintained stable, slightly overlapping home ranges during more than 40 years of observations, spanning at least five generations (Wells 2003; Wells & Scott 1999; Scott *et al.* 1990). Adjacent communities can be distinguished by genetic and behavioral differences, and are often demarcated by physiographic features (Duffield & Wells 2002; Parsons *et al.* 2006).

1.3.5 Group Size and Social Behaviour

Small groups of 2-15 individuals are typical for bottlenose dolphins, although groups of more than 1 000 have been reported on occasion (Shane *et al.* 1986; Scott & Chivers 1990). As seen in other dolphin species, bottlenose dolphins tend to form larger groups when inhabiting more open, pelagic waters (reviewed by Shane *et al.* 1986). Factors contributing to this trend seem to be the risk of predation in open habitats and a change in foraging strategies, transiting from solitary preying on reefs or shallow waters to schooling fish in the open water (Norris & Dohl 1980).

One characteristic that all populations of bottlenose dolphins appear to have in common is a fission-fusion society, with sex, age, reproductive condition, familial relationships, and affiliation histories defining their dynamic groups at any given time (Connor *et al.* 2000; Wells 2003). Unlike animals that live in groups of constant composition, social relationships in fission-fusion society may depend strongly on the social context at a given moment (Connor *et al.* 2000). Groups can be composed by females and calves, mixed sex groups of juveniles, or even strongly-bonded pairs or trios of adult males (Rogers *et al.* 2004; Owen *et al.* 2002; Connor *et al.* 2000; Wells *et al.* 1987). The patterns of association in this species seem to exhibits great variability. In Sarasota and Shark Bay strong male-male associations were found but, possibly not in the Moray Firth, Scotland (Wells *et al.* 1987; Smolker *et al.* 1992; Wilson *et al.* 1993). Some males form strong bonds with others, but some travel alone (Wells *et al.* 1987). In Shark Bay and in Sarasota some females are highly social while others are more solitary. It is possible to relate these differences between populations, and in some cases within populations, to differences in risk of predation or availability of prey (Connor *et al.* 2000).

1.3.6 Status and Conservation

In the IUCN red list, the bottlenose dolphin was classified as *Data Deficient* until 2008, when its status was changed to *Least Concern*. Although there are many threats to local populations (*e.g.* pollution, fishing interaction, direct hunt, marine traffic, tourism), as a species it does not appear to merit concern for major global population decline (Wells & Scott 2009). Likewise, the conservation status for this species in Madeira archipelago is *Least Concern* (Cabral *et al.* 2005).

The species is listed in Annex II of Habitats Directive (Natura 2000 network) and Appendix II of CITES. EU governments, throughout the Habitats Directive, are required to consider the areas where this species occurs for the establishment of Special Areas of Conservation (SACs) (Cañadas 2006; Wilson *et al.* 1997). At a regional scale, the species is legally protected in the Exclusive Economic Zone (EEZ) of the archipelago of Madeira since 1986 by the Dec.-Leg. Regional 6/86/M (Cabral *et al.* 2005).

1.4 Study area: The Archipelago of Madeira

The archipelago of Madeira (Portugal) is located in the warm-temperate waters of the northeast Atlantic Ocean (32° N, 017°W), nearly 1000 km from the European continent and 500 km of the West African coast. It is considered one of the most isolated archipelagos of the North Atlantic Ocean (Alves *et al.* 2013; Querouil *et al.* 2007), with a central geographical position between the archipelago of the Azores (at 900 km distance) and the Canaries (at 400 km). This volcanic archipelago is composed by the main island of Madeira and the smaller island of Porto Santo (~40 km Northeast), and by two uninhabited sub-archipelagos, the Desertas (~20 km Southeast) and the Selvagens (300 km South). Madeira is the largest island of the group with an area of 741 km^2 (57x22 km), a coastline of 157 km and a mountain ridge reaching 1862 meters altitude. The Madeira EEZ has approximately 446 000 km^2 and features mainly abyssal oceanic waters (Alves *et al.* 2013) (Figure1.1)

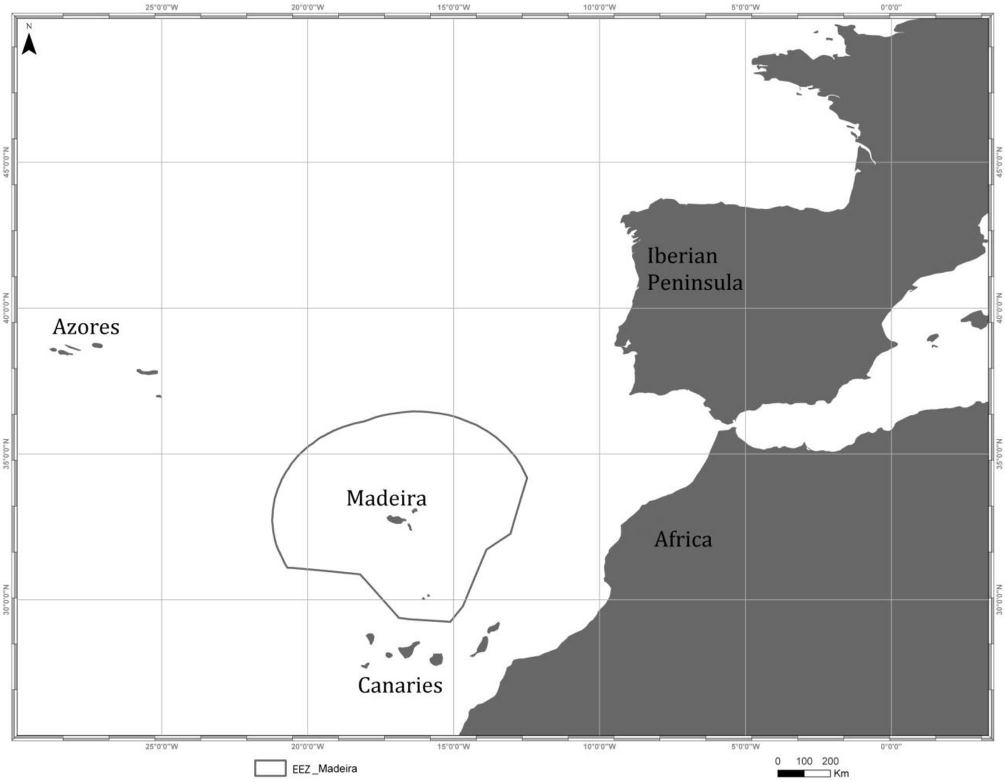

Figure 1.1- Map of the northeast Atlantic showing the location of the archipelago of Madeira and its Exclusive Economic Zone (EEZ).

The waters of Madeira archipelago are influenced by the Portuguese Current, the Azores Current, and the Canary Current, all part of the eastern anticyclonic North Atlantic subtropical gyre (Sala *et al.* 2013). The junction of the eastward division of the Azores Current with the Canary Current up north, and around the archipelago of Madeira (New *et al.* 2001) is responsible for most of its seasonal and inter-annual complex oceanographic patterns, resulting in high salinity, high temperature and low-nutrient regime waters (Johnson & Stevens 2000).

The barrier form by the islands high mountains stretch (up to 1800m) to the dominant northeast trade winds (Tomczak & Godfrey 1994) together with the underwater ridges resulting from collapsed crater rising abruptly from the deep ocean near the coast, results in the formation of productive eddies and fronts on the islands edges. The northern waters of an island are found to be consistently colder than the warm and salty southern waters, and localized cold water with relative high chlorophyll concentrations phenomena is also observed in the waters of Madeira Island (Caldeira *et al.* 2002).

Despite the wide area that comprises the Madeira EEZ, data collected in this study reports only to the inshore area that surrounds the three islands of Madeira, Porto Santo and Desertas, covering a total of 4 818 km^2 up to 20 km offshore (Figure1.2). This area is characterized by a thin continental shelf, with steep submarine canyons and deep waters (Geldmacher *et al.* 2000) (Figure 1.3).

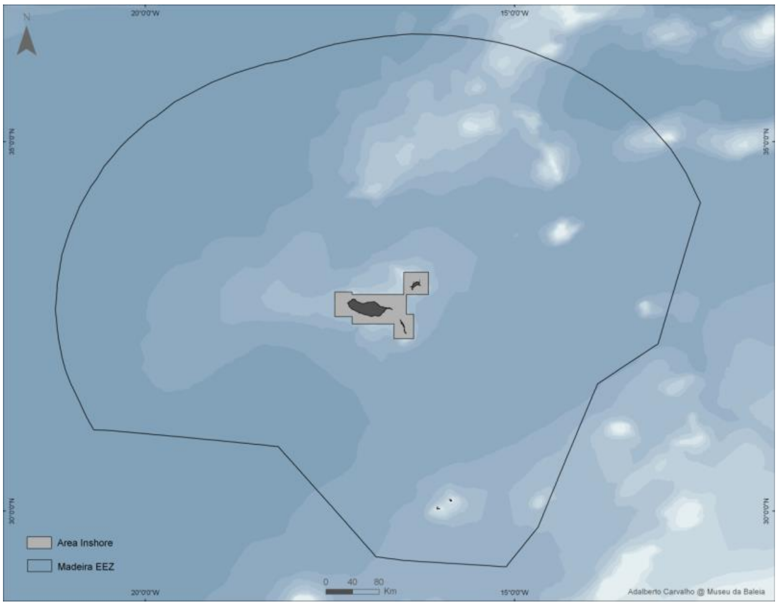

Figure 1.2- Map showing the Madeira EEZ and the inshore area where data was collected.

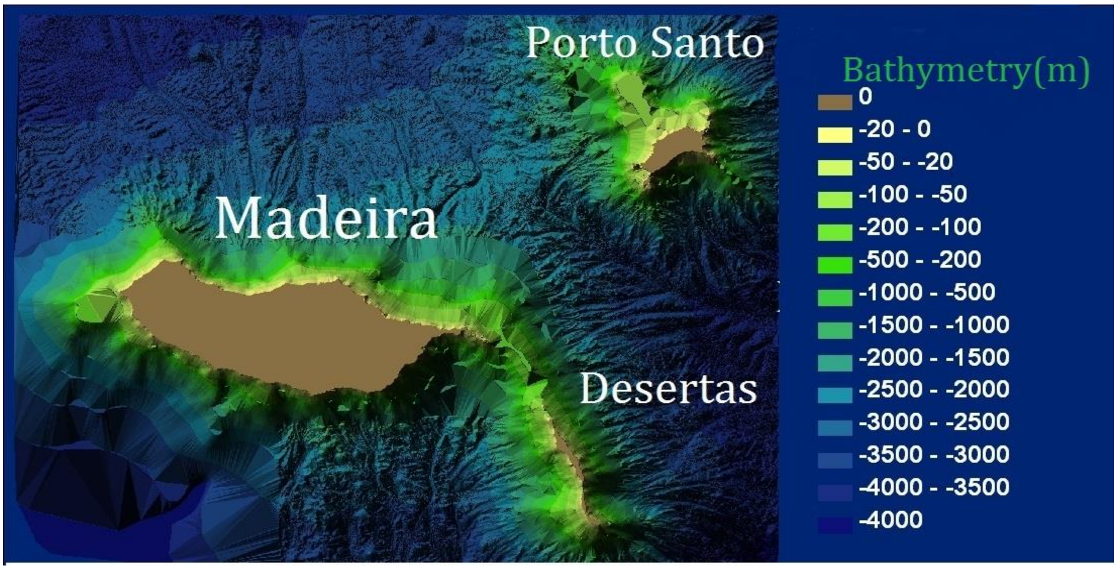

Figure 1.3- Map showing the bathymetry of the waters around Madeira, Desertas and Porto Santo. (data source: EMEPC -Estrutura de Missão para a Extensão da Plataforma Continental).

Madeira depends almost exclusively on tourism as it main source of income and over a million tourists visits the island every year (DRE 2013). Until a decade ago tourists visited Madeira for the year-round warm temperatures and exploring the mountain walks through the Laurel forests (UNESCO World Natural Heritage). In the last years the demand for marine touristic activities rapidly increased, and the whale-watching industry has grown in the same proportion. Marine tourism operators began doing sightseeing trips where they also advertised whale-watching. Nowadays, there are companies exclusively dedicated to whale-watching, including 'swimming with dolphins' activities (Vera 2012). After a 10 years period of voluntary viewing guidelines developed by the Madeira Whale Museum (Freitas *et al.* 2004), in 2013 the whale-watching activity became legally regulated by the Dec.-Leg. Regional 15/2013/M. In this legislation, the 'swimming with dolphins' activity becomes restricted to two dolphins species only: Atlantic spotted dolphin (*Stenella Frontalis*) and the short-beak common dolphin (*Delphinus delphis*), thus banning the tourists of any underwater activity with other cetacean species, including the bottlenose dolphin.

At present, there are 29 species of cetaceans reported for Madeira archipelago from which 25 are confirmed records (Freitas *et al.* 2012).

1.5 Thesis main objectives and rationale

Bottlenose dolphins are one of the most abundant species in Madeira archipelago (Freitas *et al.* 2006; Freitas *et al.* 2004). Despite this, scientific knowledge for this species in Madeira is insufficient. Ecological studies towards this species started only during the last decade, with work developed by the Madeira Whale Museum, and results are presented in this study.

The general objective of this work is to contribute to the conservation of the bottlenose dolphin in the Madeira archipelago through the investigation of aspects of the ecology of the species in this region. In order to understand the processes involved, some specific objectives were established: 1) access the population structure; 2) investigate site fidelity, residency and movement patterns; 3) estimate abundance and survival rates, and 4) investigate temporal distribution and habitat preferences related to physiographic parameters.

Social structure is known to affect ecology, genetics, population biology, and thus issues of conservation and management (Sutherland 1998). For that reason, in order to gain a better understanding of the biology of the studied animals, as well as of the effects of human activities on them, we need to study the social system of a population (Whitehead & Van Parijs 2010). Following, patterns of residency and site fidelity are often indicative of the ecology of a population; evidence of repeated sightings in the same area can be used to establish core areas or ranges of individuals and point out the importance of a habitat. Furthermore, the study of life history parameters is of fundamental importance to understanding the dynamics of animal populations. Demographic processes, such as fluctuations in survival and reproduction, are the ultimate cause of population change (Gaillard *et al.* 1998). Finally, effective conservation of wild populations requires an understanding of the relationship between populations and their habitats, and for that the first step is to determine which habitats are used with higher frequency (Cañadas *et al.* 2005).

This work represents a important contribution to the knowledge and conservation of bottlenose dolphins inhabiting Madeira archipelago waters. Prior to this, no systematic study has examined the abundance, social structure, patterns of site-fidelity or habitat use of bottlenose dolphins in Madeira archipelago. Bottlenose dolphins are apex predators, and determining the status of this population may prove to be a useful indicator of the health and stability of the habitat they live in. In addition, bottlenose dolphins that use the waters of the archipelago are subject to multiple human impacts from which the whale-watching activity stands as the major potential threat. Finally, bottlenose dolphins in Madeira are not genetically and/or geographically isolated from the population of neighbouring archipelago of Azores, and thus they are part of a single population, from a conservation standpoint (Querouil *et al.* 2007). As local threats may impact the entire population, preserving this pelagic population is critical as it may act as a pool for inshore populations (Querouil *et al.* 2007; Natoli *et al.* 2004).

The results presented here will provide baseline data and insight on the current significance of the population of bottlenose dolphins utilising the archipelago of Madeira. This information will support conservation managers in the management and protection of this population.

1.6 Chapters overview

Chapter 2 aims to examine 11 years of individual photo-identification data of the bottlenose dolphin population that occurs in Madeira archipelago in order to investigate its social structure. This was achieved by analysing the type of association indices between pairs of identified individuals, the patterns of affiliation between individual dolphins and the probabilities of associations between individuals, over time.

In Chapter 3, following the research of the previous chapter, data from individual photo-identification is used to determine group dynamics, to assess the level of residency and site fidelity, and to investigate movements patterns within and out the study area.

Chapter 4 aims to estimate apparent survival and seasonal abundance of the bottlenose dolphin population in Madeira archipelago, taking into account heterogeneity of capture probabilities by applying distinctive approaches on capture-recapture records of naturally marked individuals. The estimated aimed to resident dolphins and to the super population that used the area during the study period.

In Chapter 5, bottlenose dolphin sighting and survey effort data is used to examine habitat use and distribution of bottlenose dolphins around Madeira, Desertas and Porto Santo islands. These analyses use data from 2001-2012 (excluding 2003) to calculate encounter rates and to investigate temporal occurrence and spatial distribution of bottlenose dolphins in the study area.

References

Alves F, Querouil S, Dinis A, Nicolau C, Ribeiro C, Freitas L, Kaufmann M, Fortuna C (2013). Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: implications for conservation. *Aquatic Conservation: Marine and freshwater ecosystems,* 5: 758-776.

Ballance LT (2009). Cetacean Ecology. In: W.F. Perrin, B. Würsig, J.G.M. Thewissen (Eds.), Encyclopedia of marine mammals, second ed. Academic Press, Amsterdam.

Barros NB, Odell DK (1990). Food habits of bottlenose dolphins in the Southeastern United States. In: S. Leatherwood and R. R. Reeves (Eds.).The Bottlenose Dolphin. Academic Press, Inc. London.

Cabral MJ (coord), Almeida J, Almeida PR, Dellinger T, Almeida NF, Oliveira ME, Palmeirim JM, Queiroz AL, Rogado L, Santos-Reis M, editors (2005). Livro Vermelho dos Vertebrados de Portugal. Instituto de Conservação da Natureza, Lisboa.

Caldeira RMA, Groom S, Miller P, Pilgrim D, Nezlin NP (2002). Sea-surface signatures of the island mass effect phenomena around Madeira Island, Northeast Atlantic. *Remote Sensing of the Environment* 80: 336-360.

Cañadas A (2006). Towards the conservation of dolphins in the Alborán Sea. PhD thesis, University Autónoma de Madrid.

Cañadas A, Sagarminaga R, de Stephanis R, Urquiola E, Hammond PS (2005). Habitat preference modelling as a conservation tool: Proposals for marine protected areas for cetaceans in southern Spanish waters. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 15: 495-521

Connor RC, Mann J, Tyack PL, Whitehead H. (2000). The Social lives of Whales and Dolphins. In: J. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead (Eds.), Cetacean societies: field studies of dolphins and whales. The University of Chicago Press, Chicago and London.

Corketon P (2009). Captivity. In: W.F. Perrin, B. Würsig, J.G.M. Thewissen (Eds.), Encyclopedia of marine mammals, second ed. Academic Press, Amsterdam.

Croll DA, Tershy BR, Hewitt RP, Demer DA, Fiedler PC, Smith SE, Armstrong W, Popp JM, Kiekhefer T, Lopez VR, Urban J, Gendron D (1998). An integrated approach to the foraging ecology of marine birds and mammals. *Deep-Sea Research II*, 45: 1353-1371.

Curry BE (1997). Phylogenetic relationships among bottlenose dolphins (genus *Tursiops*) in a worldwide context. PhD thesis, Texas A&M University.

Direcção Regional de Estatística-DRE (2013). Statistical Yearbook of Região Autónoma da Madeira. Funchal, Potugal.

Duffield DA, RS Wells (2002). The molecular profile of a resident community of bottlenose dolphins, *Tursiops truncatus*. In: C.J. Pfeiffer (Ed.) Molecular and Cell Biology of Marine Mammals. Krieger Publishing Company, Melbourne, FL.

Duffield DA, Ridgway SH, Cornell LH (1983). Hematology distinguishes coastal and offshore forms of dolphins (*Tursiops*). *Canadian Journal of Zoology*, 61: 930-933.

European Union Habitats Directive (1992). http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm

Freitas L, Dinis A, Nicolau C, Ribeiro C, Alves F (2012). New records of cetacean species for Madeira Archipelago with an updated checklist. *Boletim do Museu Municipal do Funchal* 62 (334): 25-44.

Freitas L, Dinis A, Alves F (2006). Occurrence and distribution of cetaceans off Madeira archipelago (Portugal). Proceeding of the *20th Conference of the European Cetacean Society*, 2-7 April, Gdynia, Poland.

Freitas L, Dinis A, Alves F, Nóbrega F (2004). Cetáceos no Arquipélago da Madeira. Museu da Baleia, Machico, Madeira, Portugal.

Gaillard JM, Festa-Bianchet M, Yoccoz NG (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, 13: 58–63.

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

Gunter G (1951). Consumption of shrimp by the Bottlenosed Dolphin. *Journal of Mammalogy* 32:465–466.

Hersh SL, Duffield DA (1990). Distinction between northwest Atlantic offshore and coastal bottlenose dolphins based on hemoglobin profile and morphometry. In: S. Leatherwood and R. R. Reeves (Eds.). The Bottlenose Dolphin. Academic Press, Inc. London.

Hoyt E (2011). Marine Protected Areas for Whales, Dolphins and Porpoises: a World Handbook for Cetacean Habitat Conservation and Planning, second ed. Earthscan, New York.

Ingram SN, Rogan E (2002). Identifying critical areas and habitat preferences of bottlenose dolphins (*Tursiops truncatus)*. *Marine Ecology Progress Series*, 244: 247-255.

IPCC (2001). Climate Chang: Impacts, Adaptation and Vulnerability, Cambridge University Press

Johnson J, Stevens I (2000). A fine resolution model of the eastern North Atlantic between the Azores, the Canary Islands and the Gibraltar Strait. *Deep-Sea Research I,* 47: 875-899.

Kenney RD (1990). Bottlenose dolphins off the northeastern United States. In: S. Leatherwood and R. R. Reeves (Eds.) The Bottlenose Dolphin. Academic Press, Inc. London. pp: 369-386.

Learmonth JA, MacLeod CD, Santos MB, Pierce GJ, Crick HQP, Robinson RA (2006) Potential effects of climate change on marine mammals. *Oceanography and Marine Biology: An Annual Review*, 44: 431-464.

LeDuc RG, Perrin WF, Dizon AE (1999). Phylogenetic relationships among the delphinid cetaceans based on full cytochrome b sequences. *Marine Mammal Science*, 15: 619-648.

Lettink M, Armstrong DP (2003). An introduction to using mark-recapture analysis for monitoring threatened species. Department of Conservation Technical Series 28A: 5-32.

Mann, J, Connor R, Barre L, Heithaus M (2000). Female reproductive success in botlenose dolphins (Tursiops sp.): life history, habitat, provisioning, and group-size effects. *Behavioral Ecology,* 11(2): 210-219.

Mead JG, Potter CW (1995). Recognizing two populations of the bottlenose dolphin (*Tursiops truncatus*) off the Atlantic coast of North America: morphologic and ecologic considerations. *IBI Report*, 5: 31-44.

Mead JG, Potter CW (1990). Natural history of bottlenose dolphins along the central Atlantic coast of the United States. In: In S. Leatherwood, R.R. Reeves (Eds), The bottlenose dolphin. Academic Press, San Diego.

Natoli A, Peddemors VM, Hoelzel AR (2004) Population structure and speciation in the genus *Tursiops* based on microsatellite and mitochondrial DNA analyses. *Journal of Evolutionary Biology*, 17, 363–375.

New AL, Jia Y, Coulibaly M, Dengg J (2001). On the role of the Azores Current in the ventilation of the North Atlantic Ocean. *Progress in Oceanography* 48: 163-194.

Norris KS, Dohl TP (1980). The behavior of the hawaiian spinner porpoise, *Stenella longirostris*. Fishery Bulletin 77: 821-849.

Owen ECG, Hofmann S, Wells RS (2002). Ranging and social association patterns of paired and unpaired adult male bottlenose dolphins, *Tursiops truncatus*, in Sarasota, Florida, provide no evidence for alternative male strategies. *Canadian Journal of Zoology*. 80:2072-2089.

Parsons KM, Durban JW, Claridge DE, Herzing DL, Balcomb KC, Noble LR (2006). Population genetic structure of coastal bottlenose dolphins (*Tursiops truncatus*) in the northern Bahamas. *Marine Mammal Science* 22: 276-298.

Quérouil S, Silva MA, Freitas L, Prieto R, Magalhães S, Dinis A, Alves F, Matos JA, Mendonça D, Hammond P, Santos RS (2007). High gene flow in oceanic bottlenose dolphins (*Tursiops truncatus*) of the North Atlantic. *Conservation Genetics,* 8: 1405-1419.

Rice DW (1998). Marine Mammals of the World: Systematics and Distribution. Special Publication, 4, Society for Marine Mammology, Allen Press, Lawrence.

Rogers CA, Brunnick BJ, Herzing DL, Baldwin JD (2004). The social structure of bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Marine Mammal Science* 20:688-708.

Ross GJB (1977) The taxonomy of bottlenosed dolphins *Tursiops* species in South African waters, with notes on their biology. *Ann. Cape Prov. Mus. Nat. Hist.* 11, 135-194.

Sala I, Caldeira RMA, Estrada-Allis SN, Froufe E, Couvelard X (2013). Lagrangian transport pathways in the northeast Atlantic and their environmental impact. *Limnology and Oceanography: Fluids and Environments* 3: 40-60.

Schroeder PJ (1990). Breeding bottlenose dolphins in captivity. In S. Leatherwood, R.R. Reeves (Eds), The bottlenose dolphin. Academic Press, San Diego.

Schroeder PJ, Keller KV (1990) Artificial insemination of bottlenose dolphins. In S. Leatherwood, R.R. Reeves (Eds), The bottlenose dolphin. Academic Press, San Diego.

Scott MD, Chivers SJ (1990). Distribution and herd structure of bottlenose dolphins in the eastern tropical Pacific Ocean. In S. Leatherwood, R.R. Reeves (Eds) The Bottlenose Dolphin. Academic Press, San Diego, CA.

Scott MD, Wells RS, Irvine AB (1990). A long-term study of bottlenose dolphins on the west coast of Florida. In S. Leatherwood, R.R. Reeves (Eds), The bottlenose dolphin. Academic Press, San Diego.

Shane SH, Wells RS, Wursig B (1986) Ecology behavior, and social organization of the bottlenose dolphin: a review. *Marine Mammal Science*, 2: 34-63.

Skilling D (2007). The Economic Effects of Climate Change: Positioning New Zealand to respond. The New Zealand Institute.

Smolker RA, Richards AE, Connor RC, Pepper JW (1992). Sex differences in patterns of associations among Indian Ocean bottlenose dolphins. *Behaviour,* 123, 38-69.

Sutherland WJ (1998). The importance of behavioural studies in conservation biology. Animal behaviour, 56: 801-809.

Tomczak M, Godfrey JS (1994). Regional Oceanography: an introduction. Pergamon, London.

Torres LG, Rosel PE, D'Agrosa C, Read AJ (2003). Improving management of overlapping bottlenose dolphin ecotypes through spatial analysis and genetics. *Marine Mammal Science*, 19: 502-514.

Vera AH (2012). Quantification of the exposure of cetacean individuals to whale-watching vessels through the photo-identification technique in the South coast of Madeira Island (Portugal). Research Study for the Environmental Sciences Degree, Faculty of Biology, University of Murcia, Spain.

Wells RS (2003). Dolphin social complexity: lessons from long-term study and life history. In: F.B.M. de Waal and P.L. Tyack (Eds.) Animal social complexity: intelligence, culture, and individualized societies. Harvard University Press, Cambridge, MA.

Wells RS, Scott MD (2009). Common Bottlenose dolphin (*Tursiops trucatus*). In: Perrin, W.F., Würsig, B., Thewissen, J.G.M. (Eds.), Encyclopedia of marine mammals, second ed. Academic Press, Amsterdam, pp. 361-364.

Wells RS, Scott MD (1999). Bottlenose dolphin *Tursiops truncatus* (Montagu, 1821). *In*: S.H. Ridgway and R. Harrison (Eds.), Handbook of Marine Mammals, Vol. 6, the Second Book of Dolphins and Porpoises. Academic Press, San Diego.

Wells RS, Scott MD, Irvine AB (1987). The social structure of free-ranging bottlenose dolphins. In: H Genoways (Ed.) Current Mammalogy, Plenum Press: New York.

Whitehead H; Van Parijs S (2010). Studying marine mammal social systems. In: I. Boyd, W.D. Bowen, S.J. Iverson (Eds.) Marine Mammal Ecology and Conservation: A Handbook of Techniques. Oxford University Press, New York.

Wilson B, Thompson PM, Hammond, PS (1997) Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology, 34*: 1365-1374.

Wilson B, Thompson P, Hammond PS (1993). An examination of the social structure of a resident group of bottlenose dolphins (*Tursiops truncatus*) in the Moray Firth, N.E. Scotland. In *7th annual conference of the European Cetacean Society*.

CHAPTER 2

POPULATION STRUCTURE OF BOTTLENOSE DOLPHINS IN MADEIRA ARCHIPELAGO

2.1 INTRODUCTION

One of the most important attributes of any animal population is its social structure (Whitehead 2009). This is often a key element of the population biology of a species, influencing gene flows, spatial pattern and scale or predation (Wilson 1975). Mammals have complex social structures; these may vary considerably through time, both between and within species. Describing and classifying those structures is complex and challenging (Costa & Fitzgerald 1996). Knowledge regarding the identity of the interacting, associating or grouped animals is essential for social structure studies (Whitehead & Van Parijs 2010). These are based on identifying individual animals and recording their interactions (Whitehead 2008). One of the best methods to achieve this is using photo-identification. Photo-identification is based on the repeated recognition of individuals through photographs and has become an essential technique to provide information on group stability and association patterns (Würsig & Würsig 1977). Photographing certain body parts is a non-invasive method of identifying and monitoring individuals over time. Bottlenose dolphins, as well as other dolphin species can be individually identified using photo-identification of their dorsal fins (Würsig & Jefferson 1990). Each individual has a distinct and unique contour of the fin as a consequence of the interactions with conspecifics, environmental or anthropogenic factors. Thus, the posterior edge of the dolphin's dorsal fin may become irregular, resulting in recognizable patterns of notches and scars (Würsig & Jefferson 1990).

Querouil *et al.* (2007) suggest that there is a single population of bottlenose dolphins in the pelagic waters of the North-East Atlantic, and that this population is not significantly differentiated from the pelagic population of the North-West Atlantic. Madeira archipelago is one of the most isolated oceanic habitats in Northeast Atlantic; as such, one could expect to find a greater differentiation in the population structure. However, dolphins are capable of travelling large distances in short periods (Wells *et al.* 1999), making it possible that the lack of geographic structuring is explained by large home ranges and/or high dispersal in the study area (Quérouil *et al.* 2007). In terms of genetic structure the bottlenose dolphins in Madeira seem to be part of a bigger Atlantic pelagic population with high levels of gene flow (Quérouil *et al.* 2007).

Strong site fidelity, with the presence of both resident groups and resource specialization, as a consequence of different social and behavioural strategies, could be some two of the leading factors for the genetic structure (Hoelzel *et al.* 1998). Consequently, the social structure is sensitive to the genetic population structure (Whitehead & Van Parijs 2010).

Associations are often defined using spatial-temporal groups, that is, animals are associated if they are members of the same group (Whitehead 2008). The observations of associations or groups are then used to calculate relationship measures such as interaction rates and association indices. These can then be synthesized into models of social structure using ordinations, cluster analyses, network analyses, lagged association rates, and other uni- and multivariate techniques (Whitehead & Van Parijs 2010).

Previous studies on bottlenose dolphins describe them as living in a so-called fission-fusion community, individuals associate in small groups that change in composition, often on a daily or even hourly basis (Wells *et al.* 1987, Würsig & Würsig 1977). Unlike animals that live in groups of constant composition, social, relationships on fission-fusion society may depend strongly on 'who is there and who is not' (Connor *et al.* 2000). Most information about bottlenose dolphin social organization comes from three long-term studies carried out in Sarasota Bay Florida (Wells 1991), Shark Bay (Western Australia) (Smolker *et al.* 1992) and Moray Firth (Scotland) (Wilson 1995). Those studies report a great variability in social strategies within and between populations emerges, such as different gender-related bonds that could be due to differences in predation risk, availability or use of resources and mating (Connor *et al.* 2000). The same authors point that our understanding of bottlenose dolphin social relationships and its ranging patterns provides the establishment of population units that can support management. In Florida, patterns of social association facilitate the partitioning of continuously distributed resident dolphins into geographically management units (Wells 1986). The frequency of associations between individuals that inhabit overlapping or adjacent ranges can help define population units. Given this information is geo-referenced, the definition of management units makes it possible to relate specific threats to a particular population community, allowing the assessment of potential impacts and mitigation efforts (Connor *et al.* 2000). Some of the pressures bottlenose dolphins faces in Madeira are fisheries, costal development and whale-watching; this latter may be the major direct threat in the south of Madeira Island.

The aim of this study was to examine individual photo-identification data of the bottlenose dolphin population that occur in Madeira archipelago in order to investigate the species social structure. This was achieved by analysing the type of association indices between pairs of identified individuals; the patterns of affiliation between individual dolphins and the probabilities of association between individuals over time. Information on social structure is important for management and conservation plans for this species in the study area, as the potential differences in its social units may require distinctive management strategies.

2.2 Methods

2.2.1Study area

The Madeira archipelago is located in the Northeast Atlantic (32ºN; 17ºW) at app. 670 km from Morocco (Figure 2.1). It is formed of two main volcanic islands, Madeira and Porto Santo, separated by a stretch of app. ≃ 50km. It comprises also two sub-archipelagos; the Desertas Islands, located app. ≃20km southeast, and the Selvagens Islands located 300 km south of Madeira Island. Madeira and Porto

Santo are inhabited, whereas Desertas and Selvagens are not. Additionally the two latter are natural reserves (Caldeira & Sangrá 2012). These oceanic volcanic islands have a reduced continental shelf which results in deep waters and submarine canyons just a few miles offshore (Geldmacher *et al.* 2000). Depths can reach 3000m.

Figure 2.1- Map highlighting Madeira archipelago and its islands, located in the Northeast Atlantic. A gradient of bathymetry is show on a scale of blue.

Data was recorded from boat surveys around the islands of Madeira, Desertas and Porto Santo (Figure 2.2) The study area was divided in eight sectors encompassing a total of 4 818 km^2 up to 20 km offshore.

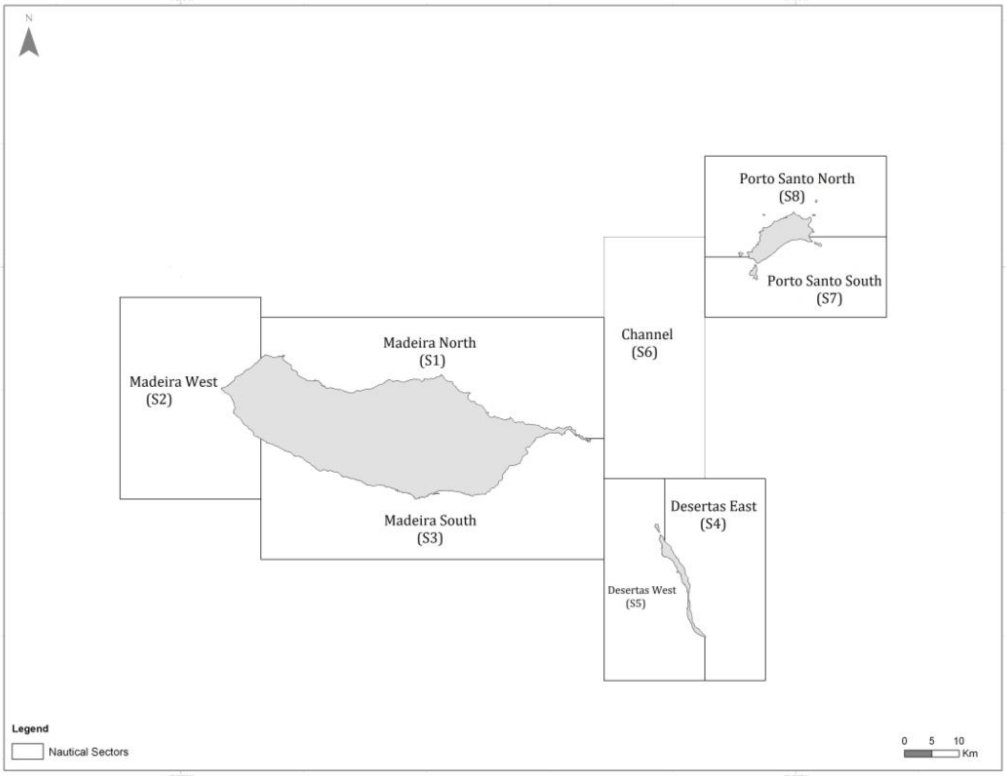

Figure 2.2 – Map of the main study area with the division of the eight sectors used in this study: S1- Madeira North; S2- Madeira West; S3- Madeira South; S4- Desertas East; S5- Desertas West; S6- Channel; S7- Porto Santo South and S8- Porto Santo North.

2.2.2 Photo-identification surveys

Photographs were taken on year-round systematic and non-systematic research boat surveys, as well as from whale-watching boats.

One hundred and seventeen systematic surveys were carried out following predetermined line-transects covering the eight sectors. Surveys were carried out between 2001-2002 and 2004, and from 2007 to 2012. In 2003 no data was collected. Two vessels were used: the 12 m vessel *Calcamar* (in 2001 and 2002; at 11 km/h), and the 18 m research yacht *Ziphius* (from 2004 to 2012; cruise speed 12 km/h). The surveys had a mean duration of 11h 30min (harbour to harbour). An average of 3 observers searched the area. The observers searched the area up to the horizon, assisted with 7 x 50 binoculars, at an eye-height of 3 m or 5 m above the sea level when using Calcamar or Ziphius respectively. The boat followed predefined equal spaced zig-zag line-transects generated by Distance 4.0

(Thomas *et al.* 2010) to ensure, as much as possible that equal geographic coverage was obtained. Data and track courses were recorded on a laptop connected to a GPS, using the data logging software Logger 2000 (developed by the International Fund for Animal Welfare). Weather, effort, and sighting information (GPS position, initial time, best group size estimation and group composition) were recorded. Effort was conducted during daylight hours and only with Beaufort Sea state ≤3. In the systematic surveys, time sometimes constrained the data collection of individual photographs of the entire group; as such the photographic coverage and identification of all the individuals present in the group was not always possible.

One hundred and eighty four non-systematic surveys were carried out between 2004 and 2012. Surveys were conducted during daylight hours and sea state ≤3 Beaufort Sea using a 6.5 m rigid inflatable boat *Roaz* (cruise speed 15-25 km/h) and the 18 m research yacht *Ziphius* (cruise speed 12 km/h). Two to four observers searched the area up to the horizon, assisted with 7 x 50 binoculars, at an eye-height of app. 2 m. No predefined transect were followed. A daily assessment was made to define which area survey; this was done based on weather conditions, tips of observers on land; tips from the whale-watching boats and areas expected to have a higher presence of dolphins. The mean duration of surveys was 6h16 and the searching effort was not equally distributed throughout the different areas.

When a group of dolphins was encountered, data on the sighting was collected. Following that, the boat slowly approached the group and an attempt was made to obtain several photographs to identify each individual. In this study, the term ‘group’ was used as the sampling unit and defined as all dolphins sighted within a 100 m radius of each other (Wells *et al.* 1987). Dolphins were classified into three categories - adults, subadults and calves according to their size, colour, and behaviour. The adult class corresponded to large and robust animals. Calves were identified by their small body size and/or permanent association with an adult (Mann *et al.* 2000). Individuals whose body size was smaller than that of adults and that were independent from an adult animal were considered subadults (Wells *et al.* 1987). Photographs were taken using digital cameras (Nikon D2H and D700) equipped with Nikkor zoom lenses ranging between 70-400 mm in both systematic and random surveys.

Digital photographs from different opportunistic platforms were analysed. These images were obtained from 2003 to 2012 in the south coast of Madeira island (sector 3; Figure 2.2). The opportunistic platforms operate year-round, with 1-3 daily trips, with no specific target species. The photographs were taken whenever bottlenose dolphins were sighted by trained observers onboard, as well by experienced skippers.

2.2.3 Photo-identification processing

A photo-identification (photo-id) catalogue was compiled. A dataset of capture histories was created using individual information taken from the photographs. (Würsig & Jefferson 1990). An individual identification within an encounter was defined as a capture.

Photographs were graded as 'good', 'fair' or 'bad' (Figure 2.3), according to their level of focus, contrast, exposure, the angle and size of the dorsal fin in the frame. Additionally, the distinctiveness of each frame was graded as 'very distinct', 'distinct', slightly distinct' or 'unmarked' (Figure 2.4). Only 'good' quality, 'very distinct' and 'distinct' photographs were used in this study in order to increase the certainty of matches. Calves were excluded from the analysis.

(a) (b) (c)

Figure 2.3 – Examples of (a) good, (b) fair and (c) bad quality photos of the same individual, Tt 250.

(a) (b) (c) (d)

Figure 2.4 – Examples of (a) very distinctive, (b) distinctive, (c) slightly distinctive and (d) unmarked individuals.

All photo processing was done using Darwin 2.0 © (Eckerd College Dolphin Research Group), including cropping the dorsal fin area and adjusting light and contrast. Then a contour was done to the trail edge, which is identifiable from both sides (Auger-Méthé & Whitehead 2007), and the program compared that fin to all others stored in the database searching for a match. Only the contour was used to compare the fins, secondary features like fin shape or scars were only used to confirm a match by naked eye. Whenever a match was found, confirmation by the researcher was made, and the same identification number from the individual stored in the database was assigned. If the program did not find a match, the researcher would make another attempt of comparison by eye, with all the individuals of the catalogue, using the number of nicks of the dorsal fin. If a match still was not found, a new identification number was attributed to that individual and it added to the catalogue.

2.2.4 Association patterns

Data for association analysis was organized to suit the needs of the software programs SOCPROG 2.4 (Whitehead 2009). Sampling period was defined as a day, and associations defined as individuals grouped within an encounter (Whitehead & Dufault 1999).

2.2.4.1 Cluster analysis

Cluster analysis can be a useful way to classify and visually display relationships among individuals by means of association indices (Whitehead 2008). A hierarchical cluster analysis was obtained from the association data and it was used to illustrate the relationships between dolphins. The cophenetic correlation coefficient (CCC), was used to determine which type of cluster analysis was more suitable to the data. The CCC is the correlation between the actual indices of association and the levels of clustering shown in the diagram. It indicates the effectiveness of the analysis in order to separate potential dendrograms from those that are truly representative of complex social structure.

The average-linkage method using simple ratio (SR) (Equation 2.1) association indices was elected as the most appropriate for this data when compared to single-, complete-, and Ward's- linkage (not shown). It provided the best CCC value, as ≥0.8 is considered to be a good fit (Bridge 1993).

$$\mathrm{SR} = \frac{X}{X\ Ya\ Yb} \qquad \text{Equation 2.1}$$

where:

X = the number of times both individual a and b were seen together in the same group,

Ya = the number of times individual a was seen,

Yb = the number of times individual b was seen.

The index most commonly used in the analysis of social structure in cetacean populations is the Half Weight Index (HWI) (Wells *et al.* 1987; Smolker *et al.* 1992; Slooten *et al.* 1993; Bedjer *et al.* 1998; Maze-Foley & Würsig 2002). This is mainly because in photo-id it is not always possible to photograph and identify all individuals within a group, making the HWI least biased when pairs are more likely to be seen separate than together (Cairns & Schwager 1987). Despite this, Ginsberg & Young (1992) argued that the general use of the SR is recommended and Whitehead (2008) refers that, if association indices are compared among dyads or within populations it is more likely that the bias will be similar for all dyads, making it of least concern. Also, the sampling period was set short (a day) in order to reduce to the minimal bias (Whitehead 2008).

Permutation tests were performed to assess if the dolphins showed any preferred/avoided associations (Manly 1995; Bedjer *et al.* 1998; Whitehead 1999). The number of permutations implemented was increased until the *P* value obtained from the Monte Carlo simulation stabilized and the confidence intervals decreased. Two options for permuting data in this kind of analysis were used in this study: 'Permuting groups within samples' and 'Permuting associations within samples'. The former investigates both short-term (within a sampling period) and long-term (between sampling periods) associations, while the latter investigates only for long-term associations (Whitehead 2008; Whitehead 2009). The same author suggested that 'Permuting associations within samples' is the more useful method because it has fewer assumptions and it controls for gregariousness although not for factors affecting the presence of group members (*e.g.* demographic effects like birth, mortality or migration). To test for both long- and short-term associations, the two described tests were included in this analysis.

In order to determine if there were divisions within the study population, modularity (Newman 2004) was investigated. Modularity is the difference between the proportion of the total association and the expected proportion, within the clusters. It ranges between 0.0 (randomly formed clusters) and 1.0 (no associations between members of different clusters) (Whitehead 2008). Newman (2004) suggests that if the modularity ≥ 3, then the division between the clusters is 'good'. Using a modification to Newman’s test, Lusseau (2007) designed a method to maximize modularity through a series of tests along the dendrogram, where maximum modularity gives a correspondent association index called 'stopping point' that is the recommended cut-off value to form sub-groups or units.

For this study, only dolphins that had been recorded at least three times between 2001 and 2012 were used. This value was selected as appropriate to ensure a more accurate representation, given the range of the existing dataset.

2.2.4.2 Temporal analyses: Standardized Lagged Association Rate (SLAR)

Whitehead (1995) introduced several analyses to address the scales of temporal patterning in social relationships. The Lagged Association Rate (LAR) (Equation 2.2) is the probability of two individuals associated at a given time, will still be associated time lags in the future, as given in the following equation:

$$g(\tau)=\frac{\sum_{j,k\backslash(t_k-t_j)=\tau}\ \sum_{X}\ \sum_{Y\neq X} a_j(X,Y)\,.\,a_k(X,Y)}{\sum_{j,k\backslash(t_k-t_j)=\tau}\ \sum_{X}\ \sum_{Y\neq X} a_j(X,Y)\,.\,a_k(X,X)} \qquad \text{Equation 2.2}$$

where:

for a time period *j*: a_j (X,Y)=1 if X and Y were recorded in association;

a_j (X,Y)=0 if either they were not associated or none of the two individuals was identified during sampling period.

The same applies to sampling period *k,* where a_k (X,X)=1 if X was identified in period *k* and a_k (X,X)=0 if X was not identified during the sampling period.

The LAR is an estimate that uses individual identification histories to calculate the ratio of the number of observed dyadic associations, occurring at different time lags to all potential associations.

In many cases, a zero in the association data do not mean that the individuals do not associate, but rather that the dyad was not observed associated during the sampling period. In other words, not all the individuals within each sampling period were accurately identified. In these cases Whitehead (1995) suggests using Standardized Lagged Association Rate (SLAR) (Equation 2.3) instead of LAR. SLAR expresses the probability of given the observed association of Y with X, a randomly chosen association of X, identified after a time lag, will be with Y.

$$g'(\tau)=\frac{\sum_{j,k\backslash(t_k-t_j)=\tau}\ \sum_{X}\ \sum_{Y\neq X} a_j(X,Y)\,.\,a_k(X,Y)}{\sum_{j,k\backslash(t_k-t_j)=\tau}\ \sum_{X}\left[\sum_{Y\neq X} a_j(X,Y)\right]\left[\sum_{Y\neq X} a_k(X,Y)\right]}$$

Equation 2.3

LARs and SLARs are plotted continuously against time lag, with a moving average method. The number of potential associations can be changed, over which the lagged associated rate and its accompanying lag are calculated. Care must be taken to find an optimal moving average that does not compromise the data, because lag will be less precise as the lagged association curve smoothes.

Like other social measures, SLARs have little value without some measures of precision. In this study a temporal jacknife was used, in which different sets of sampling periods are omitted in turn (Whitehead 2007), and implemented by SOCPROG. Jacknifing is an acceptable measure of precision even though its estimates are conservative and the assumption of independence might not be met (Whitehead 1995; Whitehead 2007). Jacknife values are displayed in the graph by error bars (Figure 2.9).

The inclusion of a null model provides an important basis for comparison to determine whether preferred associations are present in the population. It helps to consider what would be the values if the dolphins associated randomly. The standardized null association rate is the inverse of the number of identified individuals minus one, and does not change over time lag (Whitehead 2008).

Exponential models available in SOCPROG 2.4 were fitted to the SLAR using maximum likelihood and binominal loss (Table 2.1). All SLAR models were fitted to the curve and the best-fit model was chosen as that with the lowest Quasi Akaike Information Criteria (QAIC) value. The difference between the QAIC of any other model and the selected one (ΔQAIC) gives an indication of how well the data support the less favoured models following Burnham & Anderson (2002), where:

ΔQAIC: 0-2 substantial support for model
ΔQAIC: 4-7 considerably less support
ΔQAIC: >10 essentially no support.

Data used in this analysis comprised all sighting histories independently of the coverage. This is mainly because the LAR is meant to describe temporal associations between the entire population, and not just those associations within the individuals encountered more often (Whitehead 2008). Additionally, given the small sample size, the group coverage in each sampling period was not a restricting factor in order not to bias the SLAR analyses.

Table 2.1 – Description of the models that can be fitted to the SLARs, using maximum likelihood and binominal loss, in SOCPROG 2.4.

Model description	Model Equation	Model interpretation
Constant Companions (CC)	$g'=a$	Constant companions, who stay together permanently
Casual Acquaintances (CA)	$g'=a*e^{-b\tau}$	Casual acquaintances, who associate for some time, disassociate, and may re-associate
CC + CA	$g'=a+c*e^{-b\tau}$	Association followed by disassociation at some time lag to a lower level of associations where associations stabilize
Two levels of CA	$g'=a*e^{-b\tau}+c*e^{-d\tau}$	Association and disassociation occurring on two different time scales

2.3 RESULTS

2.3.1 Photo-identification surveys

Between 2001 and 2012, there were 272 encounters resultant from 231 different days; these included dedicated effort and whale-watching trips (Figure 2.5).

Individual sighting histories varied greatly during the entire study period, ranging from individuals sighted only once to individuals seen up to 13 times (median=2). A total of 501 individuals were identified and catalogued, based on the marks of their dorsal fin. The discovery curve for the overall number of individuals increased throughout the study period as new individuals kept being added to the catalogue. such finding suggests an open population with regular recruitment of new animals to the study area. Contrarily, the discovery curve for re-sighted individuals seemed to stabilize, as fewer new previously identified individuals were being added to the catalogue (Figure 2.5).

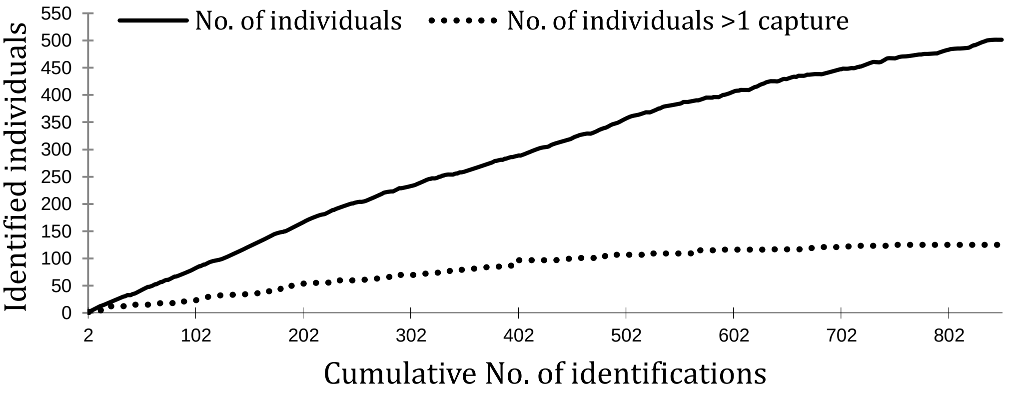

Figure 2.5- Discovery curve of the total number of marked individual dolphins (solid line) and the total number of individuals captured >1 time (....).

2.3.2 Associations patterns

Seventy dolphins were captured on three or more occasions. The overall mean association index was 0.03 (range=0.01-0.06; SD± 0.01) suggesting that, in general associations within the population were low. Also, the maximum association index for each individual had a low average of 0.38 (range=0.17-1.00; SD ± 0.18). The maximum association index of 1.00 was recorded for two individuals (Tt074 and Tt078) that showed a strong dyadic association, indicating that they were always seen together (three occasions) (Figure 2.6).

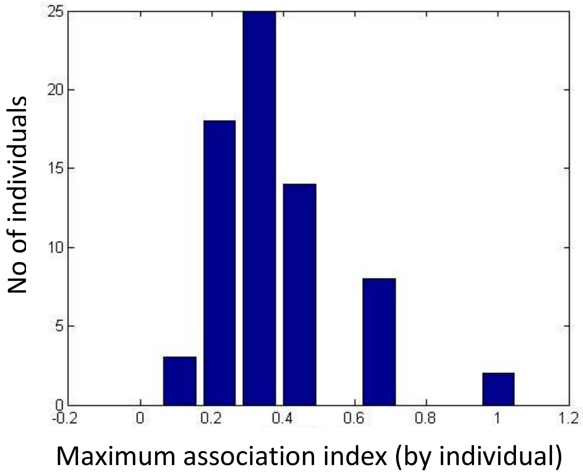

Figure 2.6 – Distribution of the maximum association index for distinctive individuals, captured ≥3 times in the study area.

The number of individuals with whom dolphins associated with was not consistent (mean=2.93; range=1.47-5.08; SD±0.90) (Figure 2.7). Although this may indicate some differences in individual gregariousness, it may also reflect low coverage of groups sampled.

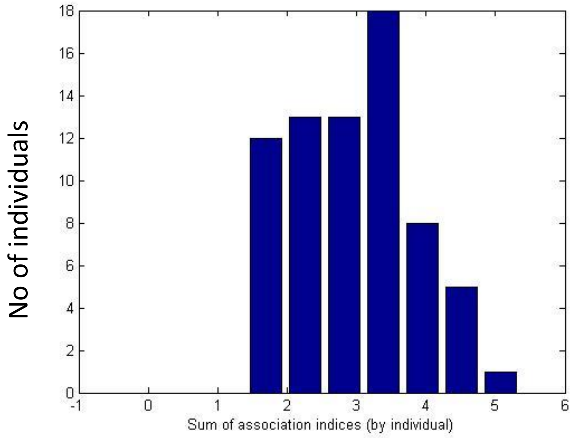

Figure 2.7 – Distribution of the sum of association index for each individual, captured more than three times in the study area.

Permutation tests for non-random associations indicated that the dolphins recorded in this study did not associate preferentially with, nor avoided other individuals. Higher SD and CV values of the real data over the permuted data were non-significant, for both permuted tests (short-term and long term associations). As such, the null hypothesis that individuals associate randomly was not rejected (Table 2.2). In addition, the observed SD was found to be slightly lower than the random value, further indicating a random association between individuals as suggested by Whitehead (1999). The permutation test supported these findings given that, no dyads were seen to be significantly different from the permuted data.

Table 2.2 – Tests for non-random associations among bottlenose dolphins seen ≥ 3 times.

	groups within samples (short and long term)	**associations within samples (long term)**
SD	Real=0,07814 permutation=0,07815 *P*=0,52200	Real=0,07814 permutation=0,07817 *P*=0,44800
CV	Real=2,83990 Permutation=2,83150 *P*=0,75200	Real=2,83990 Permutation=2,84065 *P*=0,46600
Proportion non-zero AI	Real=0,15815 Permutation=0,16017 *P*=0,04500	Real=0,15815 Permutation=0,15876 *P*=0,21400
Mean AI	Real=0,02752 Permutation=0,02752 *P*=0,33100	-
SD typical group size	Real=1,75 Permutation=1,73725 *P*=0,71800	-

2.3.2.1 Cluster analysis

The dendrogram produced (Figure 2.8) was considered representative of the structure within the studied population (CCC=0.806). All individuals were found to be associated at an association index of <0.05. Modularity -G (peak at 0.477) suggest that the best community division is at association index (AI) of 0.023. The value of the maximum modularity-G seems to meet the criteria of, if modularity ≥0.3 the divisions between clusters are 'good' (Newman 2004). Applying the variable stopping rule at AI with maximum modularity value, to the dendrogram, resulted in a rapid agglomeration of observed dyads, triads and their multiple networks, from which it becomes impossible to distinguish separate groups. There is no evidence that large groups or clusters forming a significant level of organization exist and; much of the division within this population is based on different patterns of identification, rather than preferential companionships. However there was a dyad of dolphins that was always seen together (ID 74 and 78; AI=1; N=3times) and, some dyads of dolphins spend more time together than with other individuals. Those dyads refer to dolphins 241-245; 314-344; 160-271 and 56-84 with an AI of 0.67. This hierarchical cluster analysis indicates that the level of fidelity and companionship within this population is low.

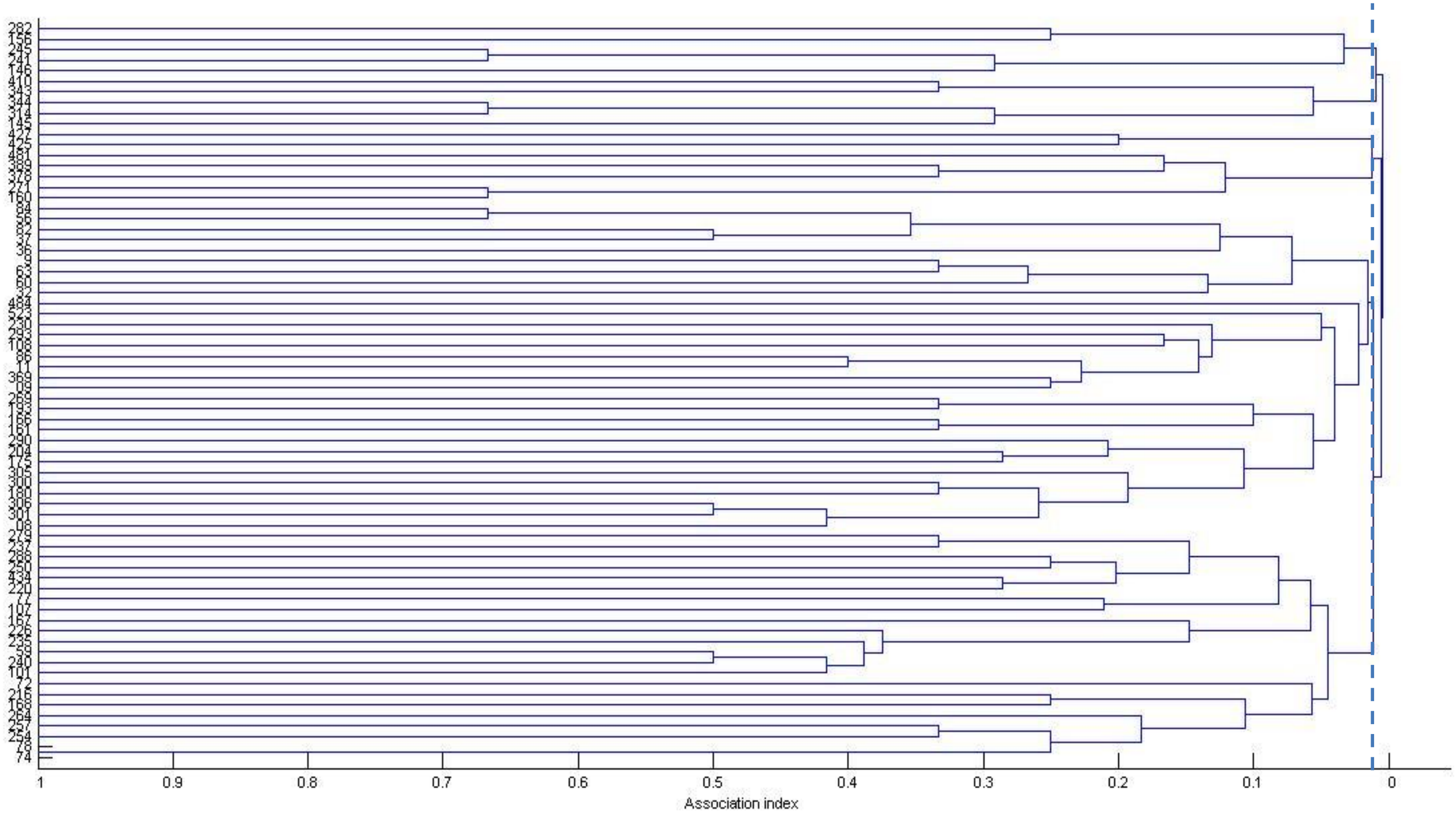

Figure 2.8 – Dendrogram of bottlenose dolphins in Madeira archipelago using hierarchical cluster analysis. The average linkage and the Simple Ratio Index for association for individuals seen ≥3 times from 2001-2012 is shown. The dashed line represents cluster division resulting from Modularity-Gmethod.

2.3.2.2 Temporal analyses: Standardized Lagged Association Rate (SLAR)

A total of 291 individuals recorded during 108 encounters, corresponding to 101 days, from 2004 to 2012 were used to access the temporal pattern of the social structure.

The model fit to the SLAR that best described this bottlenose dolphin population was 'casual acquaintances' (Whitehead 1995). (Table 2.3; Figure 2.9). An analysis of the rates of associations between individuals over time showed that the SLAR line starts to decrease at approximately 500 days and reaches the null rate (Figure 2.9) confirming the presence of random associations given by the permutation tests made in the cluster analysis. The social-system model that best fits the SLAR curve indicates casual acquaintances in a large population, possibly including rapid disassociations. However, a second model also strongly supported the SLAR (ΔQAIC= 1.60) and it suggests two levels of acquaintances: a short, casual level of association and a longer-term one, as described by Whitehead (2008). A visual inspection of the data used to generate the SLAR, indicates that a small number of individuals seems to have longer associations. For example individuals 74 and 78 were seen together twice in the same year (2005) and once five years later (2010) (AI=1). Eight individuals (56; 84; 160; 241; 245; 271; 314 and 344) had an association index of 0.67 which indicates that in more than 30% of the time they were seen associated with the same individual. However, when using LARs or SLARs to address the temporal nature of relationships it is important to make sure the results are consistent with those obtained through other methods like cluster analysis (Whitehead 2008). Hence, in accordance with the results obtain by the cluster analysis that showed an overall low association index, the model that uses casual acquaintances to explain social structure in this population was chosen despite some variation in association pattern between individuals used in this analysis.

Following the model of casual acquaintances the gregariousness of the study population was estimated at 69 individuals (1/a) if rapid disassociations do not exist, and the associations were estimated to last for 998 days (2.7 years) (1/b).

Table 2.3 – Exponential models using maximum likelihood and binominal loss, used to describe the temporal pattern of associations of bottlenose dolphins in Madeira. The best model corresponds to that with lower ΔQAIC value (highlighted in bold).

Model	Best fit	No Parameters	QAIC	ΔQAIC	Support
Constant Companions (CC)	$g'=0.009094$	1	1000.89	14.51	No support
Casual Acquaintances (CA)	$\mathbf{g'= 0.014543*e^{-0.0010022\tau}}$	**2**	**986.38**	**0**	**Best support**
CC + CA	$g'=0.0088741+0.2867 *e^{-0.57626\tau}$	3	998.80	12.42	No support
Two levels of CA	$g'=1.3895 *e^{-1.4476\tau} + 0.014029*e^{-0.00095305\tau}$	4	987.98	1.60	Strong support

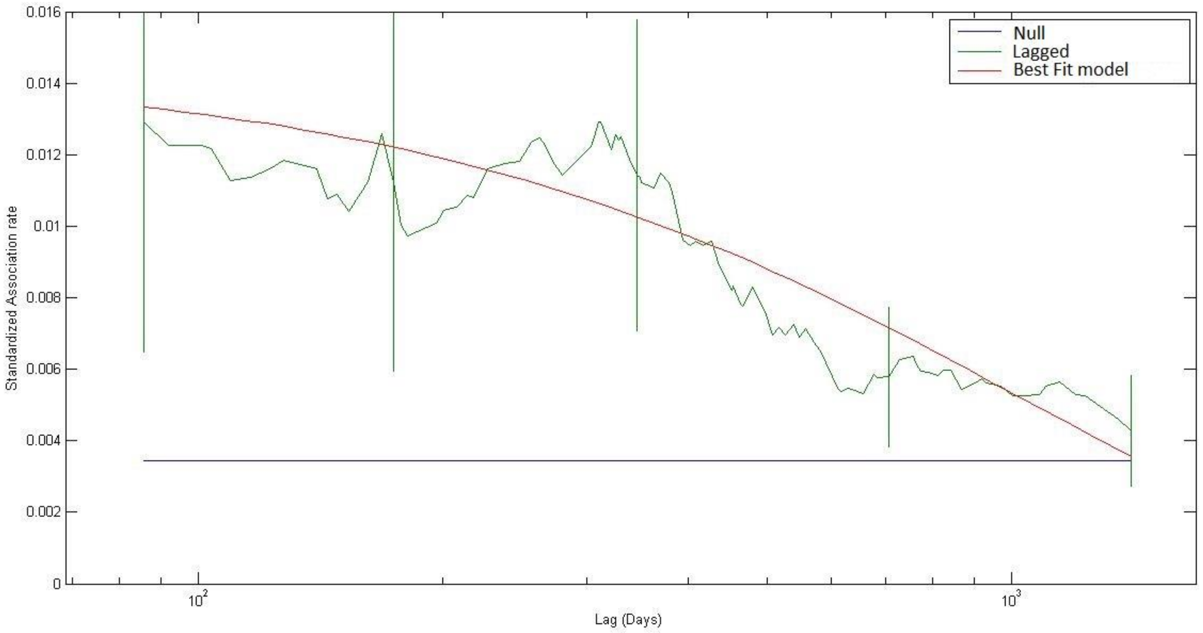

Figure 2.9 – SLAR for bottlenose dolphins captured between 2004 -2012 using a moving average of 3000 associations. Estimated SE bars were produced by jackknifing on each sampling period. The best-fit model suggests casual acquaintances and was obtained using maximum likelihood methods. The null association rate represents the expected value of the SLAR if there was no preferred association and is included for reference.

2.4 Discussion

2.4.1 Photo-identification

There is strong evidence that bottlenose dolphins seen in the archipelago of Madeira belong to an open population with regular recruitment of new animals to the area. The discovery curve for new individuals does not seem to stabilize, and thus more new individuals are expected to be captured. The large size of the study area may have contributed to this high number of catalogued individuals. Extending the survey area to all three islands (Madeira, Desertas and Porto Santo), allowed a higher chance of capturing transients or dolphins from other communities, as mentioned by Silva *et al.* (2008) referring to the archipelago of Azores. Nonetheless, the curve of the number of animals with more than one capture (recaptures) seems to be reaching a plateau in the last year of the study. This means that there might not be many more individuals with a strong site-fidelity (see Chapter 3), available to be captured in the study area, as well as that their number is low compared to the number of dolphins in the catalogue. The variations in the time gap time between many of the re-sightings of identified individuals in the study area suggested that Madeira archipelago represents part of a larger home range within the Northeast Atlantic. A genetic study by Louis *et al.* (2014), investigating habitat driven population structure of bottlenose dolphins within the Northeast Atlantic, found that individuals sampled in Azores shared a genetic structure with individuals identified in the European continental shelf, despite the large distance that separate these two places. A similar scenario seems to occur in the present study with a small percentage of individuals showing some degree of residency and the majority of the individuals being transients or migrants that move in a much wider area than the study area.

2.4.2 Association patterns

The results from the dendrogram showed that the overall association index of the dolphins was low and that there was no clear structure in the social organization. The dolphin population presented a dynamic and fluctuating social structure with little fidelity between individuals, typical of the fission-fusion system. Given the pelagic environment of Madeira archipelago, this finding is not unexpected. Highs level of associations in bottlenose dolphin populations seems to be more common in more enclosed environments, such as estuaries, bays and fjords (Lusseau *et al.* 2003). The high association levels in more enclosed communities could be, partially due to the topographic features that could pose difficulty for neighbouring communities to meet (Lusseau *et al.* 2003; Merriman 2007). Nonetheless, this scenario is not the case in an open oceanic habitat. Despite the low AI found in this study, there were two dolphins that were never seen apart and several others that revealed a higher AI than the overall mean, suggesting longer-term relationships. Some stable associations among pairs or even trios of individuals have been documented in various populations of bottlenose dolphins, although there appears to be considerable variability among populations in the types and degree of such stables associations (Connor *et al.* 2000).

Sex seems to be an important feature driving these associations, as sex-specific bonds are reported for this species in some long-term studies (Connor *et al.* 2000). The same authors point out that determining the sex of bottlenose dolphins in the field is difficult given lack of dimorphism in adults. Often sex determination is limited to individuals presumed to be females because of the consistent proximity of a small calf. That was the case in this study; only a few individuals were assumed to be females. Prey type may also play an important role in shaping school size and in the decision making whit regards to leaving or joining schools, as suggested by Lusseau *et al.* (2004). Bottlenose dolphins are often reported to circle around fish schools, with one or a few individuals at a time preying on the fishes (Connor *et al.* 2000). The Madeira archipelago is an open water habitat allowing bottlenose dolphins pursue schooling as well as pelagic solitary prey throughout the water column.

The results of the permutation test did not lead to rejecting the null hypothesis, suggesting that random associations persist in the bottlenose dolphins population studied in Madeira. Similarly, the temporal analysis also indicated the presence of random associations over time. The decline of the SLAR curve after approximately 500 days (1.4 years) suggests disassociation over that time period which can be explain by demographic events such as mortality or emigration (Whitehead 2008).

However, the associated SEs on the SLAR are quite large (Figure 2.9), so it should be noticed that this are general trends that cannot predict the association pattern of all individuals at all times.

A study carried out on bottlenose dolphins in the outer Moray Firth (Eisfield & Robinson 2004) obtained similar results to those presented here. The authors found no clear architecture or division of groups except for dyads and triads with random associations. Same results were found in the Shannon Estuary, Ireland, where social structure in a smaller population of dolphins was found to lack fidelity between individuals (Foley *et al.* 2010). Also, focal follows studies in Shark Bay, Australia describe changes in group composition occurring on average three or four times per hour (Connor *et al.* 2000). More unusual in this species are the results of a study of bottlenose dolphins in Doubtful Sound, New Zealand that demonstrated a unique fission-fusion social structure as long lasting associations were a strong feature of the community (Lusseau *et al.* 2003).

To summarize, bottlenose dolphin social structure can vary drastically, from being mainly driven by constant companionship to featuring mostly acquaintances that last only a few days (Lusseau *et al.* 2006). It would be useful to examine if different segments of the populations have different patterns of interactions, like sex-related relationships. That would be interesting future research in this population present in Madeira.

It is important to highlight that the association coefficients estimates reported here can be negatively biased, mostly owing to the inherent difficulties of the methodology applied (Stevick *et al.* 2001); those difficulties lie, manly in the inability to photograph each individual present during each encounter. In addition, as the study was restricted only to well-marked individuals (0.68, see Chapter 4), potential associations between unmarked individuals (like calves and juveniles) and the rest of the population is not being accounted for. Mother/calf pairs of bottlenose dolphins living in a fission-fusion community are expected to present long-term associations as calves are known to stay with their mother for up to eight years after birth (Greiller *et al.* 2003).

In conclusion, the bottlenose dolphin population that lives in Madeira waters did not exhibit any signs of group fidelity and social stability like it has been documented in other bottlenose dolphin populations (*e.g*. Lusseau *et al.* 2003). This population exhibits a fission-fusion society that is predominantly formed of short-term acquaintances with only a few long-lasting associations similar to the well-studied bottlenose dolphin population present in Sarasota Bay, Florida (Wells *et al.* 1987) or in the Scottish east coast (Lusseau *et al.* 2006). This lack of community structure should be considered in future conservation efforts.

Understanding the social relationships among individuals is important to define management guidelines for the population of bottlenose dolphins in Madeira and this dynamic should be taken into consideration in future government managing plans.

References

Auger-Méthé M, Whitehead H (2007). The use of natural markings in studies of long-finned pilot whale (Globicephala melas). *Marine Mammal Science,* Volume 23, pp. 77-93.

Bedjer L, Fletcher D, Bräger S (1998). A method for testing association patterns of social animals. *Animal Behaviour,* Volume 56, pp. 719-725.

Borgatti S (2002). *Netdraw Network Visualization.* Analytic Technologies: Harvard, MA, USA.

Bridge P (1993). Classification. In: J. Fry, ed. *Biological Data Analysis: A Practical Approach.* New York: Oxford University Press, pp. 219-242.

Burnham KP, Anderson DR (2002). Model selection and multimodel inference: a practical information-theoretic approach. New York: Springer-Verlag.

Cairns SJ, Schwager SJ (1987). A comparison of association indices. *Animal Behaviour,* Volume 35, p. 1454 – 1469.

Caldeira R, Sangrá P (2012). Complex geophysical wake flows: Madeira Archipelago case study. *Ocean Dynamics,* Volume 62, pp. 683-700.

Connor R, Wells R, Mann J, Read A (2000). The Bottlenose Dolphin: Social Relationships in a Fission-Fusion Society. In: J. Mann, R. Connor, P. L. Tyack & H. Whitehead, eds. Cetacean Societies: Field Studies of Dolphins and Whales. Chicago: University of Chicago Press, pp. 91-126.

Costa J, Fitzgerald T (1996). Developments in social terminology: semantics battles in a conceptual war. *Trends Ecology Evolution,* Volume 11, pp. 285-289.

Eisfield S, Robinson K (2004). *The sociality of bottlenose dolphins in the outer Moray Firth NE Scotland: Implications for current management proposals.* Proceedings of the 18th Annual Conference of the European Cetacean Society, Kolmården, Sweden, 28-31 March.

Foley A, MacGrath D, Berrow S, Gerristsen H (2010). Social Structure Within the Bottlenose Dolphin (*Tursiops truncatus*) Population in the Shannon Estuary, Ireland. *Aquatic Mammals,* Volume 36(4), pp. 372-381.

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

Ginsberg JR, Young TP (1992). Measuring association between individuals or groups in behavioural studies. *Animal Behaviour*, 44:377-379

Greiller S, Hammond PS, Wilson B, Sanders-Reed CA, Thompson PM (2003). Use of photo-identification data to quantify mother-calf association patterns in bottlenose dolphins. *Canadian Journal of Zoology,* Volume 81(8), pp. 1421-1427.

Hoelzel A, Potter C, Best P (1998). Genetic differention between parapatric 'nearshore' and 'offshore populations of the bottlenose dolphin. *Proceedings of the Royal Society Series B, Biological Sciences,* Volume 265(1402), pp. 1177-1183.

Kendall W, Nichols J, Hines J (1997). Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology,* Volume 78, pp. 563-578.

Louis M, Viricel A, Luca T, Peltier H, Alfonsi E, Berrow S, Brownlow A, Covelo P, Dabin W, Deaville R, de Stephanis R, Gally F, Gauffier P, Penrose R, Silva MA, Guinet C, Simon-Bouhet B (2014). Habitat-driven population structure of bottlenose dolphins, *Tursiops truncatus*, in the North-East Atlantic. Molecular Ecology, Volume 23(4), pp. 857-874

Lusseau D (2007). Why are male social relationships complex in the Doubtful Sound bottlenose dolphin population? PLoS ONE, Volume 2(4):e 348

Lusseau D, Wilson B, Hammond PS, Grellier K, Durban JW, Parsons KM, Barton TR, Thompson PM (2006). Quantifying the influence of sociality on population structure in bottlenose dolphins. *Journal of Animal Ecology,* Volume 75, pp. 14-24.

Lusseau D, Williams RJ, Wilson B, Grellier K, Barton TR, Hammond PS, Thompson PM (2004). Parallel influence of climate on the behaviour of Pacific killer whales and Atlantic bottlenose dolphins. *Ecology Letters,* Volume 7, pp. 1068-1076.

Lusseau D, Schneider K, Boisseau OJ, Haase P, Slooten E, Dawson S (2003). The bottlenose dolphin community of Doubtful Sound features a large porportion of long-lasting associations: can geographic isolation explain this unique trait?. *Behavioral Ecology and Sociobiology,* Volume 54, pp. 396-405.

Mahaffy S (2012). *Site Fidelity, Assocations and Long-Term Bonds of Short-Finned Pilot Whale off the island of Hawai'i.* Master Thesis, Portland State University.

Manly B (1995). A note on the analysis of species co-occurrences. *Ecology,* Volume 76(4), pp. 1109-1115.

Mann, J., R. C. Connor, L. M. Barre and M. R. Heithaus. 2000. Female reproductive success in bottlenose dolphins (Tursiops sp.): Life history, habitat, provisioning, and group-size effects. *Behavioral Ecology* 11:210–219.

Maze-Foley K, Würsig B (2002). Patterns of social affiliation and group composition for bottlenose dolphins (*Tursiops truncatus*) in San Luis Pass, Texas. *Gulf of Mexico Science,* Volume 20(2), pp. 122-134.

Merriman MG (2007). Abundance and behavioural ecology of bottlenose dolphins (*Tursiops truncatus*) in the Marlborough Sounds, New Zealand. Master thesis, Massey University, New Zeland.

Newman M (2004). Analysis of weighted networks. *Physical review,* Volume E70, p. 056131.

Pradel R, Hines JE, Lebreton JD, Nichols JD (1997). Capture–recapture survival models taking account of transients. *Biometrics,* Volume 53, pp. 60-72.

Quérouil S, Silva MA, Freitas L, Prieto R, Magalhães S, Dinis A, Alves F, Matos JA, Mendonça D, Hammond P, Santos RS (2007). High gene flow in oceanic bottlenose dolphins (*Tursiops truncatus*) of the North Atlantic. *Conservation Genetics,* Volume 8, pp. 1405-1419.

Silva MA, Prieto R, Magalhães S, Seabra MI, Santos RS, Hammond PS (2008). Ranging patterns of bottlenose dolphins living in oceanic waters: implications for population structure. *Marine Biology,* Volume 179, pp. 179-192.

Slooten E, Dawson SM, Whitehead H (1993). Associations among photographically identified Hector's dolphins. *Canadian Journal of Zoology,* Volume 71, p. 2311 – 1328.

Smolker R, Richards A, Connor RC, Pepper J W (1992). Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour,* Volume 123, pp. 38-69.

Stevick PT, Palsbøll PJ, Smith TD, Bravington MV, Hammond PS (2001). Errors in identification using natural markings: rates, sources, and effects on capture-recapture estimates of abundance. *Canadian Journal of Fisheries and Aquatic Science,* Volume 58, p. 1861 –1870.

Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, Hedley SL, Bishop JRB, Marques TA, Burnham KP (2010). Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* 47: 5-14.

Wells R (1991). The role of long-term study in understanding the social structure of a bottlenose dolphin community. In: K. Pryor & K. Norris, eds. Dolphin societies: discoveries and puzzles. Berkeley: University of California Press, pp. 199-225.

Wells R (1986). *Population structure of bottlenose dolphins along the central west coast of Florida,* Southeast Fisheries Center: Contract Report to National Marine Fisheries Service.

Wells R, Rhinehart H, Cunningham P, Whaley J, Baran M, Koberna C, Costa D (1999). Long distance offshore movements of bottlenose dolphins. *Marine Mammal Science*, Volume 15(4), pp. 1098-1114.

Wells R, Scot M, Irvine A (1987). The social structure of free-ranging bottlenose dolphins. In: H. Genoways, ed. *Current mammalogy.* New York: Plenum Press, pp. 247-305.

Whitehead H (1995). Investigating structure and temporal scale in social organizations using identified individuals. *Behavior Ecology,* Volume 6, pp. 199-208.

Whitehead H (1999). Testing association patterns of social animals. *Animal Behaviour,* Volume 57, pp. 26-29.

Whitehead H (2007). Selection of models of lagged identification rates and lagged association rates using AIC and QAIC. *Communication in Statistics- Simulation and Computation ,* Volume 36, pp. 1233-1246.

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

Whitehead H (2009). SOCPROG programs: analysing animal social structures. *Behaviou Ecology Sociobiology,* Volume 63, pp. 765-778.

Whitehead H, Dufault S (1999). Techniques for analysing vertebrate social structure using identified individuals: review and recomendations. *Advanced Study Behaviour,* Volume 28, pp. 33-74.

Whitehead H, Van Parijs S (2010). Studying marine mammal social systems. In: I. Boyd, W. Don Bowen & S. Iverson, eds. Marine Mammal Ecology and Conservation: A handbook of Techniques . New York: Oxford Univerdity Press, pp. 263-282.

Wilson D (1995). *The ecology of bottlenose dolphins in the Moray Firth, Scotland: a population at the northern extreme of the species' range,* Aberdeen, Scotland: Aberdeen University.

Wilson EO (1975). *Sociobiology: The New Synthesis.* Cambridge, Massachusetts: Belknap Press.

Würsig B, Jefferson T (1990). Methods of photo-identification for small cetaceans. In: *Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters.* Report of the International Whaling Commission, special issue 12.Cambridge: International Whaling Commission, pp. 43-52.

Würsig B, Würsig M (1977). The photographic determination of group size, composition and stability of coastal porpoises (*Tursiops truncatus*). *Science,* Volume 198, pp. 755-756.

CHAPTER 3

GROUP DYNAMICS, SITE FIDELITY, RESIDENCY AND MOVEMENT PATTERNS

3.1 INTRODUCTION

Patterns of residency and site fidelity are often indicative of the ecology of a population; evidence of repeated sightings in the same area can be used to establish core areas or ranges of individuals and point out the importance of a habitat. Residency is generally defined based on the amount of time an individual spends in a certain geographic area (Wells & Scott 1990). The parameters used to define residency in studies with cetaceans vary widely and most of the times are influenced by the local geography and access to the population of interest. This often requires long-term studies of populations, which can be particularly challenging when studying highly mobile species like bottlenose dolphins. Bottlenose dolphins tend to form resident or semi-resident populations across their distribution range. For instance, bottlenose dolphins are year round residents in the Moray Firth and Sarasota Bay (Scott *et al.* 1990; Wilson *et al.* 1997), while dolphins identified in Bahia Kino (Gulf of California, Mexico) and in the Shannon Estuary (Ireland) are not (Balance 1992; Ingram & Rogan 2003). The pelagic waters of Madeira archipelago are one of the most isolated oceanic habitats of the North Atlantic (Alves *et al.* 2013). Residency of animals in isolated oceanic habitats is harder to establish than in more enclosed areas. Sheltered areas, by offering predictable and highly concentrated prey, are more likely to support resident communities, often with fewer individuals with similar residency pattern. Studies in remote open-ocean systems often rely on site fidelity, the tendency for individuals to return to or remain in the same area over time (Baird *et al.* 2008).

Commonly, the size of the area typically surveyed in open-ocean (e.g., 4818 Km2 in Madeira archipelago in Alves *et al.* 2013) is much larger than areas like bays and estuaries (*e.g*. 336 km2 in Martinho, 2012). It is then expected a lower encounter rate in the open ocean and thus, the definition of residency should be adjusted accordingly. These remote oceanic habitats, such as Madeira, are prone to localized upwellings, eddies and convergence zones, which may enhanced primary productivities and promote biomass accumulation at specific sites (Caldeira *et al.* 2002).

Little is known about residency and movement patterns of bottlenose dolphins in Madeira archipelago. Previous studies have shown that these dolphins are one of the most frequently sighted cetaceans from both research surveys and whale-watching trips (Dinis *et al.* 2009; Ferreira, 2008) but more detailed information on population dynamics is still lacking. The importance of determining whether a population or part of it is dependent of a specific area is crucial for future management decisions that aim those areas and/or species.

In this chapter, long-term photo-identification data of bottlenose dolphins from both research surveys (systematic and non-systematic), was used to determine group dynamics. Moreover, data from opportunistic encounters of whale-watching boats was added to access the level of residency and site fidelity, as well as investigate movement patterns within and off the study area.

3.2 METHODS

3.2.1 Study area, field surveys and photo-identification

Data collection was conducted on eight pre-established sectors for systematic surveys around the islands of Madeira, Desertas and Porto Santo, from 2001-2002 and 2004-2012 (see chapter 2: Figure 2.2). Photographs were obtained from year-round systematic and non-systematic surveys, in addition to whale-watching boats trips. Details of the surveys, photo-identification procedures and analysis of photographs are presented in the previous chapter (see Chapter 2).

3.2.2 Group dynamics

In the present study, the term 'group' was used as the sampling unit and defined as all dolphins sighted within 100 m radius of each other (Wells *et al.* 1987). Group size was determined as best estimated at sea. Group composition was determined by counting the minimum number of adults, juveniles and calves present. For this analysis only data from research surveys was considered; whale-watching data was excluded due to possible errors on estimating the group size/composition.

A one-way ANOVA was used to investigate if there were significant differences in group size across months. Data was pooled after confirmation that there were no significant differences between years (not shown). One Kruskal-Walis ANOVA was used to see if there were significant differences in the percentage of calves per group observed between months. Also, a Kruskal-Walis ANOVA was use to infer if the percentage of groups with calves were significant across months. The assumptions for the ANOVA ($\alpha=0.05$) analysis were tested using Shapiro-Wilk and Levene's test. All the analyses were made in R 3.0.2 software (R Development Core Team, 2012). Additionally, the percentage of encounters that displayed inter-specific relationships was calculated.

3.2.3 Site fidelity

Site fidelity was determined by the sighting frequency, number of years observed and mean monthly sighting rate (MMSR). Data from whale-watching boats was included in the analysis of the sighting frequency and number of years observed. The monthly sighting rate was calculated using the proportion of months a given individual was seen in relation to the number of months surveyed during the year(s) it was observed in the study area. Then, averaging this value across the years the animal was observed, the overall mean was obtained (Silva *et al.* 2008). When the maximum value of the MMSR is reached (MMSR=1), it means that an individual was seen in all the surveyed months in the years it was observed in the study area. Kruskal-Walis ANOVA was used to see if there were significant differences between the MMSR and the numbers of years the dolphins were seen. Shapiro-Wilk and Levene's test were used on the ANOVA assumptions (α=0.05).

3.2.4 Residency

Residency to the study area was examined using social network analysis and Lagged Identification Rates (LIRs).

Social network diagrams were produced with Netdraw 2.136 (Borgatti 2002). Social networks are a useful tool as they display visually the social system of the population in a clear and accessible manner. Using nodes to represent individuals and lines in between to link the associated individuals, it graphically displays the social organization within a population.

The residency pattern was included as an individual attribute. Residency patterns were assigned to the individual dolphins based on their capture histories. The term 'resident' was used to designate dolphins that were regularly seen during the study period in the study area (three seasons in a year and more than two consecutive years). Following the nomenclature used in capture-recapture studies, 'transients' dolphins are those dolphins seen just once in the main area (Pradel *et al.* 1997); animals seen more than once but in non-consecutive years were considered 'migrants' (Kendall *et al.* 1997). All individuals seen in association between 2004 and 2012 were used in this analysis.

The amount of time individuals spent within all the eight sectors of the study area was examined through the Lagged Identification Rates, calculated in SOCPROG 2.4 (Whitehead 2009). Given that an animal of the study population can only be identified if present in the study area, it is important to assess the potential for the animals to leave the area. LIRs give us the probability that an individual observed in the study area at a given time will still be present (τ) time lags in the future (Whitehead 2001), as showed in Equation 3.1:

$$\mathrm{R}(\tau) = \frac{\sum_{j,k(t_k - t_j)=\tau} \; mjk}{\sum_{j,k(t_{k-t_j})=\tau} \; n_j - n_k} \qquad \text{Equation 3.1}$$

where:

n_i is the number of individuals identified in sampling period j;

m_{jk} is the number of individuals identified in both periods j and k.

Both Lagged Association Rates (see Chapter 2) and Lagged Identification rates are temporal analysis. However, this latter is not a dyadic association measure, but rather the probability of an individual remaining in the study area divided by the size of the population of interest within that same area.

Movements in and out from the whole study area were investigated using photo-id data of all individuals photographed between 2004 and 2012. LIRs were displayed graphically and models generated in SOCPROG 2.4 (Whitehead 2009) were fit to the data using maximum likelihood and binominal loss (Table 3.1). The model with the lowest Quasi Akaike Information Criteria (QAIC) was elected the most appropriate to explain the data.

Table 3.1 - Models that can be fitted to Lagged Identification Rates. The terminology of the fitted models must be interpreted with care: 'emigration' means emigration from the database, there is no way of knowing if the dolphins actually died, left the study area or simply were not captured again.

Model	Equation	Explanation (N is the population size)
A	a1	Closed (1/a1=N)
B	1/a1	Closed (a1=N)
C	a2*exp(-a1*td)	Emigration/mortality (*a1*=emigration rate; 1/*a2*=*N*)
D	(1/*a1*)*exp(-*td*/*a2*)	Emigration/mortality (*a1*=*N*; *a2*=Mean residence time)
E	a2+a3*exp(-a1*td)	Emigration + reimmigration (*a1*=emigration rate; *a2*/(*a2*+*a3*)=proportion of population in study area at any time)

F	$(1/a1)*((1/a3)+(1/a2)*\exp(-(1/a3+1/a2)*td))/(1/a3+1/a2)$	Emigration + reimmigration ($a1=N$; $a2$=Mean time in study area; $a3$=Mean time out of study area)
G	$a3*\exp(-a1*td)+a4*\exp(-a2*td)$	Emigration + reimmigration + mortality

LIRs were calculated using the sighting histories of all individuals, including transients, and represents an average residency rate for the animals that were included in the analysis. The same dataset used for building the social network was also used in the LIR analysis, with an established sampling period of a day.

3.2.5 Movement patterns

Transition probabilities for movements between sectors within the main study area were calculated in SOCPROG 2.4 (Whitehead 2009). Also, an undefined area outside the study area was included in the analysis. This undefined area represents the whole area outside the study area, and it was included to account for movements from a specific sector to an area that was not being surveyed. A parameterized Markov model was used to access movements among sectors. This model generates estimates for each time unit in which individuals have a certain probability of moving from one area to another, while accounting for permanent emigration in a single day (Whitehead 2009). The probability of an individual remaining in the study area one sampling period later (μ) was also calculated following Whitehead (2009): one minus the sum of the transition probabilities on its corresponding row. The same dataset used for LIR analysis was used here.

3.3 RESULTS

3.3.1 Group dynamics

Group size and composition were examined for 242 independent groups encountered between 2004 and 2012. Group size ranged from 2 to 90 individuals, with an average of 17 individuals (median=12, ±SE 0.97). The majority of groups contained between 6 and 10 dolphins (n=56) (Figure 3.1).

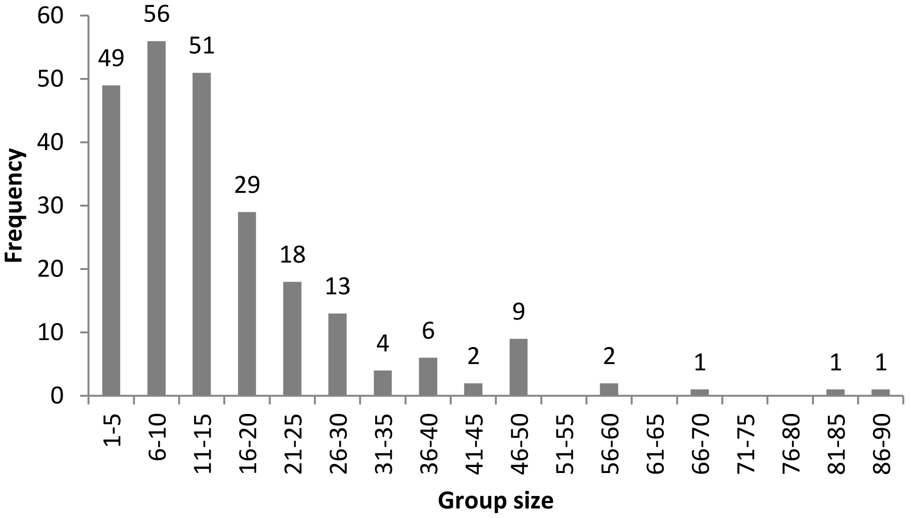

Figure 3.1 – Frequency of group size of bottlenose dolphins based on field counts between 2004 and 2012 in Madeira archipelago.

The one-way ANOVA showed no significant differences in group size across months (P=0.23) (Figure 3.2).

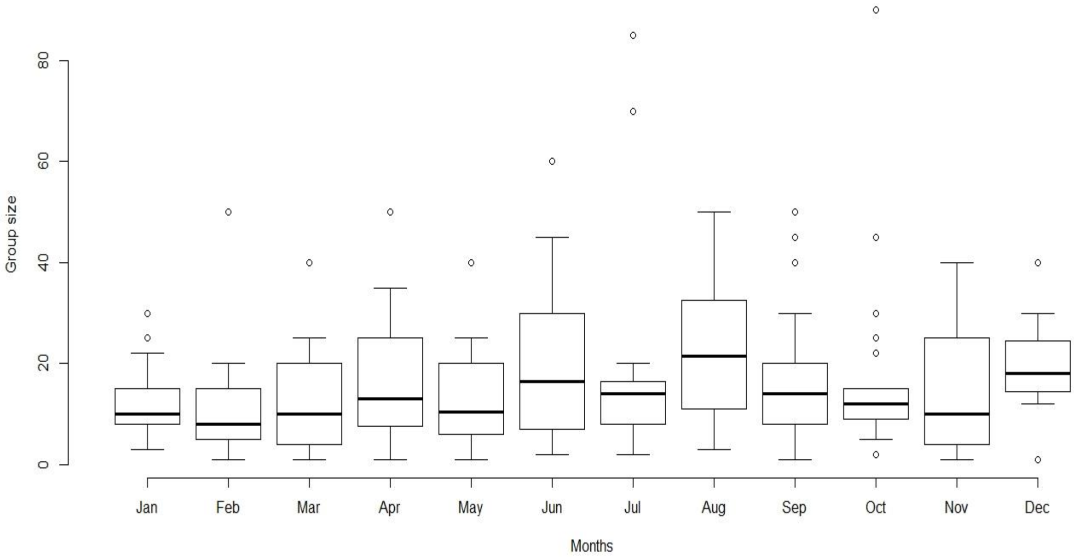

Figure 3.2 – Group size across months. The bottom and top of the box represent the first and third quartiles respectively; the band inside the box is the median. Vertical bars correspond to maximum and minimum group size and points (O) represents outliers.

The analysis of group composition revealed that the calves were observed in 26.4%; the remainder groups were formed either by adults or by adults together with juveniles. Groups with calves were seen year-round, with a peak in the early spring and another in late summer/autumn (Figure 3.3). Kruskal-Wallis ANOVA found significantly different results in the percentage of groups with calves observed between months ($P<0.001$) but, no significant differences between the percentage of calves per group across months ($P=0.70$).

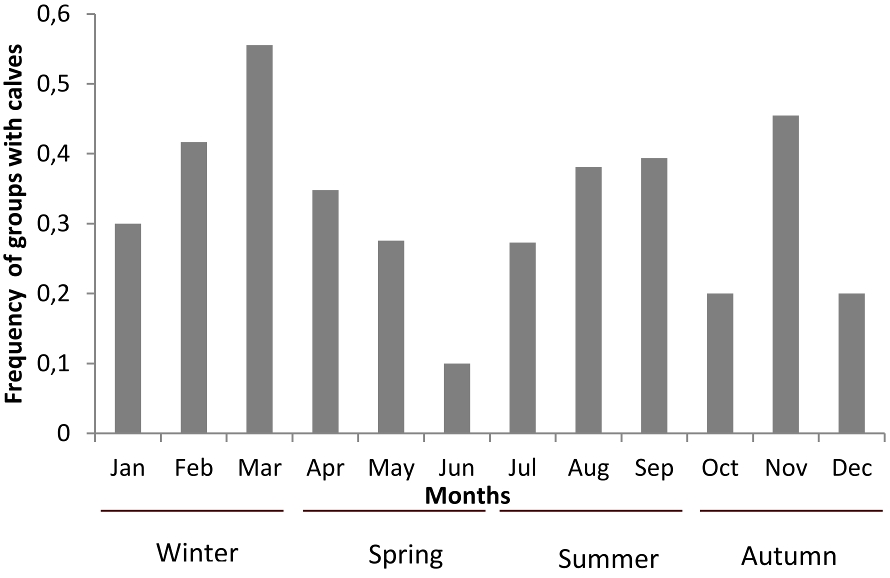

Figure 3.3 – Frequency of groups containing calves across months.

In 36 encounters (14.9%), the dolphins were observed in association with another cetacean (Figure 3.4). Short-finned pilot whale (*Globicephala macrorhynchus*) was the species most commonly found in association with bottlenose dolphin followed by Bryde's whale (*Balaenoptera edeni*). In the former case the dolphins were always outnumbered by the pilot whales and in the latter case the dolphins were seen in the vicinity of the whale.

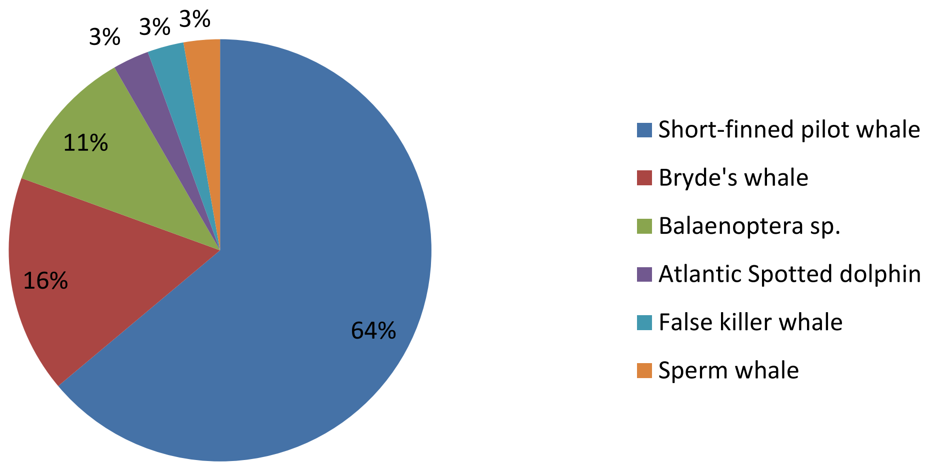

Figure 3.4 – Species seen in association with bottlenose dolphins. Short-finned pilot whale (*Globicephala macrorhynchus*), n=23; Bryde's whale (*Balaenoptera edeni*), n =6; *Balaenoptera* sp., n=4; Atlantic spotted dolphin (*Stenella frontalis*), n=1; false killer whale (*Pseudorca crassidens*) and sperm whale (*Physeter macrocephalus*), n=1.

3.3.2 Site fidelity

Individual sighting histories varied greatly. Some individuals were sighted only once, others up to 13 times (median=2), during the entire study period. From the total of 501 individuals catalogued (see Chapter 2), a total of 108 (21.5%) were re-sighted in more than 1 year, 16 individuals span over 4 y (3.2%) (Figure 3.5). Individuals Tt032 and Tt086 were first documented in 2002 and subsequently re-sighted 12 and 13 times respectively during different months and years until 2012. Tt009 was recorded in 8 years, seen in nearly every year of the study period with the exception of 2004, 2006 and 2009. To note that there was no data collection in 2003.

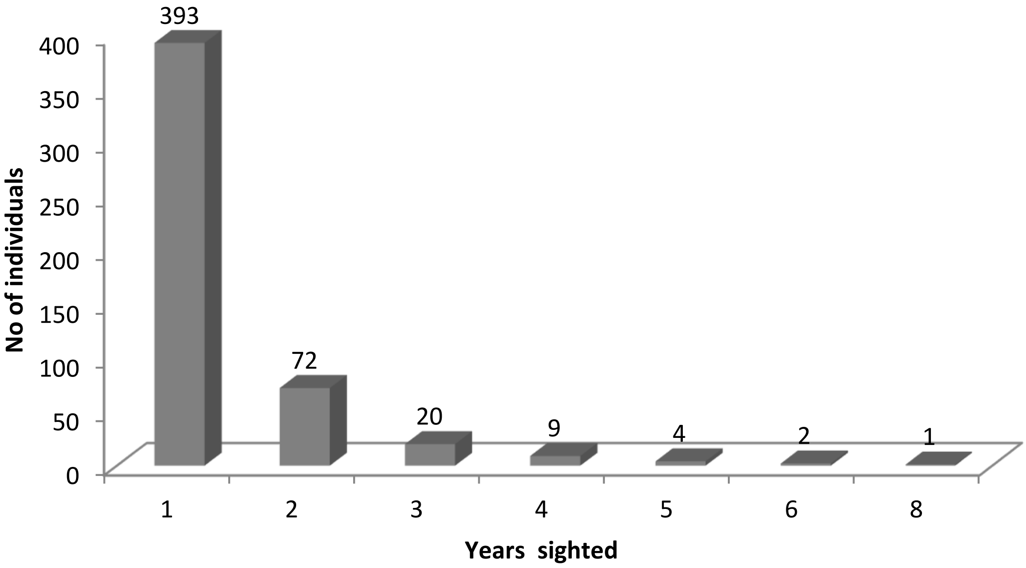

Figure 3.5 – Number of identified bottlenose dolphins in the Madeira archipelago *versus* the number of years they were sighted in, between 2001-2002 and 2004-2012.

The Mean Monthly Sighting Rate (MMSR) was, generally low (range 0.12-0.45; Median 0.23; SE ± 0.008). Figure 3.6 shows that the MMSR seems to increase with the number of years the dolphins were seen although the Kruskal-Wallis ANOVA found no significant correlation between these two factors (*P*=0.41).

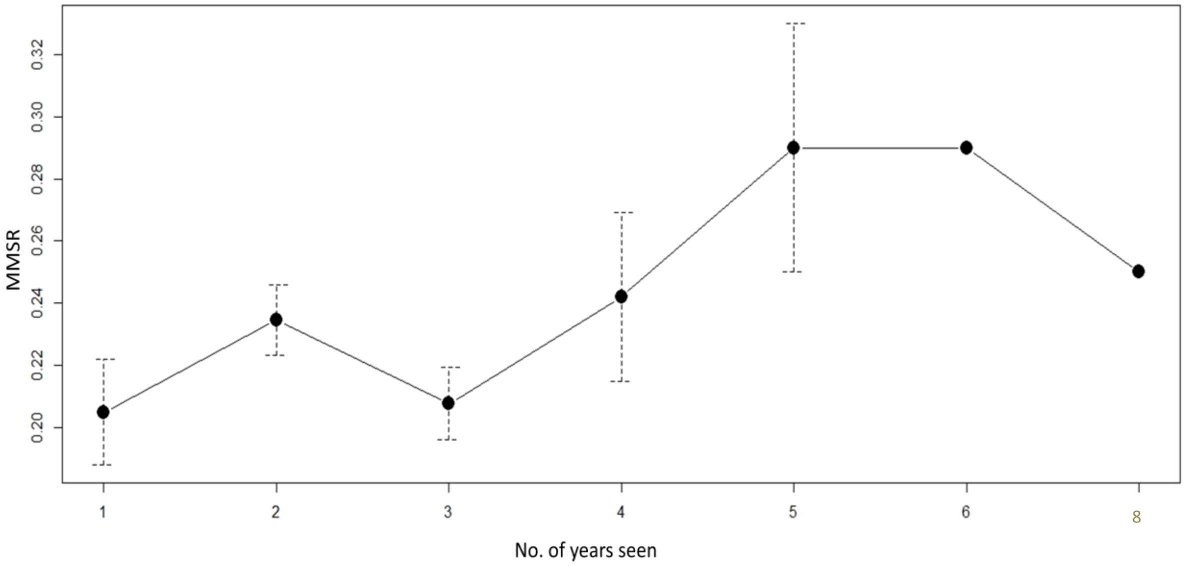

Figure 3.6 –Mean Monthly Sighting Rate (MMSR) *vs* the number of years the dolphins were sighted in. Confident intervals are represented by vertical bars.

3.3.3 Residency

All individuals seen in association between 2004 and 2012 were used for this analysis resulting in a total of 441 dolphins. Based on the previously established residency criteria, 19 residents (4.3%), 41migrants (9.3%) and 381 transients (86.4%) were identified. The social network diagram recognized a core network formed by 380 individuals (86.1%) and 12 satellite clusters (range 2-9)with no link to the main cluster, containing 61 dolphins in total (Figure 3.7). All the individuals present in the satellite clusters are transient while the main cluster is composed by dolphins of all three residency patterns. The visual inspection to the main cluster shows the centrality of resident dolphins (Figure 3.8).

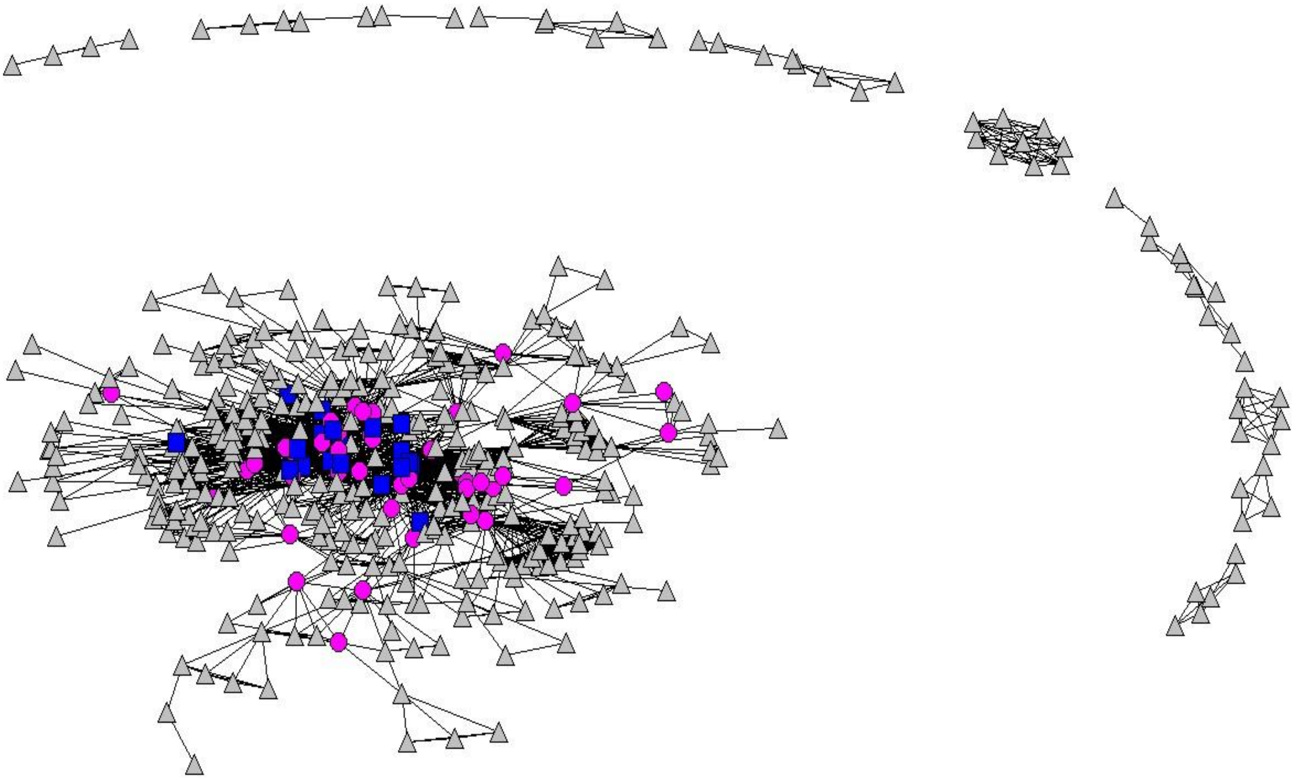

Figure 3.7 – Social network diagram illustrating the associations of 441 dolphins identified in the study area. Individual dolphins are represented by nodes; associations are shown by the lines between nodes. Residency patterns are indicated by the different shapes and colours of the symbols: residents are represented as blue boxes, migrants as pink circles and transient as grey triangles.

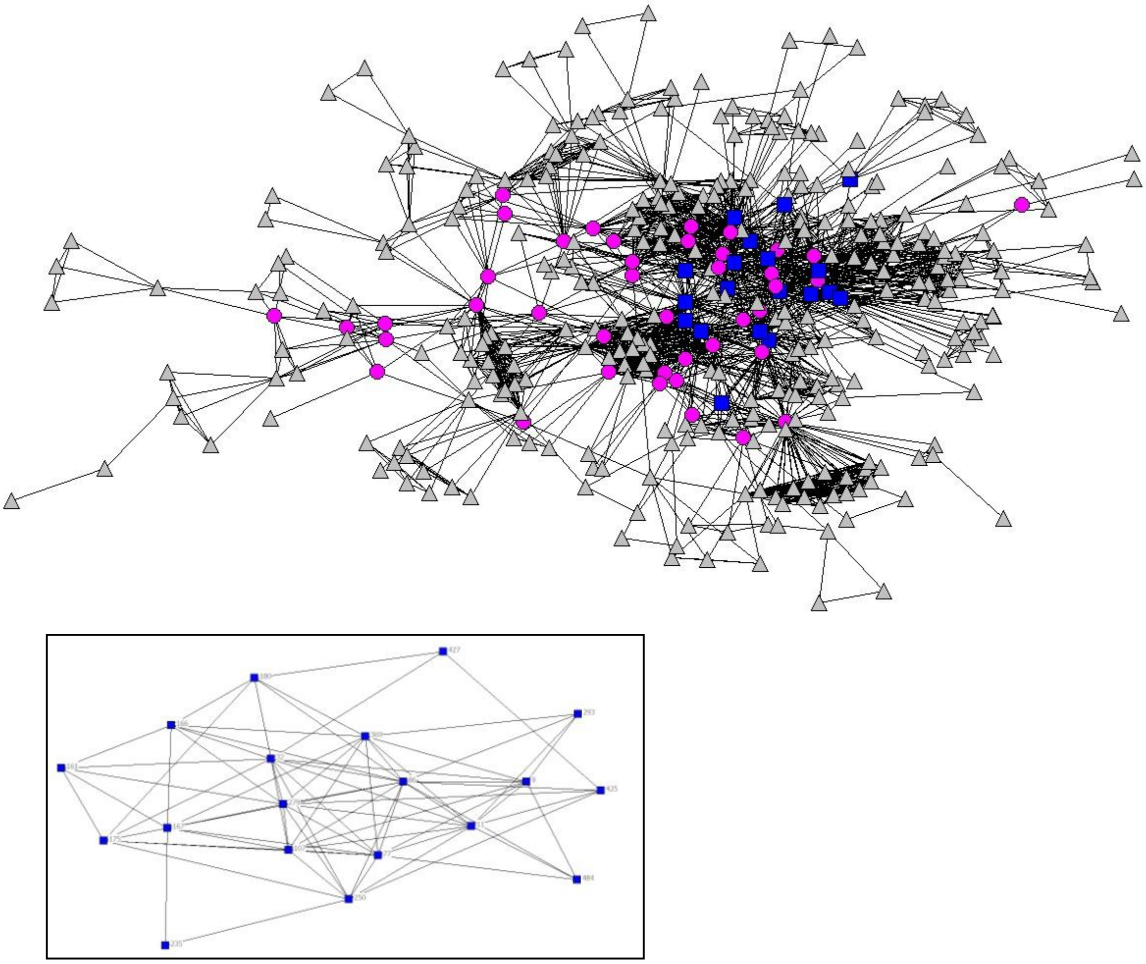

Figure 3.8 – Zoom of the main cluster taken from Figure 3.6 were the centrality of resident individuals is highlighted. Bottom left: detailed view of resident dolphins.

Lagged Identification Rates (LIRs) revealed that the model that best described the movements of the study population in Madeira archipelago was Emigration+Reimmigration (model F on Table 3.2; Figure 3.9). The model indicates that on average, 178 individuals were in the study area at any one time and that an individual remained in the study area an average of 90 days. The average time an individual spent outside the study area was estimated to be of 313 days.

Table 3.2 – Models fit to LIRs for bottlenose dolphins observed in Madeira archipelago: residence times and movements in and out the study area, for all individuals captured, between 2004 and 2012 (*n*=estimated population size in the study area).* marks the best fit model (with the lowest QAIC value) fitted to the LIR graph.

Model	Maximum-likelihood value for parameters	QAIC value	Summed log likelihood	Mean residence time in	Mean residence time out
*a1=N; a2=Res time in; a3=Res time out	*n*= 177,890	7526,4115	-5063,831	90,28	312,93
a1=N; a2=Res time in; a3=Res time out; a4=Mort	*n*= 87,324	7528,6852	-5064,0152	-	-
a1=N; a2=Mean residence	*n*= 200,002	7530,5667	-5067,9744	-	-

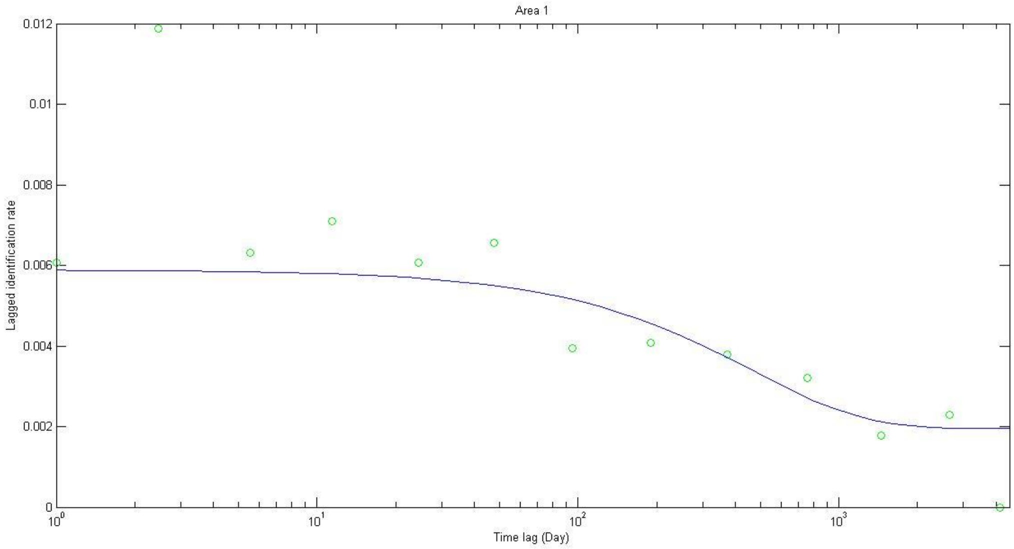

Figure 3.9–Lagged identification rate (LIR) for all individuals captured between 2004 and 2012. Data points are represented by circles and the best fit model (Emigration+reimmigration) is displayed by a solid line.

3.3.4 Movement patterns

Transition probabilities were estimated for movements between all sectors within the study area (see Chapter 2: Figure 2.2), as well as to an undefined external area within one day (Table 3.3). Sector 2 (Madeira West) was excluded from the analysis due to the fact that only one encounter was recorded there, and no dolphin was identified in sector 4 (Desertas East).

Table 3.3 – Probability of individual bottlenose dolphins to move between sectors (1-8) and to areas outside the main study area (OUT), within one day period. (μ)is the probability that an individual remains in a given sector one sampling period later.

To From	1	3	5	6	7	8	OUT	μ
1	-	0,1035	0,1180	0,1031	0,1007	0,1081	0,1041	0,9288
3	0,0998	-	0,0994	0,0973	0,1042	0,1267	0,1000	0,3726
5	0,1088	0,1032	-	0,1116	0,0962	0,0965	0,1036	0,3801
6	0,1235	0,0989	0,0748	-	0,1027	0,1040	0,0988	0,3973
7	0,1069	0,0971	0,1040	0,1045	-	0,0977	0,1051	0,3847
8	0,0950	0,1122	0,1071	0,0874	0,1054	-	0,0998	0,3931
OUT	0,0966	0,0979	0,0991	0,1003	0,0894	0,1083	-	0,4084

Sector 3 (Madeira S) showed higher probabilities of movements to sector 8 (Porto Santo N) than movements to any other sector. Also, movements from sector 6 (Travessa), which is located between Madeira Island and Porto Santo, were higher to sector 1 (Madeira N); sector 7 (Porto Santo S) and sector 8. Sector 1 was also the sector dolphins have the highest probability of remaining in that area. The external undefined area outside the study area show relatively high values of movements into, indicating that dolphins can leave the study area in short periods of time.

3.4 DISCUSSION

3.4.1 Group Dynamics

Groups of bottlenose dolphins in Madeira archipelago seem to be skewed towards small sizes. Although large groups were encountered, the median value was similar to those found in other studies with the same species (Merriman *et al.* 2009;

Eisfeld 2003; Constantine 2002). One group was estimated to be formed by of 90 individuals, a group size more commonly found in open ocean habitats. Dolphin species that inhabit pelagic habitats generally form larger groups (Shane *et al.* 1986). The average group size may also vary according to location; small groups (3-7 animals) tend to be found in coastal areas (Ben Naceur *et al.* 2004; Bearzi *et al.* 1997) whereas larger groups (up to 35 and as high as 180) in offshore waters (Cañadas & Hammond 2006; Forcada *et al.* 2004). Madeira archipelago is an oceanic habitat; larger groups are likely to be aggregations of transient pelagic dolphins. Two factors may contribute to this - the risk of predation in open habitats and preying upon schooling fish in the pelagic environment (Wells *et al.* 1980). Lusseau *et al.* (2003) suggest that oceanographic features such as isolated regions and depth could influence bottlenose dolphin social organization; as such those could also influence group size. Additionally, the definition of 'group' used here (Wells *et al.* 1987) explains in part the results; the dolphins were often seen in small groups separated from each other by a few hundred meters.

Bottlenose dolphins were recorded in every month of the year and, groups tended to be larger in the summer and autumn, even though no significant differences were found in group size frequency between months. This may be due to the presence of the transient pelagic bottlenose dolphins observed during the summer months.

Groups with calves were recorded year-round although more often in the spring and late summer/autumn in Madeira archipelago, as expressed by the significant differences found in the ANOVA analysis. This suggests that there is a preferential period of the year for birthing and calving as similarly recorded in other parts of the world (Wells *et al.* 1987; Grigg & Markowitz, 1997; Mann *et al.* 2000). As the risk of predation is low (e.g. sharks and killer whales) in Madeira archipelago this birth seasonality may be due to the warmer temperatures of water in theses months. Mann *et al.* (2000) suggests that warm water is thermally efficient for small calves or for mothers, and that food availability may fluctuate sufficiently to favour seasonal births. Nonetheless, there is not sufficient information about prey availability to relate both factors in Madeira archipelago.

Bottlenose dolphins were seen associated with other species in 15% of encounters being the short-finned pilot whale the most frequent of these associations. Bottlenose dolphins are commonly found in mixed-species groups in pelagic waters. In the Eastern Pacific a significant increase in mixed-groups was found with increasing of distance from shore, and 40% of these groups were made up of bottlenose dolphins and short-finned pilot whale (Scott & Chivers 1990). This association, although common is poorly understood. Kraus & Gihr (1971) found scars from squid suckers on one of two bottlenose dolphins captured in a drive fishery together with a group of 101 pilot whales in the Faeroe Islands. As these whales feed extensively on squid (Connor *et al.* 2000), the most likely reason for those associations is opportunistic feeding. Pilot whales are deep divers and this type of prey in more distant to shore pelagic waters, may be out of range for bottlenose dolphins. The associations recorded of bottlenose dolphins and baleen whales may also be related to feeding as the whales were seen lunge feeding at surface with the bottlenose dolphins in the proximity (own observations).

3.4.2 Site Fidelity

Despite the large number of dolphins identified and catalogued during the study period (*n*=501, see Chapter 2), only a small number of individuals was re-sighted in more than one year (21.5%) and even a smaller number (3.2%) showed long-term site fidelity (i.e. seen at least in 4 years). Data on sighting frequency indicates a small group of dolphins with high levels of site fidelity, the majority of the individuals showed several different kinds of occurrence. Individuals infrequently re-sighted also showed some degree of site fidelity to Madeira Island, and individuals seen only once in the study area were likely to be pelagic dolphins just passing through Madeira archipelago. However, it is not possible to say that even the individuals with a high level of site fidelity were always present in the study area as MMSR was generally low. Even though the ANOVA analysis showed no significant differences between the MMSR and the numbers of years the dolphins were seen, this is likely due to the fact that only few dolphins were seen in more than five years. Such hypothesis is supported by the apparent increase of the MMSR with the number of years the dolphins were seen in. Large populations of dolphins characterized by a low number of individuals with re-sightings are considered typical of open water habitats (Defran *et al.* 1999), although they can also occur in costal environments (Shane 2004). Silva *et al.* (2003) referring to the neighbouring archipelago of Azores, suggests that seems reasonable to speculate that dolphins occurring in the surrounding ocean areas may be drawn to the islands due to the great productivity of waters around the islands. When compared to open oceanic waters, these island habitats can act like 'oasis' responsible for attracting several cetacean species that use the area as a foraging or migration stop. A similar situation seems to occur in Madeira archipelago, where different degrees of site fidelity to the islands indicate various patterns of occurrence.

3.4.3 Residency

The analysis of the social network diagram shows that individuals from different residency patterns (residents, transients and migrants) associate with each other (Figure 3.7). Only a small number of dolphins were found to be resident (4.3%) according to the definition established. All resident dolphins formed a complex network, located in the centre of the main cluster. Satellite clusters were formed exclusively by transient individuals suggesting that some transient dolphins mix with residents and migrants, while others do not. Individuals Tt86 and Tt32 showed a high level of betweeness centrality (a measure of centrality of a node in the network), indicating that they may act as a 'social glue' that links other individuals, favouring their position in the network (Lusseau & Newman 2004). Similarly to the findings of Lusseau and Newman (2004), the removal of those two individuals from the network, would not cause the loss of network connectivity. However according to those authors, some individuals are more important to the network connectivity than others, and their removal may cause an effect not immediately evident from a representation of the network. The mixture of different patterns of occurrence, with the presence of resident, transients and migrants, is also seen in other populations of bottlenose dolphins worldwide (Baird *et al.* 2009, Silva *et al.* 2008, Connor *et al.* 2000), as well as in another cetacean species (*Globicephala macrorhynchus*) in Madeira archipelago (Alves *et al.* 2013). Also, this is supported by the lack of genetic structure found by Quérouil *et* *al.* (2007) in the Northeast Atlantic, indicating that those associations might serve as a stimulus for gene flow. The Madeira archipelago seems to have an open population of bottlenose dolphins with a small number of individuals showing residency to the area.

The Lagged Identification Rate (LIR) estimated that, on average, an individual remains 90 days in the study area. As above, calling resident to some dolphins does not imply that these individuals never leave the area; rather, they may travel over a large range which was not covered by surveys in the present study. The LIR curve starts to decay after approximately 100 days (Figure 3.10) indicating that the dolphins leave the area through emigration or mortality. Nevertheless, after this fall (≃2.7 y) the curve starts levelling again suggesting that some of those individuals that leave the population return to the study area after this period. Also, this levelling of the LIR curve may be an evidence of a mixed population of residents, migrants and transients revealed by the social network diagram (Whitehead 2008).

3.4.4 Movement patterns

The movement probabilities obtained indicate rapid movements between sectors. However the survey effort was higher in sector 3 (Madeira S) which means that movements can be under-represented on the remaining areas. Nonetheless, the transitions probabilities seem to indicate movements between Madeira Island and Porto Santo which are separated by approximately 50 km. The sector which seems to be of some importance is sector 1 (Madeira N) with the highest probability of dolphins remain in. Porto Santo N had the highest probability of dolphins moving into from the sector 3, one of the greatest distance covered in the study area. This suggests that dolphins covered 50 km within a day which is in accordance to Lynn (1995) findings that found through radiotracking data that dolphins are able to travel as much as 55 km in 12h. Similarly a dolphin was recorded moving 50.2 km in one day in Tampa Bay (Florida) (Mate *et al.* 1995). Madeira, Desertas and Porto Santo are within a daily range reported for this species, so these rapid movements between the islands are not unexpected. Sectors 1 and 8 had the highest probabilities of dolphins moving into, from the remaining sectors. Both sector 1 and 8 correspond to unsheltered and shallower sides of the islands Madeira and

Porto Santo respectively. Potential explanations for such movements may include foraging strategies related to vertical prey distribution and/or some human disturbance. Although I cannot infer on the former due to the lack of knowledge on prey distribution in Madeira archipelago, Silva (2007) found that in the neighbouring archipelago of Azores, bottlenose dolphins used preferentially shallow areas, between 100 and 600 m. This could be related to the fact that those areas provide a more suitable habitat compared to open waters where dolphins can take advantage of bottom fishes in addition to schooling prey. Potential explanations for this preference for unsheltered areas of the islands might be the occurrence of any dynamic environmental phenomenon linked to such areas, and the lower exposure to human impact (*e.g*. whale-watching).

References

Alves F, Querouil S, Dinis A, Nicolau C, Ribeiro C, Freitas L, Kaufmann M, Fortuna C (2013). Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: implications for conservation. *Aquatic Conservation: Marine and freshwater ecosystems,* 5: 758-776.

Auger-Méthé M,.Whitehead H (2007). The use of natural markings in studies of long-finned pilot whale (*Globicephala melas*). *Marine Mammal Science,* 23:77-93.

Baird RW, Webster DL, Mahaffy SD, McSweeney DJ, Schorr GS, Ligon AD (2008). Site fidelity and associations patterns in a deep-water dolphin: rough-toothed dolphins (*Steno Bredanensis*) in the Hawaiian Archipelago. *Marine Mammal Science,* 24:535-553.

Baird RW, Gorgone AM, McSweeney DJ, Ligon AD, Deakos MH, Webster DL, Schorr GS, Martien KK, Salden DR, Mahaffy SD (2009). Population structure of island associated dolphins: evidence from photo-identification of common bottlenose dolphins (*Tursiops truncatus*) in the main Hawaiin Islands. *Marine Mammal Science,* 25: 251-274.

Balance LT (1992). Habitat use Patterns and Ranges of the Bottlenose Dolphin in the Gulf of California, Mexico. *Marine Mammal Science,* 8(3): 262-274.

Bearzi G, Notarbartolo di Sciara G, Politi E (1997). Social ecology of bottlenose dolphins in the Kvarneric (northern Adriatic Sea). *Marine Mammal Science,* 13(4): 650-668.

Bedjer L, Fletcher D, Bräger S (1998). A method for testing association patterns of social animals. *Animal Behaviour,* 56: 719-725.

Ben Naceur L, Gannier A, Bradai MN, Drouot V, Bourreau S, Laran S, Khalfallah N, Mrabet R, Bdioui M (2004). Recensement du grand dauphin *Tursiops truncatus* dans les eaux tunisiennes. *Bulletin Institut National des Sciences et Technologies de la Mer de Salammbô,* 31: 75-81.

Borgatti S (2002). *Netdraw Network Visualization.* Analytic Technologies: Harvard, MA, USA.

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

Cañadas A, Hammond P (2006). Model-based abundance estimates for bottlenose dolphins off southern Spain: implications for conservation and management. *Journal of Cetacean Research and Management,* 8(1): 13-27.

Connor R, Wells R, Mann J, Read A (2000). The Bottlenose Dolphin: Social Relationships in a Fission-Fusion Society. In: J. Mann, R. Connor, P. L. Tyack & H. Whitehead, eds. *Cetacean Societies: Field Studies of Dolphins and Whales.* Chicago: University of Chicago Press, pp. 91-126.

Constantine R (2002). *The behavioural ecology of the bottlenose dolphins (Tursiops truncatus) of the Notheastern new Zeland: A population exposed to turism.* Auckland, New Zeland: Unpublished PhD Thesis, University of Auckland.

Defran R, Weller D, Kelly D, Espinosa M (1999). Range characteristics of Pacific coast bottlenose dolphins (*Tursiops truncatus*) in the Southern California Bight. *Marine Mammal Science,* 15: 381-393.

Dinis A, Ribeiro C, Nicolau C, Alves F, Carvalho A, Freitas L (2009). Common bottlenose dolphin (*Tursiops truncatus*) occurrence, distribution and conservation status in Madeira Archipelago (Portugal). SC/61/SM13, 61ª Annual meeting of the International Whaling Commission (IWC). Funchal

Eisfeld S (2003). The social affiliation and group composition of bottlenose dolphins (Tursiops truncatus) in the outer southern Moray Firth, NE Scotland. Master thesis, School of Biological Sciences, University of Wales, Bangor, U.K.

Eisfield S, Robinson K (2004). *The sociality of bottlenose dolphins in the outer Moray Firth NE Scotland: Implications for current management proposals. Proceedings of the 18th Annual conference,* Kolmärden, Sweden.

Ferreira RB (2007). Monitorização da actividade de observação de cetáceos no Arquipélago da Madeira, Portugal. Master thesis, Universidade of Lisbon.

Foley A, MacGrath D, Berrow S, Gerristsen H (2010). Social Structure Within the Bottlenose Dolphin (*Tursiops truncatus*) Population in the Shannon Estuary, Ireland. *Aquatic Mammals,* 36(4): 372-381.

Forcada J, Gazo M, Aguilar A, Gonzalvo J, Fernandez-Contreras M (2004). Bottlenose dolphin abundance in the NW Mediterranean: addressing heterogeneity in distribution. *Marine Ecology Progress Series,* 275: 275-87.

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

Grigg E, Markowitz H (1997). Habitat use by bottlenose dolphins (*Tursiops truncatus*) at Turneffe Atoll, Belize. *Aquatic Mammals,* 23(3): 163-170.

Ingram S, Rogan E (2003). *Bottlenose dolphins (Tursiops truncatus) in the Shannon estuary and selected areas of the west-coast of Ireland.,* s.l.: Report to the National Parks and Wildlife Service.

Kendall W, Nichols J, Hines J (1997). Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology,* 78: 563-578.

Kraus C, Gihr M (1971). On the presence of *Tursiops truncatus* in schools of Globicephala melaena on the Faeroe Islands. *Investigating Cetacea,* 3(1): 180-182.

Lusseau D, Newman M (2004). Identifying the role that animals play in social networks. *Proceedings of the Royal Society of London,* 271: doi: 10.1098/rsbl.2004.0225,.

Lusseau D, Schneider K, Boisseau OJ, Haase P, Slooten E, Dawson S (2003). The bottlenose dolphin community of Doubtful Soun features a large porportion of long-lasting associations: can geographic isolation explain this unique trait?. *Behavioral Ecology and Sociobiology,* 54: 396-405.

Lusseau D, Williams RJ, Wilson B, Grellier K, Barton TR, Hammond PS, Thompson PM (2004). Parallel influence of climate on the behaviour of Pacific killer whales and Atlantic bottlenose dolphins. *Ecology Letters,* 7: 1068-1076.

Lusseau D, Wilson B, Hammond PS, Grellier K, Durban JW, Parsons KM, Barton TR, Thompson PM (2006). Quantifying the influence of sociality on population structure in bottlenose dolphins. *Journal of Animal Ecology,* 75: 14-24.

Lynn S (1995). Movements, site fidelity, and surfacing patterns of bottlenose dolphins on the central Texas coast, MS Thesis, Texas A&M University.

Manly B (1995). A note on the analysis of species co-occurences. *Ecology,* 76(4): 1109-1115.

Mann, J, Connor R, Barre L, Heithaus M (2000). Female reproductive success in botlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. *Behavioral Ecology,* 11(2): 210-219.

Martinho F (2012). Residency and behavioural patterns of coastal bottlenose dolphin (*Tursiops truncatus*) in the Arrabida and Troia shores (Portugal). Master thesis. Universidade de Lisboa, Departamento de Biologia Animal, Lisboa.

Mate B, Rossbach KA, Nieukirk SL, Wells RS, Irvine AB, Scott MD, Read AJ (1995). Satellite-monitored movements and dive behavior of a bottlenose dolphins (*Tursiops truncatus*) in Tampa Bay, Florida. *Marine Mammal Science,* 11: 452-463.

Maze-Foley K, Würsig B (2002). Patterns of social affiliation and group composition for bottlenose dolphins (*Tursiops truncatus*) in San Luis Pass, Texas. *Gulf of Mexico Science,* 20(2): 122-134.

Merriman M, Markowitz T, Harlin-Cognato A, Stockin K (2009). Bottlenose Dolphin (*Tursiops truncatus*) Abundance, Site Fidelity, and Group Dynamics in the Marlborough Sounds, New Zeland. *Aquatic Mammals,* 35(4): 511-522.

Newman M (2004). Analysis of weighted networks. *Physical review,* E70, p. 056131.

Pradel R, Hines JE, Lebreton JD, Nichols JD (1997). Capture–recapture survival models taking account of transients. *Biometrics,* 53: 60-72.

Quérouil S, Silva MA, Freitas L, Prieto R, Magalhães S, Dinis A, Alves F, Matos JA, Mendonça D, Hammond PS, Santos RS (2007). High gene flow in oceanic bottlenose dolphins (*Tursiops truncatus*) of the North Atlantic. *Conservation Genetics,* 8: 1405-1419.

Scott M, Chivers S (1990). Distribution and herd structure of bottlenose dolphins in the eastern tropical Pacific Ocean. In: S. Leatherwood & R. Reeves, eds. *The bottlenose dolphin.* San Diego: Academic Press.

Shane S (2004). Residence Patterns, Group Characteristics, and Association Patterns of Bottlenose Dolphins Near Sanibel Island, Florida. *Gulf of Mexico Science,* 1: 1-12.

Shane S, Wells R, Würsig B (1986). Ecology, behabior and social organization of the bottlenose dolphin: A review. *Marine Mammal Science,* 2: 34-63.

Silva M (2007). *Population Biology of bottlenose dolphins in the Azores archipelago,* University of St. Andrews: PhD Thesis.

Silva MA, Prieto R, Magalhães S, Cabecinhas R, Cruz A, Gonçalves J, Santos RS (2003). Occurrence and distribution of cetaceans in the waters around Azores (Portugal), Summer and Autumn 1999-2000. *Aquatic Mammals,* 29(1): 267-274.

Silva MA, Prieto R, Magalhães S, Seabra MI, Santos RS, Hammond PS (2008). Ranging patterns of bottlenose dolphins living in oceanic waters: implications for population structure. *Marine Biology,* 179: 179-192.

Slooten E, Dawson SM, Whitehead H (1993). Associations among photographically identified Hector's dolphins. *Canadian Journal of Zoology,* 71: 2311 – 1328.

Smolker R, Richards A, Connor RC, Pepper JW (1992). Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour,* 123: 38-69.

Team R, Developement Core (2012). *R: A language and environment for statistical computing.* Vienna, Autria: URL: Http://www.R-project.org/.

Wells R (1991). The role of long-term study in understanding the social structure of a bottlenose dolphin community. In: K. Pryor & K. Norris, eds. Dolphin societies: discoveries and puzzles. Berkeley: University of California Press, pp. 199-225.

Wells R, Rhinehart H, Cunningham P, Whaley J, Baran M, Koberna C, Costa D (1999). Long distance offshore movements of botllenose dolphins. *Marine Mammal Science,* 15: 1098-1114.

Wells R, Scott M (1990). *Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques,* s.l.: Reports of the International Whaling Commission (Special Issue), 407-415.

Wells R, Scott M, Irvine A (1987). The social structure of free-ranging bottlenose dolphins. In: H. Genoways, ed. *Current mammalogy.* New York: Plenum Press, pp. 247-305.

Wells R, Irvine A, Scott M (1980). The social ecology of inshore odontocetes. In: L. Herman, ed. *Cetacean behavior: Mechanisms and functions.* New York: Jonh Wiley and Sons.

Whitehead H (2009). SOCPROG programs: analysing animal social structures. *Behavior Ecology and Sociobiology,* 63: 765-778.

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

Whitehead H (2007). Selection of models of lagged identification rates and lagged association rates using AIC and QAIC. *Communication in Statistics- Simulation and Computation,* 36: 1233-1246.

Whitehead H (2001). Analysis of animal movement using opportunistic individual identifications: application to sperm whales. *Ecology,* 82: 1417-1482.

Whitehead H (1999). Testing association patterns of social animals. *Animal Behaviour,* 57: 26-29.

Whitehead H (1995). Investigating structure and temporal scale in social organizations using identified individuals. *Behavior Ecology,* 6: 199-208.

Whitehead H, Dufault S (1999). Techniques for analysing vertebrate social structure using identified individuals: review and recomendations. *Advanced Study Behaviour,* 28: 33-74.

Wilson D (1995). *The ecology of bottlenose dolphins in the Moray Firth, Scotland: a population at the northern extreme of the species' range,* Aberdeen, Scotland: Aberdeen University.

Wilson E (1975). *Sociobiology: The New Synthesis.* Cambridge, Massachusetts: Belknap Press.

Wilson B, Thompson PM, Hammond PS (1997). Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology,* 34: 1365-1374.

CHAPTER 4

SURVIVAL AND ABUNDANCE ESTIMATES OF BOTTLENOSE DOLPHINS IN MADEIRA ARCHIPELAGO

4.1 INTRODUCTION

The study of life history parameters is of fundamental importance to understanding the dynamics of animal populations (Chapron *et al.* 2003). Demographic processes, such as fluctuations in survival and reproduction, are the ultimate cause of population change (Gaillard *et al.* 1993). As these processes can be influenced by both ecological and anthropogenic factors, they are of great importance for several research areas, like evolutionary, population and behavioural ecology, as well as for management and conservation (Brooks *et al.* 2004). The abundance of a species can seldom be determined by census; *i.e.*, is not always possible to count all the individuals of a population. This is especially true for marine mammals, which pose particular problems of access and scale. Most marine mammals live entirely in the water, typically spend a large amount of time submerged and can have very large populations ranging over wide areas (Hammond 2010).

Demographic analyses often rely on following the fate of individually marked animals using mark-recapture sampling (Lebreton *et al.* 1992). In this method animals are captured, marked in some way and then released back into the population. The initial marking is followed by one or more capture occasions where live animals are recaptured or re-sighted, and/or dead animals are recovered. The combination of these multiple recapture occasions results in individual capture histories: a record denoting whether each individual was observed or not in each sampling occasion (White & Burnham 1999). The estimate obtained from mark-recapture method represents the number of animals that use the study area during the study period; it does not represent the density of animals in the study area as in line transect sampling (Hammond 2010).

The estimation of population size in cetacean populations can be achieved using data from photo-identification (photo-id) (Hammond 2010). Photo-id of natural marks has allowed individuals cetaceans to be monitored in photographic 'capture and recapture' samples (Hammond *et al.* 1990). This technique is commonly used to study movements and behaviour of cetaceans worldwide and it was first applied to bottlenose dolphins by Würsig & Würsig (1977). It works on the principle of photographing individual animals and identifying them by their unique natural markings. It is important though, to distinguish the application of this method in open and closed population mark-recapture studies can be made between open and closed population mark-recapture studies. A closed population will remain constant in size and composition during the study, while an open population will be subject to animals leaving and entering the population through births, deaths, emigration and immigration. Although one might think that there is no such thing as a closed population, it may be possible to have a closure by conducting a study over a short time frame, and this scenario is often desirable. Mark-recapture studies in closed population are used to estimate its absolute abundance. In open population mark-recapture studies the estimates can take into account births, deaths, immigration and emigration during the study period; additionally, it can also be used to estimate survival, recruitment and population growth rates (reviewed by Schwartz & Seber 1999).

4.1.1Model assumptions

Dependent on the state of the population (opened or closed), mark-recapture methods rely on different assumptions; these are described below.

Open population methods (Pollock *et al.* 1990)

1. All animals have the same survival probability until the next sampling occasion;
2. All animals have the same capture probability;

3. Marks are not lost or overlooked;
4. Individuals are immediately released after being sampled and intervals between sampling occasions are longer than the duration of a sample;
5. Marking does not affect future catchability.

Cosed population methods (Otis *et al.* 1978)

In addition to the assumptions outlined above:

6. There are no births, deaths or emigration during the study period.

On one hand, photo-id does not require physical capture, handling or marking which represents a huge advantage, but on the other hand it also makes it more difficult to meet the assumptions described above.

Errors in the identification of individuals will lead to the violation of the third assumption; they may result from the poor quality of photographs used, lack of distinctiveness of the individual markings and lack of permanency of markings throughout time (Hammond 1986; Stevick *et al.* 2001). To reduce the chances of missing or misidentifying marks, the dataset analysed in this study only included well-marked individuals and high-quality photographs. In spite of this precaution, the chance of making identification an error is still present in the study; the catalogue analysed here is quite extensive, and thus there is always possible biases associated with violating the third assumption.

A long-standing issue with capture–recapture models involves the matter of heterogeneity introduced by transient individuals passing through the sample area at the time of sampling. These animals usually do not return in subsequent years (permanent emigration), or they may be part of the population but not always be present in the study area (temporary emigration). The emigration process can be described in three ways:

a) Markovian temporary emigration (non-random emigration), where the probability of an animal being captured at time t + 1 depends on whether it was available for capture at time t;
b) Permanent emigration, a special case of the Markovian emigration, where the probability of a subsequent capture is zero for animals available for capture at time t;

c) Random temporary emigration, in which the probability of capture at time t + 1 does not depend on whether the animal was available for capture at time t.

Permanent emigration provokes a confounding effect between emigration and mortality (Williams *et al.* 2002) because it violates the assumption that all animals alive at time t have the same chance of survival and capture until time t+1 (Lebreton *et al.* 1992).Open models fail to distinguish permanent emigration from death not taking into account transience. This leads to negatively bias survival rates (Pradel *et al.* 1997). Also, apparent temporary emigration occurs when members of the population are available for capture; nonetheless, this seems to happen on some sampling events and not in others (Silva *et al.* 2009). It is possible to account for transience when estimating population size on cetaceans as has been the case in some studies for estimating abundance (e.g. Silva *et al.* 2009, Tezanos-Pinto *et al.* 2013; Conn *et al.* 2011; Madon *et al.* 2012). This study used models for both open and close population mark-recapture methods, to analyse long-term photo-id data of a bottlenose dolphin population with strong evidences of transience and temporary emigration (see Chapter 2 and 3). In Chapter 3 it is discussed that these dolphins are likely to have larger home ranges than the study area and that transient individuals mixed with resident dolphins. These different patterns of occurrence of the dolphins denote a wide ranging behaviour, causing unequal capture probabilities and consequently introducing problems in the analysis.

There are no previous studies in Madeira archipelago that determined this species abundance or survival. Estimating abundances for the resident dolphins can be important to address the impacts of localized disturbances (Conn *et al.* 2011). Despite this, estimating the absolute abundance could also be important to define protected areas or management plans. In this chapter I estimated the apparent survival and abundance in Madeira archipelago, using capture-recapture records of naturally marked individuals from 2004 to 2012. The open population model Cormack-Jolly Seber (CJS) was used to estimate survival between years and capture probabilities for each year for Madeira archipelago. Abundance was estimated applying two approaches:

1) The Schwarz and Arnason parameterization of the Jolly-Seber model (POPAN) (Schwarz & Arnason 1996) with data pooled by seasons was used to gain an understanding of the seasonal pattern of abundance of animals that visited the area in each season (residents and migrants; see definitions in Chapter 3, section 3.2.4 Residency). This approach was also used to provide an estimate of the 'super-population', *i.e.* the total number of dolphins that used the area during the entire study period.

2) The 2-sample Chapman-modified Peterson estimator (Hammond 2009) was used to estimate the total number of animals present in the study area during each pairs of seasons.

4.2 METHODS

4.2.1 Photo-id surveys

Photographs were obtained year round from two different types of surveys: systematic and non-systematic. Systematic surveys were carried out between 2001 and 2004, and from 2007 to 2012 and two vessels were used: the 12 m vessel Calcamar (in 2001 and 2002; at 11 km/h), and the 18 m research yacht Ziphius (from 2004 to 2012; cruise speed 12 km/h) in Beaufort Sea states ≤3. Non-systematic surveys were carried out using a 6.5m rigid inflatable boat (cruise speed 20 km/h), in Beaufort Sea states ≤4, from 2004 to 2012 (see Chapter 2 for details). Data collected during the surveys included GPS positions, group size, age-class composition, behaviour and individual photo-identification. Each collection of photos would end when all the dolphins in a group were thought to be photographed or when the group started avoiding the vessel, suggesting disturbance. During the systematic surveys it was not always possible to collect photos of each individual in the group due to time and logistic constrains. However, in all encounters an attempt to photograph without bias towards distinctively marked dolphins was made (as per Wursig & Jefferson 1990).

Digital photographs taken from different opportunistic platforms were also analysed. These were obtained from touristic boats that make two trips per day to search for cetaceans and/or other marine life; photos were collected from 2003 until 2012, mainly in the south coast of Madeira island (Figure 4.1). Data was collected by experience observers on board as well by trained whale-watching operators. Despite all types of surveys had been performed from 2001 to 2012, only a subset was used in this analysis (see section 4.2.5 Data organization and analysis).

Photographs were taken using digital cameras (Nikon D2H and D700) equipped with Nikkor zoom lenses ranging between 70-400 mm in both systematic and non-systematic surveys

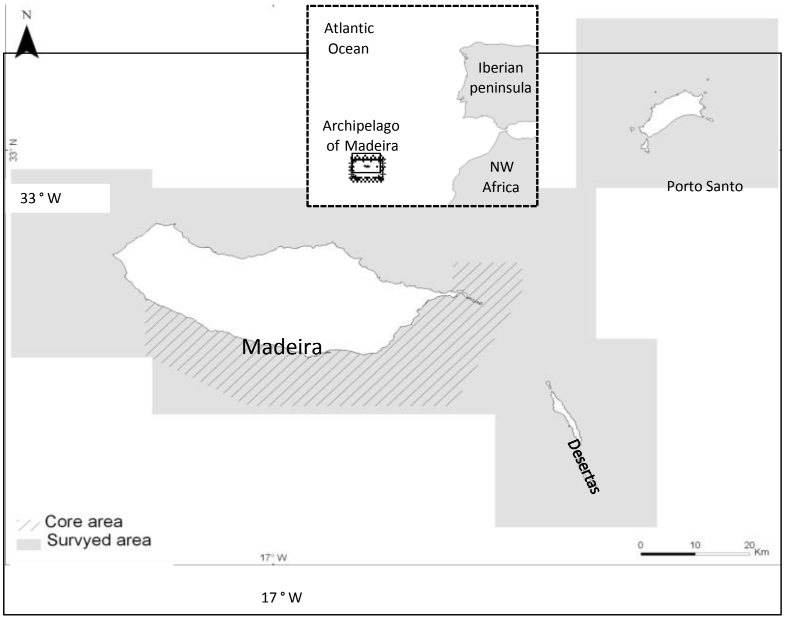

Figure 4.1 – Map of the Madeira archipelago in the Northeast Atlantic (small picture) and the study area (in grey on the larger picture), showing the area of operation of the whale-watching boats (diagonal stripes)(adapted from Alves *et al*. 2013).

4.2.2 Photo-id processing

A photo-id catalogue was compiled and a dataset of capture histories was created using individual information taken from the photographs analysed (as per Würsig & Jefferson 1990). An individual identification within an encounter was defined as a capture (see Chapter 2 for details). Only 'good' quality, photographs and 'very distinct' and 'distinct' animals were used in this analysis in order to ensure the certainty of matches. Calves were excluded from the analysis. After applying constraints for photographic quality and individual distinctiveness, the sample used in the analysis was restricted to 301 individuals.

4.2.3 Construction of capture history

Capture histories were constructed by grouping the records of sighting for each of distinct animals through time. Data was displayed in a series of '1's and '0's, where '1' indicates that the animal was captured at a given time (and as such, known to be alive and in the sampling area) and '0' shows that the animal was not captured on sampling occasion.

4.2.4 Data organization and analysis

4.2.4.1 Survival rates and capture probabilities

Data was pooled by years from 2001-2012 (excluding 2003) for the entire study area as it was assumed that survival would not change greatly over areas, as bottlenose dolphins are long-lived mammals. Goodness-of-fit (GOF) tests (TEST 2 and TEST 3) were run in RELEASE (Burnham *et al.* 1987) and with U-CARE V 2.3.2 (Choquet *et al.* 2009) to investigate potential violations of the assumptions. TEST 2 checks for differences in capture probabilities (heterogeneity) while TEST 3 assesses the assumption that all marked individuals have the same probability of survival between sampling occasions. In order to address the possible violation of equal probability of capture that would result in a lower survival rate, an *ad doc* method introduced by Pradel *et al.* (1997) was used. The first capture of each individual was excluded from the analysis to overcome the transience problem. This left truncation of the dataset suppresses the influence of the individuals captured only once (permanent emigration) with a null rate of recapture probability (Pradel *et al.* 1997). After truncation resulting sample size was 69 individuals and five years of data (2008-2012).

Overdispersion is a common occurrence in most capture-recapture data. This is especially true in the case of gregarious species, such as dolphins, because the fate of each individual within a group (seen *versus* not seen) is not independent of the fate of the others (Anderson *et al.* 1994). Conversely, underdispersion is rarer and it means that there was less variation in the data than predicted. Data were examined for overdispersion by calculating the variance inflation factor ($\hat{c}$). This factor can be calculated using several methods currently available. One option is to estimate $\hat{c}$ using the chi-square (x^2) statistics provided by programs RELEASE (Burnham *et al.* 1987) and U-CARE (Choquet et al, 2009), and divide it by the number of degrees of freedom. This approach is not always the best for live encounter capture-recapture data and the resulting estimate of $\hat{c}$ can be biased estimate from the true overdispersion. Plus, it can only be used in a limited type of models, such as the full-time dependent (Cooch & White 2010). Alternatively, the median $\hat{c}$ approach estimates $\hat{c}$ as the value for which the observed $\hat{c}$ falls halfway in the distribution of all possible $\hat{c}$ generated, under the hypothesis that a given value of $\hat{c}$ is the true value. On average, the median $\hat{c}$ is closer to truth than the $\hat{c}$ estimated from RELEASE or U-CARE, although it is usually biased high (Cooch & White 2010). Here, all three methods were used to estimate $\hat{c}$ and a conservative approach was taken by selecting the largest resulting estimate.

Data was then analysed with Cormack-Jolly Seber (CJS) model in MARK Vs. 7.0 (White & Burnham 1999), to estimate the survival between years and the capture probabilities for each year. The general full-time dependent model was fitted to the data and then, progressively simpler models of few parameters were tested. Model selection was based on the Quasi-likelihood Akaike's Information Criteria (QAICc); this criterion provides a good way to deal with overdispersion (Seber, 1982; Anderson *et al.* 1994) and also accounts for differences in the sample size between models (Burnham & Anderson 2002). The model with the lowest QAICc value was selected as the best fitting model.

4.2.4.2Abundance

Data was restricted to the south of Madeira (Figure 4.1) because of the constrains imposed by the utilization of photographs taken by the whale-watching operators that only use this area (increasing the effort in this area). Two approaches were made to estimate seasonal abundance, the open Arnason-Schwarz model (Schwarz & Arnason 1996) and the closed 2-sample Chapman-modified Peterson estimator (Hammond 2009).

Estimates of abundance from the used models ($\widehat{N}$) do not apply to the whole population, only to the well-marked individuals that were used in the analysis. These estimates had to be corrected for the total population (N_{tot}- marked and unmarked individuals). The N_{tot} was calculated by dividing N by the mean proportion of well-marked individuals ($\hat{\theta}$). This proportion was estimated dividing the well-marked individuals by the total number of photographed individuals, using 14 good quality images with 3-7 individuals in the photograph, captured from 2005-2012, resulting in a sample of 60 individuals.

For estimating the seasonal abundance of animals that use the area and the total number of animals that used that area during the course of the study (super population), data was pooled by seasons from 2004-2012 (n=237 individuals). GOF tests (TEST 2 and TEST 3) were run in U-CARE V 2.3.2 (Choquet *et al*. 2009) to investigate potential violations of the assumptions. Then, data was analysed with POPAN in MARK Vs. 7.0 (White & Burnham 1999) abundance. This approach is based on a reparameterization of the Jolly-Seber (JS) model with an additional parameter, N_{super} that denotes the size of the super population (Schwarz & Arnason, 1996). A range of models was investigated allowing survival (φ), capture probability (*p*) and probability of entry (β) to vary over time (*t*) or not (.). The Logit function was specified for survival (φ) and capture probability (*p*); the Multinomial Logit link function for the probability of entry parameter (β) and the Log link function for the estimate of abundance (Cooch & White 2010). Again, model selection was based on the QAICc value. Additionally, this approach also provides an estimate of the 'super population'. The variance of N_{tot} was estimated using the delta method following Wilson *et al.* 1999 (Equation 4.1).

$$\text{Var } N_{tot}=N_{tot}^2\left[\frac{varN}{N^2}+\frac{var\theta}{\theta^2}\right] \qquad \text{Equation 4.1}$$

For estimating the total number of animals present in the study area during each pairs of seasons, this dataset data was also pooled into seasons but using only one month of each season (to meet the closure assumption)(Table 4.3). Then, it was analysed by pair of seasons using a closed model, the 2-sample Chapman-modified Peterson estimator (Hammond 2009) (Equation 4.2):

$$N=\frac{(n1+1)(n2+1)}{(m2+1)}-1 \qquad \text{Equation 4.2}$$

where: $n1$ is the number of dolphins identified in the first sampling occasion; $n2$ is the number of dolphins identified in the second sampling occasion and $m2$ is the number of dolphins identified in both sampling occasions.

Given the small number of recaptures on the sample, this estimator was chosen as the most adequate because it reduces small sample bias. Plus, it has a robust estimate of variance. Variance was estimated according to the bootstrap simulation procedure described in Stevick *et al.* 2001 (Equation 4.3).

$$\text{Var}N_{tot}=\frac{(n1+1)(n2+1)(n1-m2)(n2-m2)}{(m2+1)^2(m2+2)} \qquad \text{Equation 4.3}$$

Sequential Chapman estimates were calculated for 4 pairs of seasons from 2011 to 2012 due to higher number of captures. Since there is no GOF test available for closed population models, these estimations were not adjusted for overdispersion.

For both open and closed models, lower and upper log-normal CIs for N_{tot} were calculated as MNA+N/C to MNA+N*C (Thompson *et al.* 1998) (Equation 4.4), where:

$$C=e^{1.96\sqrt{\ln(1+CV^2N)}} \qquad \text{Equation 4.4}$$

and MNA is the minimum number of animals known to be alive in the population (number of animals captured).

In addition, any possible trend in the seasonal abundance over time was investigated, by fitting a linear regression to the data.

4.3 RESULTS

4.3.1 Photo-id surveys

Between 2001 and 2012, there were 272 encounters corresponding to 231 days of effort that resulted in captures for photo-identification. Individual sighting histories varied greatly, ranging from individuals sighted only once to individuals seen 13 times (median=2), during the entire study period. A total of 501 individuals were identified and catalogued, based on the marks of their dorsal fin. The discovery curve for the total number of individuals increased throughout the study period as new individuals kept being added to the catalogue, suggesting an open population with regular recruitment of new animals to the study area. Contrarily, the discovery curve for re-sighted individuals seemed to stabilize as fewer new individuals were recaptured (Figure 4.2, Table 4.1). As mentioned above, after applying restrictions of quality photographs and individual distinctiveness the sample used in this analysis was reduced to 301 dolphins.

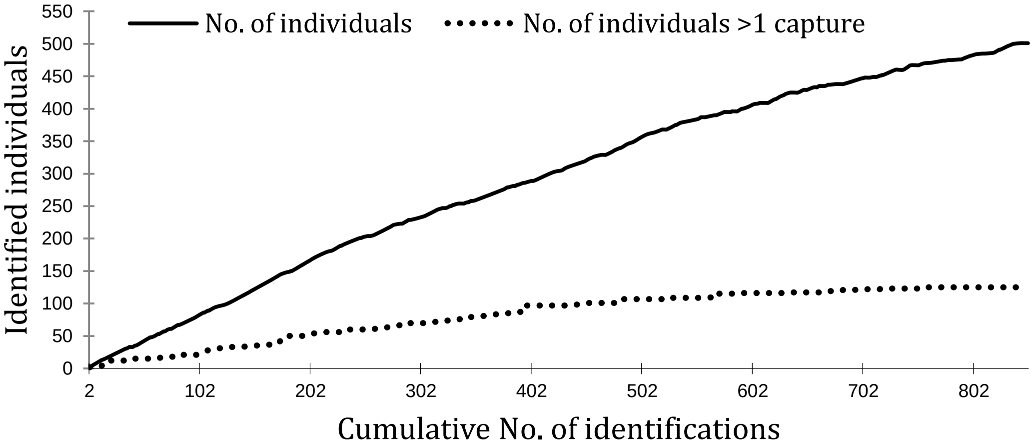

Figure 4.2 - Discovery curve of the total number of marked individual dolphins (solid line) and the total number of individuals recaptured >1 time (dashed line).

Table 4.1 – Summary of captures history with the number of individuals marked and recaptured in each year from 2011 to 2012.

Year	2001	2002	2004	2005	2006	2007	2008	2009	2010	2011	2012
Total marked individuals	13	33	61	95	143	167	218	253	329	451	501
Total recaptured individuals	4	13	18	30	40	53	64	74	101	122	125
New marked individuals	13	20	28	34	48	24	51	35	76	122	50
Recaptured Individuals per year	0	5	10	7	4	5	21	24	58	129	84

4.3.2. Capture-recapture data used

For POPAN the dataset used included data from 23 seasons for 2004-2012 and only for the south of Madeira Island (Table 4.2). After GOF tests showed significance for TEST 3.SR (transience) the first capture of every individual was remove from the dataset (see Goodness of Fit tests below). This resulted on the removal of 174 individuals and 15 seasons from the analysis.

Table 4.2 – Summary data for POPAN as implemented in MARK, including type of pooling, period of data collection, number of sampling occasions, number of uniquely marked individuals captured and number of individuals captured after removal of the 1st capture.

Year	Season	Period	Sampling Occasions	No. of individuals captured	No. of individuals captured (no first capture)
2004	Spring	17 May-23 June	5	10	0
	Summer	2 Sept-29 Sept	2	4	2
2005	Winter	26 Jan-22 Feb	2	1	0
	Spring	27 Apr-14 Jun	5	8	0
	Summer	12 Jul-21 Sept	5	4	1
2006	Winter	22 Feb	1	2	0
	Spring	11 May-30 Jun	3	7	0
	Summer	19 Jul-19 Sept	4	5	0
2007	Summer	29 Aug-22 Sept	7	6	0
2008	Spring	28 Apr-20 Jun	9	2	0
	Summer	7 Jul-7 Sept	4	18	2
2009	Spring	26 Mar-26 Jun	12	22	4
	Summer	4-Jul-12 Aug	7	8	4
	Autumn	13-Oct-18 Nov	7	6	1
2010	Spring	17 May-30 Jun	10	8	3
	Summer	14 Jul-22 Sept	17	39	12
	Autumn	13 Oct-2 Dec	9	13	3
2011	Winter	4 Jan-21 Mar	6	4	1
	Spring	4 Apr-24 Jun	25	31	10
	Summer	2 Jul-29 Sept	41	56	15
	Autumn	4 Oct-28 Dec	21	35	17
2012	Winter	7 Jan-25 Mar	14	39	25
	Spring	9-Apr-29 Jun	19	18	7

For the Chapman estimator data used in this analysis included captures from spring 2011 until spring 2012 totalizing 173 uniquely marked individuals (Table 4.3).

Table 4.3 - Summary data used in the 2-sample Chapman-modified Peterson estimator, including type of pooling, period of data collection, number of sampling occasions, number of uniquely marked individuals captured and number of individuals recaptured.

Year	Season	Period	Sampling Occasions	No individuals captured	No of individuals recaptured
2011	Spring	3-27 May	9	21	-
	Summer	11-28 Aug	18	32	5
	Autumn	4-30 Nov	3	18	7
2012	Winter	13-25 Mar	7	29	15
	Spring	8-23 May	3	12	7

4.3.3. Goodness of Fit tests

For survival and capture probabilities dataset, both GOF tests conducted in U-CARE and in RELEASE were inconclusive. There was not sufficient data to run the tests, and the only test that was performed was TEST 3.SR (test for transience). This resulted in an overall test with an unexpected ĉ value of 0.20 indicating underdispersion of the data. Then, ĉ was estimated through another method described above (see section 4.2.4.1), the Median ĉ, implemented in MARK (White & Burnham 1999). This test gave a ĉ value of 2.23 indicating significant overdispersion of the data. While the latter case is more common on this type of data and at the same time more conservative this ĉ value was used to adjust for lack of fit of the data.

For abundance estimation using open model POPAN, GOF tests run in U-CARE indicated some overdispersion of the data (Table 4.4). There was no evidence of 'trap effect' and that that effect lasted for more than one interval (TEST 2.CT and 2 CL). There was also no evidence of an effect of capture on survival (TEST 3.SM), however there was a significant transience effect as showed by the result of TEST 3.SR. To account for this, the same approach used for the annual survival dataset was used here, and the first capture of every individual was excluded from seasonal data (Pradel *et al.* 1997). Dataset was reduced to 46 individuals and 8 seasons (2010-2012). Then, the data was reran in U-CARE (Table 4.4).

Table 4.4 – Results from the GOF tests run in U-CARE for the seasonal dataset used in POPAN, including the results of the overall test (TEST 2+3). $\hat{C}$ was estimated by dividing the $\chi^2$by the degrees of freedom (df). * are significant *p* values.

		Test3SR	Test3SM	Test2CT	Test2CL	Global test
by seasons	*p* value	0,001*	0,86	0,49	0,77	0,12
	χ2	33,63	3,99	9,49	11,61	58,74
	df	13	8	10	16	47
	$\hat{c}$					1,25
by seasons without 1st capture	*p* value	0,06	-	0,81	0,33	0,26
	χ2	7,50	-	0,43	0,94	8,87
	df	3	-	2	1	7

4.3.4 Survival rates and capture probabilities

The best fitting model was with constant survival and time variation capture probabilities (φ (.) p (t)) (Table 4.5). The annual survival rate for this model was 0.95 (0.12 SE, CI=0.13-0.99).

Table 4.5 - Model selection for CJS candidate models. Data was pooled by years and without the first capture. φ = survival; *p*= capture probabilities ;(.)=constant ;(t)=time.

Model	QAICc	Delta QAICc	QAICc weight	Model Likelihood	No. Parameters	Deviance
1 φ(.) *p*(t)	133,0877	0	0,74447	1	5	18,1690
2 φ(t) *p*(t)	135,8937	2,806	0,18303	0,25	7	16,0760
3 φ(t) *p*(.)	137,7459	4,6582	0,07250	0,10	5	22,8272

Figure 4.3 shows that there were fluctuations in capture rates between years. There is an increase from 2010 onwards, but generally the values were low ranging from 0.16 (±0.23) in 2010 to 0.50 (±0.26) in 2011.

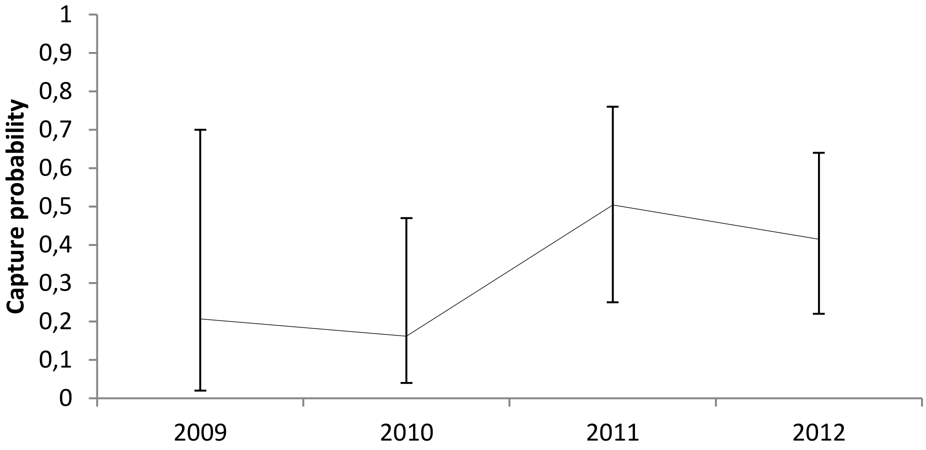

Figure 4.3 – Annual capture probabilities estimated from CJS model. Vertical bars represent the 95% confidence intervals.

4.3.5 Abundance

4.3.5.1Arnason-Schwarz model (POPAN)

The POPAN candidate models for the seasonal dataset without the first capture were adjusted for the estimated ĉ value (1.25) and are presented in Table 4.6 Standard models with constant and time-variation in survival and capture rates were produced and fitted to the data. Model with constant survival and time-variation in capture and entrance probabilities received best support from the data (Model 1, Table 4.6). Thus, parameter inference was done using only this model.

Table 4.6 – Model selection for POPAN data pooled by seasons without the first capture.φ= apparent survival; *p*= capture and β= probability of entry; (.)=constant; (t)=time

	Model	QAICc	ΔQAICc	QAICc weight	Model Likelihood	No. Parameters	Qdeviance
1	φ(.) *p*(t) β(t)	260,395	0	0,86484	1	23	-
2	φ(t) *p*(.) β(t)	264,538	4,143	0,10894	0,13	18	-
3	φ(.) *p*(.) β(t)	267,387	6,992	0,02622	0,03	13	-

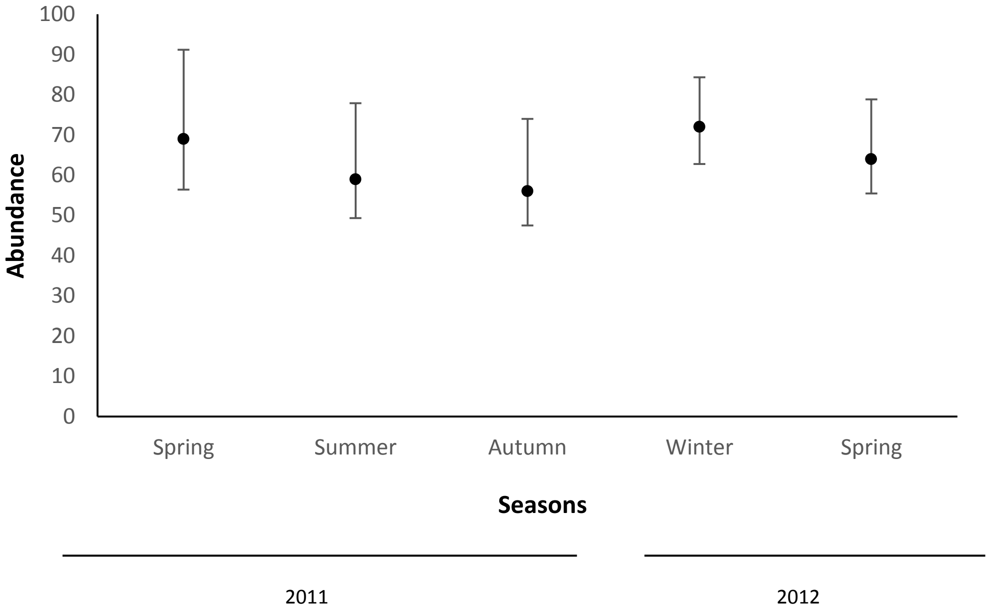

Figure 4.4 – Seasonal abundance estimates (marked and unmarked) in the South sector of Madeira Island, obtained with POPAN (excluding transients). Vertical bars represent 95% confidence intervals.

Due to higher number of captures, and thus more representatives, only estimates from spring 2011 to spring 2012 are presented here. There were only minor fluctuations on seasonal abundance of resident dolphins (Figure 4.4, Table 4.7). Seasonal estimates of abundance, excluding the first capture of each individual, and after correcting for the proportion of unmarked individuals, varied from 56 (95% CI=48-74) dolphins in autumn of 2011 to 72 dolphins in winter 2012 (95% CI=63-84).

Table 4.7 - Averaged estimates of seasonal population size (Ntot). $\widehat{N}$ is the seasonal estimate of well-marked individuals. L CI= lower confident interval; U CI= upper confident interval; 95% CI are corrected for the total population (marked and unmarked). Proportion of well-marked = 0.68.

Year	Season	$\widehat{N}$	SE($\widehat{N}$)	CV	Ntot	L CI	U CI
2011	Spring	47	11,69	0,25	69	56	91
	Summer	40	9,75	0,24	59	49	80
	Autumn	38	9,12	0,24	56	48	74
2012	Winter	49	6,26	0,13	71	59	92
	Spring	44	7,32	0,17	65	53	89
	Res	125	1,42	0,16	183	155	218
	Res+Trans	299	1,42	0,16	438	394	486

The super population that used the South of Madeira Island through the study period was estimated in 299 dolphins. This was done by adding the transient animals (n=174) that had been excluded to the estimated number of resident dolphins (n=125). Correcting this value for the unmarked proportion of the population (32%), the total super population estimation was 438 bottlenose dolphins (SE=1.42, 95% CI=394-486) (Table 4.7).

4.3.5.2 Chapman-modified Peterson estimator

The estimates represent an entire year (spring 2011- spring 2012). The number of recaptures ($m2$) is much higher in autumn-winter of 2011/2012 which represents also the lowest estimate of abundance (Table 4.8).

Table 4.8 –Number of dolphins captured each season ($n1$ and $n2$), number of matches ($m2$) and estimates of abundance for each pair of seasons ($\widehat{N}$).

Year	Seasons	$n1$	$n2$	$m2$	$\widehat{N}$	SE($\widehat{N}$)	CV($\widehat{N}$)
2011	Spr-Sum	21	32	5	120	1,97	0,02
	Sum-Aut	32	18	7	77	3,22	0,04
	Aut-Win	18	29	15	35	0,40	0,01
2012	Wint-Spr	29	12	7	48	1,25	0,03

In Table 4.9 are presented the seasonal estimates of abundance after correcting for the proportion of unmarked individuals (0.32). The highest estimate is 176 dolphins in spring-summer 2011and the lowest is 51 dolphins in autumn-winter of 2011/2012. There were considerable variations in the seasonal estimates of population size of bottlenose dolphins in the study area throughout an entire year with the regression presenting a negative trend (r^2=0.81). The four seasonal estimates are independent estimates of population size as the number of matches should be independent and CV values indicate that this estimation should be precise.

Table 4.9 – Number of total abundance after correcting for the proportion of unmarked dolphins (Ntot) and 95% confident intervals. L CI= lower confident interval; U CI= upper confident interval; Proportion of well-marked = 0.68.

Year	Seasons	^N	SE	CV	Ntot	L CI	U CI
2011	Spri-Sum	120	1,97	0,02	176	97	363
	Sum-Aut	77	3,22	0,04	113	66	248
	Aut-Win	35	0,40	0,01	51	44	76
2012	Wint-Spr	48	1,25	0,03	70	56	96

4.4 DISCUSSION

4.4.1 Model assumptions

The analysis of survival rates and abundance estimates presented here rely on a set of assumptions derived from both open and close methods (see section 4.1: Introduction). The violation of those assumptions has the potential to bias estimates and need to be considered (Seber 1982).

The assumption that marks are not lost was unlikely violated in this study. The characteristics used to identify individual bottlenose dolphins were nicks and notches in the dorsal fin that are generally persistent and can last throughout the lifetime of an individual (Lockyer & Morris 1990; Würsig & Jefferson 1990). Those nicks and notches make the individuals reliable for posterior identification. Additionally, by using only well-marked individuals and excluding calves (that lack distinctive marks) (Würsig & Jefferson 1990), from the analysis helped mitigate possible misidentification.

Captures of individuals are assumed to be independent events in mark-recapture analysis. For animal populations that form groups though this can be problematic because the capture of an individual can be dependent on the capture of another individual. That can give a false sense of precision as lead to underestimating the variance of the estimates. Excluding calves from the analysis eliminates the major source of this potential bias. Also, the fluid nature of the bottlenose dolphin population in Madeira (see Chapter 2), with individuals associating and disassociating rapidly, reduces the impact of social structuring in this analysis (Wilson *et al.* 1999).

Perhaps the most difficult assumption to satisfy in capture-recapture studies is that of equal probability of capture within a sampling occasion (Silva 2007). Individual preferences for certain areas may affect the probability of encountering a animal (Hammond 2010). In this study, in order to increase sample size (and thus precision) the whale-watching opportunistic data was added to the analysis. By doing this, the study area had to be reduced to the south of Madeira Island, and the bias resulting from different photo-id effort was minimized. In Chapter 3 the movements probabilities indicate that dolphins had a higher probability of staying in sector 1 (Madeira North, Figure 4.1) which is an area that was not considered for this analysis. In addition to this, the different patterns of occurrence of the dolphins in Madeira archipelago (see Chapter 2 and 3) makes this violation even more likely to occur. In addition, approximately 82% of the individuals of the datasets used in this analysis were transients and were only captured once, representing individuals that either died or permanent emigrated. As expected the GOF tests gave significant values for transience and by applying the left truncation (elimination of the first capture of every individual) the effect of transience was minimized. The GOF tests indicated that the model structure was correct and the small variance inflator ($\hat{c}$=1.25) points out that the excess of variation was not large and was within the acceptable limits.

Besides the general assumptions earlier discussed, the assumption of closure for the 2-sample Chapman-modified Peterson estimator was addressed by using sampling occasions within one month period. However, even so, given the results of movements patterns that showed that these dolphins can travel from one area to another within one day (see Chapter 3), and thus leaving this study area it is unlikely that the assumption held. This will certainly bias the population estimation but, the direction and extension of that bias was not further investigated.

4.4.2 Survival

This study failed to estimate accurate annual survival rates for this population. The GOF tests were inconclusive, both from U-CARE and RELEASE due to insufficient data. By leaving all the transients in the dataset this leads to negatively bias survival rates (Pradel *et al.* 1997). When removing them the captures were insufficient to estimate annual survival parameter. Age effect cannot explain this result because the analysis was restricted to well-marked individuals as explain in the previous section, Model assumptions. Although the estimate of survival resulting from the CJS models on the truncated dataset is expected ($\varphi=0.95$) (within the range of other long-lived mammal), the CIs are wider and the performance of GOF tests indicated that there are structural problems with this dataset, that is probably too sparse or has too much variability. In open models, permanent emigration is confounded with apparent survival and temporary emigration is not estimated. This can affect capture probability with a secondary effect on survival (Tezanos-Pinto *et al.* 2013). Silva *et al.* (2009) found higher values of survival in the Azores archipelago for a populations that similarly had high number of transient's dolphins ($\varphi=0.97$, ± 0.029 SE). Contrarily, a population of dolphins in Croatia with low levels of transience was found to have one of the lowest rate of survival for cetaceans populations ($\varphi=0.82$, CI 0.694 - 0.908, Fortuna 2006). The estimate of 0.95 from this study is in the range of values found in other bottlenose dolphin populations (Sado estuary, Portugal $\varphi=0.961$, SE=0.012 Gaspar 2003; Moray Firth $\varphi=0.942$, SE=0.048 Sanders-Reed *et al.* 1999; Sarasota Bay $\varphi=0.96$, SD=0.008 Wells and Scott 1990). These differences in survival estimates are likely to be related to ecological differences between study sites (Currey *et al.* 2008) or to different levels of natural or anthropogenic impacts (Silva *et al.* 2009). Caution must be taken though when interpreting the estimate found in this study, due to its lack of precision. Nonetheless, this value should be acceptable as there is no apparent reason for this population to have low rates of survival. There are also no major visible signs of threats in the study area that would differentiate the population in Madeira from other similar bottlenose dolphin populations, such the one studied by Silva *et al.* (2009) in the Azores.

4.4.3 Capture probabilities

Capture probability was highest in 2011, likely due to a higher research effort in that year. There was great variation in the annual values, suggesting time-dependency, as expected in the majority of mark-recapture studies in cetaceans (Hammond 2009). The variability observed in the capture probabilities may be explained by the variations in the effort, as sampling effort certainly influenced the number of dolphins identified each year.

4.4.4 Population size

Hammond *et al.* (1990) refers that cetacean abundance studies that are carried out as a by-product of general purpose photo-identification studies frequently suffer from violations of the assumption, including that of unequal capture probabilities. Although the photo-id catalogue analysed here is large and includes captures since 2001, the majority of the dedicated sampling effort was done in the last three years (2010-2011). In order to minimize this potential bias, the captures made prior to this period were excluded from the analysis. The seasonal differences found in abundance in the last three years do not seem to be due to any methodological problem and should reflect natural oscillations in the global abundance of bottlenose dolphins in the study area. This study estimated that 183 resident dolphins (95% CI= 140 to 246) used the south of Madeira Island from the autumn of 2010 until the spring of 2012. Both open and closed models estimates followed the same temporal variability throughout seasons. A consistent value of high winter estimates of resident dolphins decreasing in spring is evident through the study period. When comparing these results to the ones of Chapman estimator, the tendency of the population size of the total number of dolphins that use the area, is inverse. Here the lowest value was found to occur in the autumn-winter. The data suggest that there was an increase on the number of dolphins in this area from spring-summer until autumn, decreasing in winter and increasing again in the following spring. Results showed in Chapter 3 indicated that, even though there were no significant differences in group size across moths, there were some larger groups seen from June to October. Those groups may represent an influx of transients and seasonal residents moving into the study area, which can explain the higher number of dolphins in that period. The higher abundance estimates generated from the Chapman estimator for spring-summer and summer-autumn seems to corroborate that influx of non-resident dolphins. The residents, however seem to be slightly higher during winter indicating that they might move out of the area in the other seasons. This could be due to a shift in prey distribution; it may also be due to the fact that by having more dolphins in the area during spring and summer and that they mixed with resident individuals (see Chapter 3) the chances of capturing resident dolphins decreases during that period. Often mark-recapture studies assume that all animals are members of the same homogeneous population, ignoring potential complications that arise from heterogeneous social structure and different residency patterns (Conn *et al.* 2011). Similar patterns of seasonal variability in abundance have been reported for other bottlenose dolphin populations (New Zeland, Tezanos-Pinto *et al.* 2013; South Carolina, USA, Speakman *et al.* 2010).

The south coast of Madeira Island is only a part of the range of a larger population of bottlenose dolphins. The super population estimates from POPAN indicated that 438 (95% CI= 394-486) dolphins used the area at least once from 2004-2012. This estimate includes those animals that may have died or emigrated permanently.

The estimate of population size provided here for the total number of dolphins using the study area from 2010 to 2012 was higher than that published for bottlenose dolphin population in the Moray Firth, Scotland (129 animals, 95% CI= 110-174; Wilson *et al.* 1999), in the Shannon Estuary, Ireland (107 animals, 95% CI= 83-131; Berrow *et al.* 2012) and in North Carolina, USA (141 animals, 95% CI=112-200; Read *et al.* 2003). This finding was to be expected as those studies focused on areas that were inhabited by dolphins with a high degree of site-fidelity and well-defined and smaller ranges (Silva *et al.* 2009).

As discussed previously, the violations of the model assumptions may lead to biases in the abundance estimates to an uncertain level. This is specially so for the assumption of equal capture probability in the Arnanson-Schwartz model, and the assumption of geographic closure for the Chapman estimator. Nonetheless, this study presents the first abundances estimates of bottlenose dolphins in Madeira archipelago. Providing separate estimates for the overall super population as well as the resident population is important, as population size of residents alone, may often be more important for managers when handling a specific area and its localized impacts (Conn *et al.* 2011).

References

Alves F, Querouil S, Dinis A, Nicolau C, Ribeiro C, Freitas L, Kaufmann M, Fortuna C (2013). Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: implications for conservation. *Aquatic Conservation: Marine and freshwater ecosystems,* 5: 758-776.

Anderson DR, Burnham KP, White GC (1994). AIC model selection in overdispersed capture–recapture data. *Ecology*, 75: 1780–1793.

Berrow S, O'Brien J, Groth L, Foley A, Voigt K (2012). Abundance estimate of bottlenose dolphins (*Tursiops truncatus*) in the Lower River Shannon candidate Special Area of Conservation, Ireland. *Aquatic Mammals*, 38(2): 136-144

Brooks SP, Catchpole EA, Coulson T, Lebreton JD, Morgan BJT (2004). Recent progress in using marked individuals to understand animal population biology. Statistical Laboratory Research Reports 2004-7, 32p. University of Cambridge.

Burnham KP, Anderson DR&, White G, Brownie C, Pollock KH (1987). Design and analysis of fish survival experiments based on release-recapture data. *American Fisheries Society Monograph*. 5, Bethesda, MD.

Burnham KP, Anderson DR (2002). Model Selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer Verlag, New York.

Caldeira RM, Sangrá P (2012). Complex geophysical wake flows: Madeira Archipelago case study. *Ocean Dynamics* DOI 10.1007/s10236-012-0528-6.

Chapron G, Quenette PY, Legendre S, Clobert J (2003) Which future for the French Pyrenean brown bear (*Ursos actos*) population? An approach using stage-structured deterministic and stochastic models. Comptes Rendus - Biologies, 326(1): 174-182

Choquet R, Lebreton JD, Gimenez O, Reboulet AM, Pradel R (2009). U-CARE: Utilities for performing goodness of fit tests and manipulating CApture-REcapture data. *Ecography,* 32:1071-1074.

Cooch E, White G (2010). Program Mark: 'A gentle introduction'. Colorado State University, Fort Collins, CO.

Conn PB, Gorgone AM, Jugovich AR, Byrd BL, Hansen LJ (2011). Accounting for transients when estimating abundance of bottlenose dolphins inChoctawhatchee Bay, Florida. *Journal of Wildlife Management*, 75:569-579

Currey RJC, Dawson SM, Slooten E, Schneider K, Lusseau D, Boisseau OJ, Haase P, Williams JA (2008). Survival rates for a declining population of bottlenose dolphins in Doubtful Sound, New Zealand: an information theoretic approach to assessing the role of human impacts. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19: 658–670.

Fortuna CM (2006). Ecology and conservation of bottlenose dolphins (*Tursiops truncatus*) in the north-eastern Adriatic Sea. PhD dissertation, University of St. Andrews.

Gaspar R (2003). Status of the resident bottlenose dolphin population in the Sado Estuary: past, present and future. PhD dissertation, University of St Andrews.

Gaillard JM, Festa-Bianchet M, Yoccoz NG (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, 13: 58–63.

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

Hammond PS (1986). Estimating the size of naturally marked whale populations using capture-recapture techniques. Report of the International Whaling Commission, Special Issue 8: 253-282.

Hammond PS (2009). Mark-Recapture. In: Perrin, W.F., Würsig, B. and Thewissen, J.G.M. (Eds.) *Encyclopedia of marine mammals, second ed*. Academic Press, Amsterdam, pp. 705-709.

Hammond P (2010). Estimating the abundance of marine mammals. In: Boyd, I. Bowen, D. and Iverson, S. Eds. *Marine Mammal Ecology and Conservation*. *A handbook of techniques*. Oxford Press. 42-67.

Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992). Modeling survival and testing biological hypotheses using marked Animals: A unified approach with case studies. *Ecological Monographs,* 62(1):67-118

Lockyer CH, Morris RJ (1990). Some observations on wound healing and persistence of scars in *Tursiops truncatus*. Report of the International Whaling Commission,Special Issue 12: 113–18.

Madon B, Garrigue C, Pradel R, Gimenez O (2012). Transience in the humpback whale population of New Caledonia and implications for abundance estimation. *Marine Mammal Science,* 29(4): 669-678.

Mann J, Connor R, Barre L, Heithaus M (2000). Female reproductive success in bottlenose dolphins (Tursiops sp.): life history, habitat, provisioning, and group-size effects. *Behavioral Ecology,* 11(2): 210-219.

Otis DL, Burnham KP, White GC, Anderson DR (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monographs,* 62

Pollock KH, Nicholls JD, Brownie C, Hines JE (1990). Statistical inference for capture-recapture experiments. *Wildlife Monographs,* 107.

Pradel R, Hines JE, Lebreton JD, Nichols JD (1997). Capture–recapture survival models taking account of transients. *Biometrics,* 53:60–72

Read AJ, Urian KW, Wilson B, Waples DM (2003). Abundance of bottlenose dolphins in the bays, sounds and estuaries of North Carolina, USA. *Marine Mammal Science,* 19: 59-73

Sanders-Reed CA, Hammond PS, Grellier K, Thompson PM (1999). Development of a population model for bottlenose dolphins. Survey and Monitoring Rep. No. 156, Scottish Natural Heritage, Battleby, Redgorton, Perth, UK.

Schwarz CJ, Arnason AN (1996). A general methodology for the analysis of open-model capture recapture experiments. *Biometrics,* 52: 860–873.

Schwarz CJ, Seber GAF (1999). Estimating animal abundance: review III. *Statistical Science*, 14:427–456

Seber GAF (1992). A review of estimating animal abundance II. *International Statistical Review,* 60: 129-166

Seber GAF (1982). The Estimation of Animal Abundance and Related Parameters. 2nd ed. Arnold, London, UK.

Silva M, (2007). *Population Biology of bottlenose dolphins in the Azores archipelago,* University of St. Andrews: PhD Thesis.

Silva MA, Magalhães S, Prieto R, Santos RS, Hammond PS (2009). Estimating survival and abundance in a bottlenose dolphin population taking into account transience and temporary emigration. *Marine Ecology Progress Series,* 392:263-276.

Speakman TR, Lane SM, Schwacke LH, Fair PA, Zolman ES (2010). Mark-recapture estimates of seasonal abundance and survivorship for bottlenose dolphins (*Tursiops truncatus*) near Charleston, South Carolina, USA. *Journal of Cetacean Research and Management,* 11: 153-162.

Stevick PT, Palsbøll PJ, Smith TD, Bravington MV, Hammond PS (2001). Errors in identification using natural markings: rates, sources, and effects on capture-recapture estimates of abundance. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 1861-1870.

Tezanos-Pinto G, Constantine R, Brooks L, Jackson JA, Mourão F, Wells S, Scott-Baker C (2013). Decline in local abundance of bottlenose dolphins (*Tursiops truncatus*) in the Bay of Islands, New Zealand. *Marine Mammal Science,* 29(4): 390–410. doi: 10.1111/mms.12008.

Thompson WL, White G, Gowan C (1998). Monitoring vertebrate populations. Academic Press, New York

Wells R, Scott M, Irvine A (1987). The social structure of free-ranging bottlenose dolphins. In: H. Genoways, ed. *Current mammalogy*. New York: Plenum Press, pp. 247-305.

Wells RS, Scott MD (1990). Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. Report of the International Whaling Commission, Special Issue 12:407-415.

Williams BK, Nichols JD, Conroy MJ (2002). Analysis and Management of Animal Populations. San Diego: Academic Press, USA.

White GC, Burnham KP (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study (Suppl),* 46:120-138

Wilson B, Hammond PS, Thompson PM (1999). Estimating Size and Assessing Trends in a Coastal Bottlenose Dolphin Population. *Ecological Applications,* 9: 288-300

Würsig B, Jefferson T (1990). Methods of photo-identification for small cetaceans. In: Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters. Report of the International Whaling Commission, Special Issue 12: 43-52.

Würsig B, Würsig M (1977). The photographic determination of groupsize, composition, and stability of coastal porpoises (*Tursiops truncatus*).*Science,* 198: 755-56.

CHAPTER 5

SPATIAL AND TEMPORAL DISTRIBUTION OF BOTTLENOSE DOLPHINS IN MADEIRA ARCHIPELAGO

5.1 INTRODUCTION

Effective conservation of wild populations requires an understanding of the relationship between populations and their habitats and for that, the first step is to determine which habitats are used with higher frequency (Cañadas *et al.* 2005). Physiographic, oceanographic and biological variables can be used as proxies for prey availability (known to most often determine the cetacean distribution patterns as a predator response) (de Stephanis *et al.* 2008), which often are not available at the required spatial resolution to be used for habitat use analysis (Redfern *et al.* 2006). Foraging cetaceans are known to concentrate over areas of abrupt topography, such as shelf breaks, steep slopes, canyons, shallow banks and seamounts (Cañadas *et al.* 2002; 2005; Yen *et al.* 2004; Baumgartner *et al.* 2001; Croll *et al.* 1998). These habitats are characterized by higher productivity, as a result of upwelling-driven nutrient availability (Genin 2004).

The bottlenose dolphin (*Tursiops truncatus*) occurs in populations that range from far offshore waters to mostly or even exclusively coastal, along the continents or around islands (Forcada *et al.* 2004). In Madeira archipelago the bottlenose dolphin is one of the most common species (Dinis *et al.* 2009; Freitas *et al.* 2004), and this study estimates that approximately 430 bottlenose dolphins have used the area at least once, of which a small part was classified as residents based on their long-term and year-round site fidelity (see Chapters 2,3 and 4).

Several anthropogenic activities in Madeira with potential impact on cetaceans, especially the whale-watching industry (Ferreira 2007, Vera 2012) are growing, and

this urges for an assessment of appropriate habitat use and distribution studies, in order to identify possible preferences and to indicate if critical habitats do exist.
Despite the difficulties of investigating the marine environment, one of the more common approaches to conservation is the establishment of marine protected areas (MPAs) and although their effectiveness is the subject of much debate, they are considered an important tool for conservation (Cañadas *et al.* 2005). In Madeira archipelago MPAs covers only the coastal waters up to 100 m depth (Menezes *et al.* 2011), which is hardly effective for such a mobile species as bottlenose dolphins. These animals usually have ranges that are too large to be included within a single MPA, but addressing areas where threatening human activities significantly overlap with the population range or important habitat can contribute effectively for the species conservation (Silva *et al.* 2012). Protected areas design requires knowledge of the spatial-temporal distribution and habitat requirements of the population of interest, in order to adjust the size of the management area to the biological needs of the target population (Silva *et al.* 2012). In addition the large habitat area usually required for a species like the bottlenose dolphin can protect many other species (Hoyt 2011) as these dolphins can act as an umbrella and a flagship at the same time for the preservation of the marine environment.

Here, bottlenose dolphin sighting and survey effort data were used to examine habitat use and distribution of bottlenose dolphins around Madeira, Desertas and Porto Santo islands. These analyses use data from 2001 through 2012 (excluding 2003) to calculate encounter rates and to investigate temporal occurrence and spatial distribution of bottlenose dolphins in the study area.

5.2 METHODS

5.2.1 Study area

This study was conducted in the archipelago of Madeira, Portugal. The archipelago is located in the warm-temperate waters of the northeast Atlantic Ocean, at approximately 1000 km of the European continent and 500 km of the West African coast (see Chapter 1, section 1.4 - Study area). The study area covers about 4818 km^2, and is characterized by a narrow continental shelf, with steep submarine canyons and deep waters (ca. 1500 m) (Geldmacher *et al.* 2000). The area was divided in eight (see Chapter 2 and 3 - study area) and four sectors for systematic and non-systematic surveys respectively (Figure 5.1).

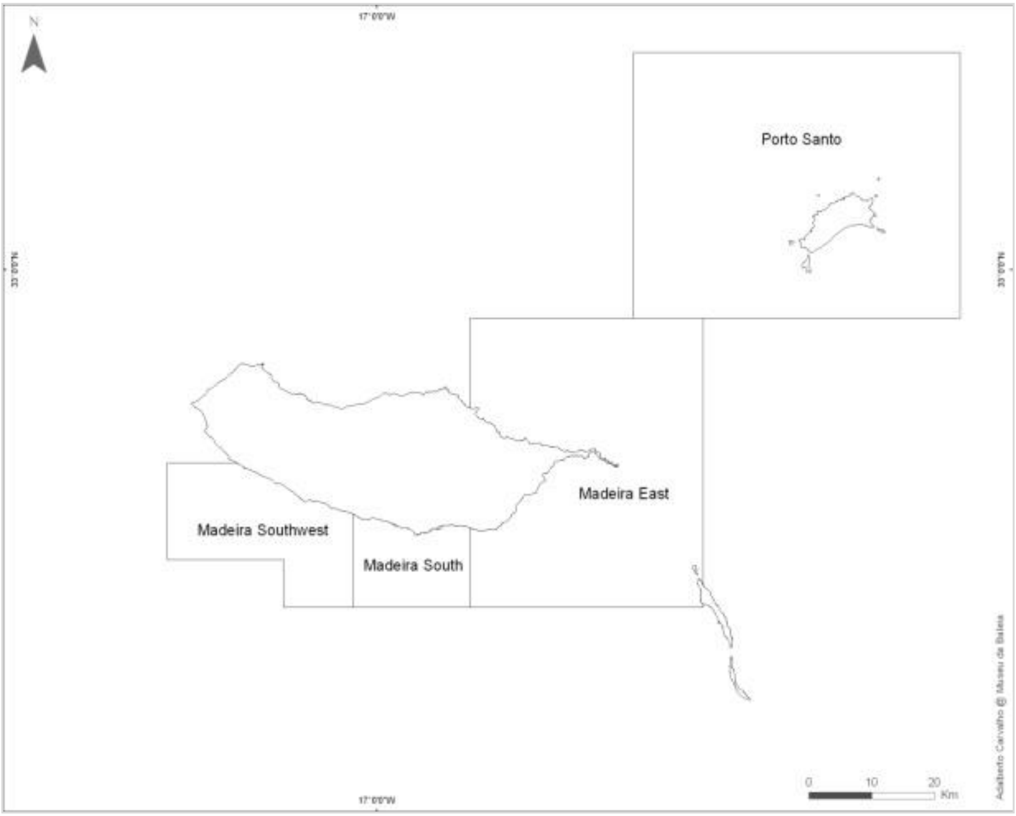

Fig. 5.1- Map representing the different sectors for non-systematic surveys.

5.2.2 Field methods

Sightings and search effort from dedicated surveys (systematic and non-systematic) collected between 2001 and 2012 (excluding 2003) were used in the analysis (see chapter 2 for survey methodologies details; Table 5.1).

5.2.3 Data analysis

Search effort was quantified as the number of km covered on effort mode under Beaufort Sea state ≤3. In order to reduce bias sightings from radio calls from other vessels were excluded. Effort and sighting data were then transferred into ArcView 9.3.1 (ESRI, Inc.), which was used for data processing.

5.2.3.1 Spatial distribution

Search effort, sighting data, and static variables such as mean depth, mean slope and minimum distance to coast were associated with each grid cell using Geographic Information System (GIS) tools. Spatial distribution was investigated by dividing the study area into a 2' x 2' grid of cells and calculating an encounter rate for each grid cell. Encounter rate was calculated as the number of sightings by 100 km surveyed. Data analysis was independent for each type of survey due to different methodologies, and grid cells with <5 km of search effort were excluded from the analysis to avoid small sample biases (Alves 2013); Panigada *et al.* 2005, de Stephanis *et al.* 2008).

For the analysis of the encounter rate in relation to physiographic variables these were ranked into bins. Depth and distance from the coast were measured in meters and kilometres respectively, while slope was expressed in degrees. Polynomial regressions were used to assess the best fit prediction between the response variable encounter rate and each static covariate.

5.2.3.2 Temporal distribution

Monthly encounter rate was calculated using inter-annual data of each type of survey. Encounter rate was calculated as the number of sightings/100km and pooled by month.

Kruskal-Walis ANOVA was used to explore if there were significant differences in the encounter rate between months for both systematic and non-systematic survey data. Shapiro-Wilk and Levene's test were carried out for the ANOVA assumptions (α=0.05). All the analyses were made in R 3.0.2 software (R Development Core Team 2012).

5.3 RESULTS

5.3.1 *Effort and sightings*

One hundred and ten groups of bottlenose dolphins were recorded along 10 596 km of search effort during non-systematic surveys, and 89 sightings were registered along 14 318 km of effort during systematic surveys, which totalizes 199 sightings and 24 914 km of search effort from 2011-2012 (Table 5.1; Figure 5.2). During systematic surveys, 2001 was the most surveyed year while 2011 was the year with more encounters. Also, 2011 was the year with more effort and sightings in non-systematic surveys.

Table 5.1 - Km surveyed, number of groups and encouter rate(ER) of bottlenose dolphins sighted per year and type of survey.

	Non-systematic surveys			Systematic surveys			Total	
Year	km	Groups	ER	Km	Groups	ER	Km	Groups
2001			-	2 577	7	0,27	2 577	7
2002			-	1 943	7	0,36	1 943	7
2004	455	17	3,74	652	7	1,07	1 107	24
2005	1 853	17	0,92			-	1 853	17
2006	2 005	11	0,55			-	2 005	11
2007	649	6	0,92	919	6	0,65	1 568	12
2008			-	2 274	15	0,66	2 274	15
2009			-	500	4	0,80	500	4
2010	953	13	1,36	1 551	10	0,64	2 504	23
2011	3 266	26	0,80	2 510	17	0,68	5 776	43
2012	1 415	20	1,41	1 392	16	1,15	2 807	36
Total	10 596	110		14 318	89		24 914	199

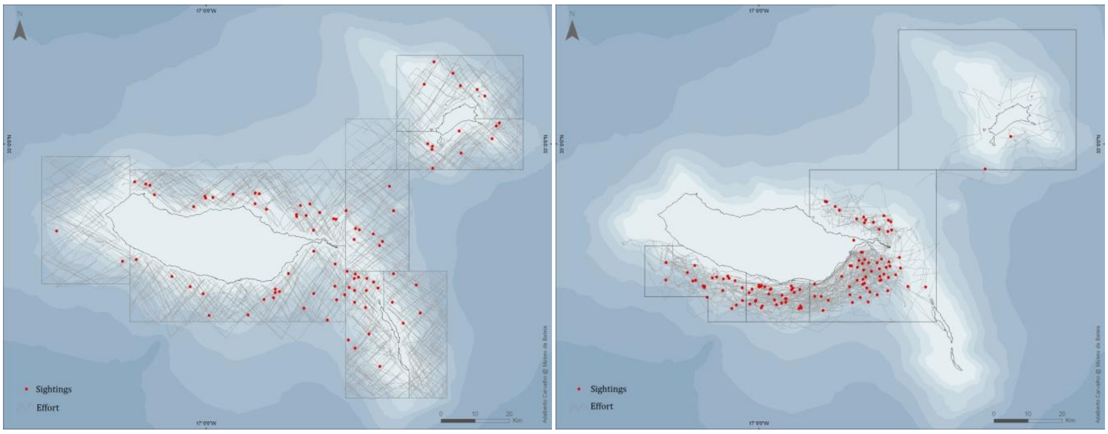

Figure 5.2 - Effort tracks and sightings from systematic surveys (left) and non-systematic surveys (right).

5.3.2 Spatial distribution

The exclusion of the cells with ≤5 km of search effort resulted in the elimination of 288 km of transect line from non-systematic surveys, and of 109 km from systematic surveys. No sightings were cut off by this truncation.

Although covering all sectors during systematic surveys, effort was not homogeneous and sectors 2 (Madeira West) and 8 (Porto Santo North) were less covered mainly due to weather conditions and distance from the port. The most covered areas during non-systematic surveys were South and southeast of Madeira also, due to the reasons pointed out before (Figures 5.3 and 5.4).

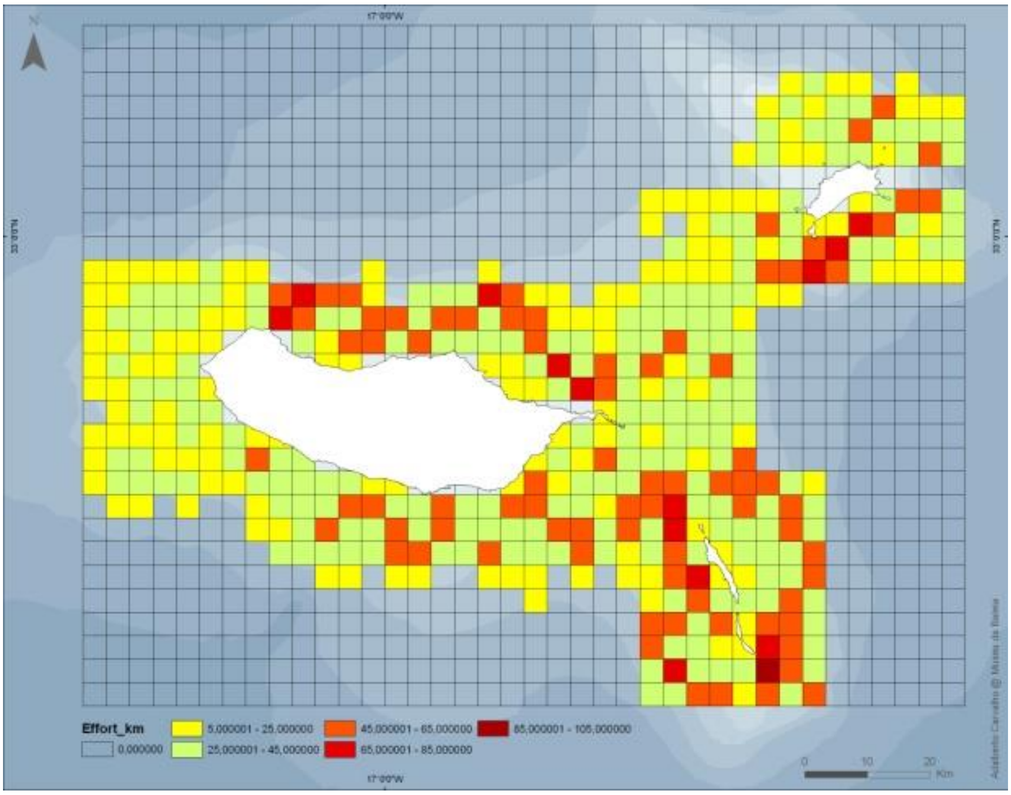

Figure 5.3 - Effort distribution in systematic surveys, excluding grid cells with ≤5km of effort.

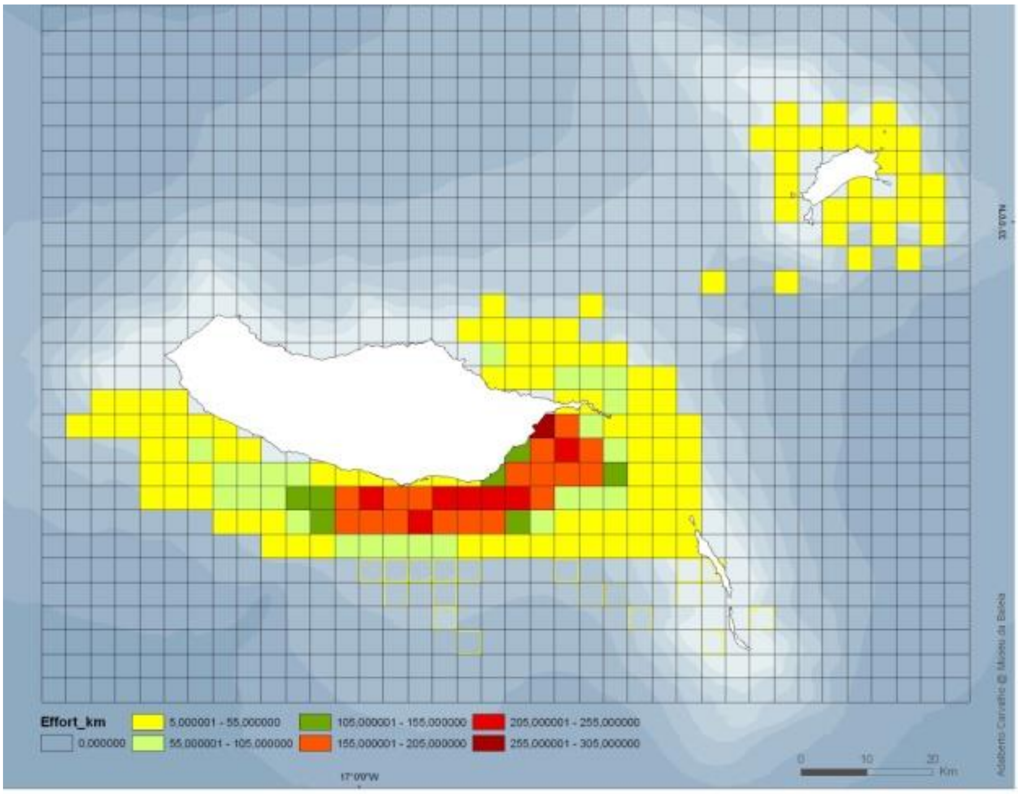

Figure 5.4 - Effort distribution in non-systematic surveys, excluding grid cells with ≤5km of effort.

Dolphins were encountered in 75 of the grid cells (16%), during systematic surveys and in 56 grid cells (21%) during non-systematic surveys (Figure 5.5).

With the exception of one grid cell in the Southwest coast of Madeira, cells with highest encounter rates were found on the East side of Madeira and in Porto Santo. The Northeast of Madeira presented the cell with the highest encounter rate (ER=13.5; effort=7km) in non-systematic surveys, followed by a grid cell in sector Porto Santo North during systematic surveys (ER=7.5; effort=13km)

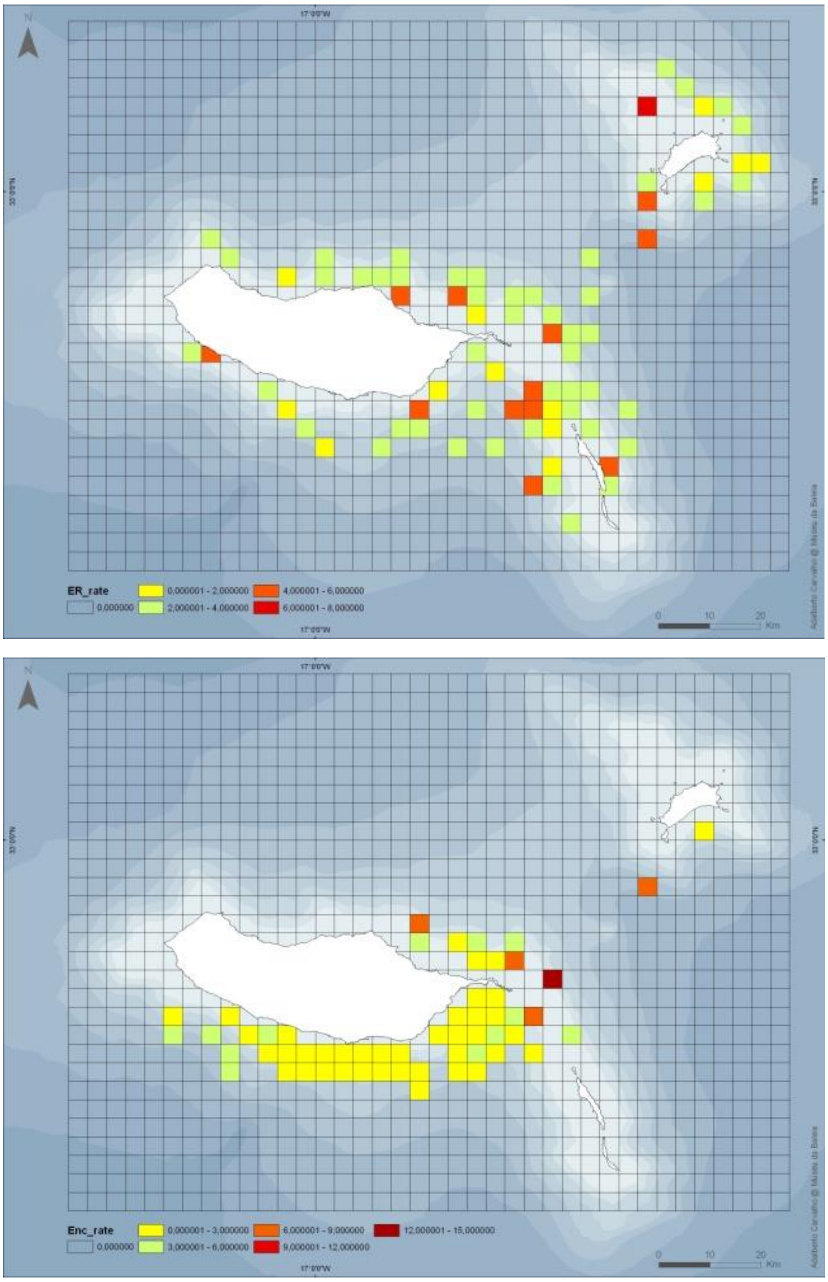

Figure 5.5 - Encounter rate by grid cells for systematic surveys (top) and non-systematic surveys (bottom) over the pre-established sectors.

The encounter rate distribution in relation to physiographic covariates revealed different values for systematic and non-systematic surveys for all variables, except for slope where the tendency was similar (Figure 5.6). Higher encounter rates occurred over bathymetries ranging between 500 and 1 000m during systematic surveys whereas in non-systematic surveys relative high encounter rates were also found in depths of 2 000 and 2 500m. Encounter rates related to distance from the coast was decreasing in systematic surveys while in non-systematic surveys the 5-10 km bin showed the highest value. Lastly, encounter rate in relation to slope ranged between 5 and 20° with the highest values appearing in bins 5-10° and 10-15°, for both types of surveys.

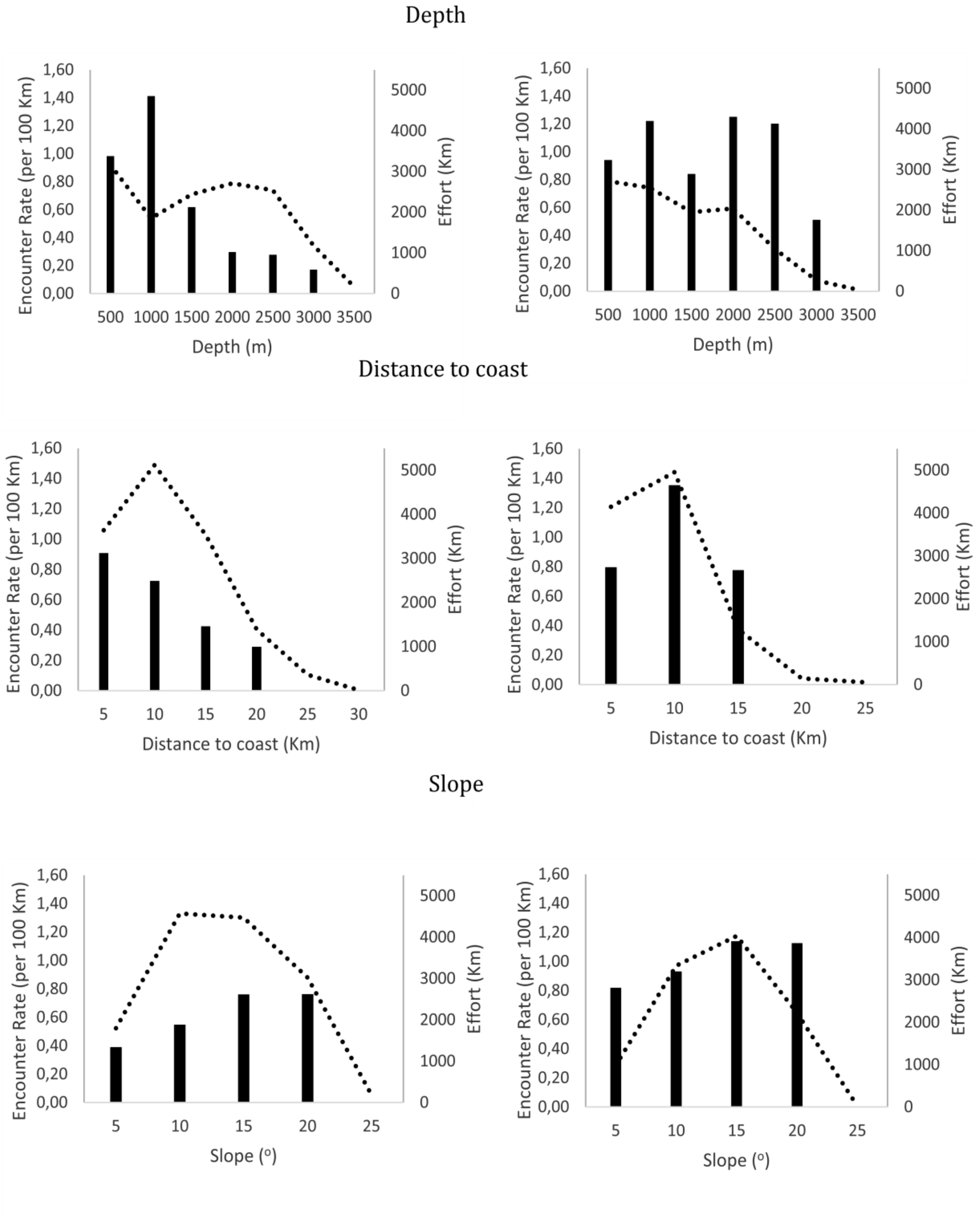

Figure 5.6 - Distribution of encounter rate (bars) and search effort (•) in relation to depth, distance to coast and slope, per type of survey: left- systematic surveys; right - non-systematic.

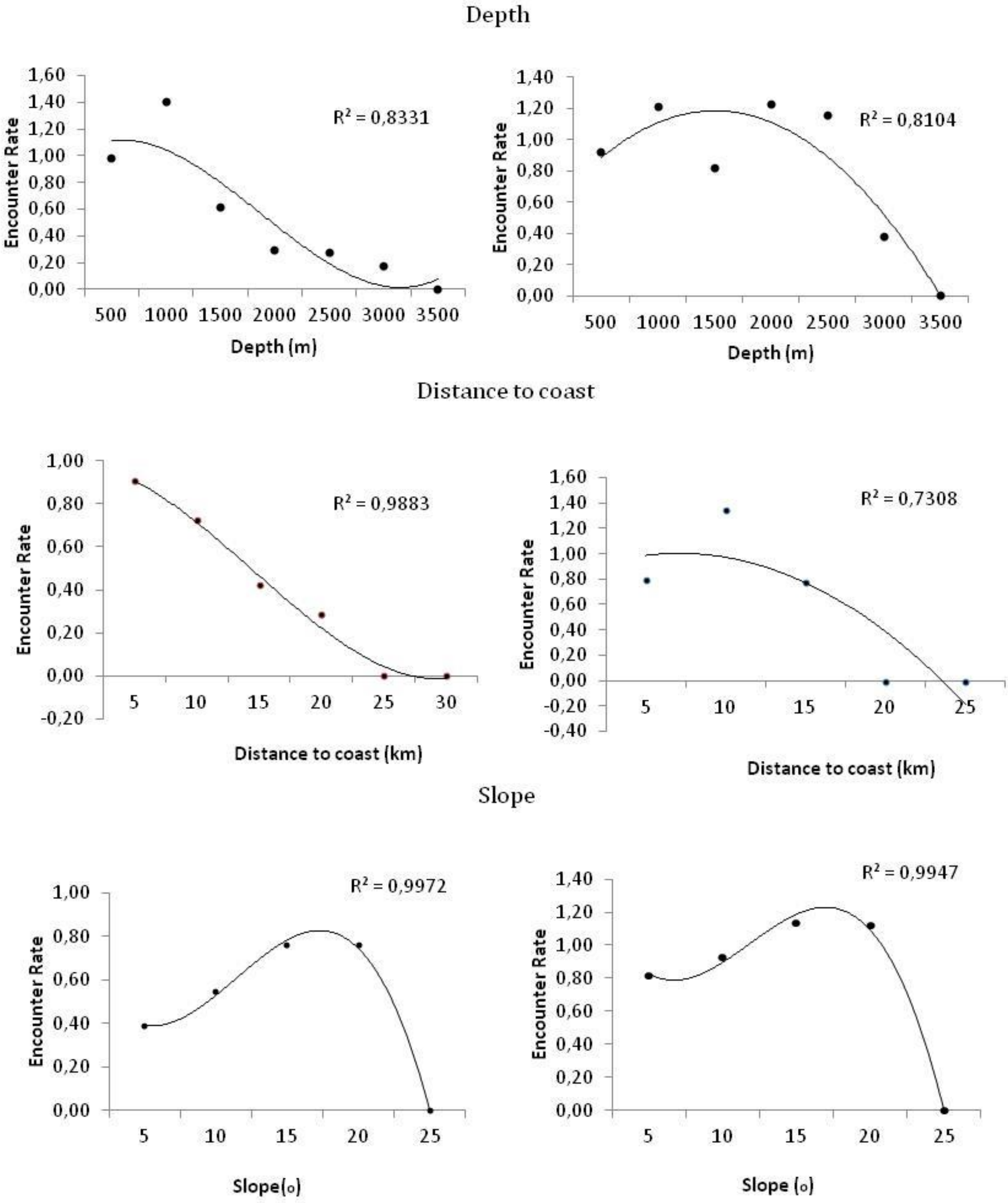

Figure 5.7 - Best fit predictions between the response variable (encounter rate) and three static variables: depth (top); distance to coast (middle) and slope (bottom). Systematic surveys are plotted on the left and non-systematic surveys are plotted on the right.

In general, all the curves presented high r^2 values indicating strong relations between the encounter rate and each covariate (Figure 5.7). Systematic surveys revealed slightly better fits than non-systematic surveys. Depth and distance to coast shown identical curves between them for both types of surveys. The slope curves were identical between the two types of surveys, presenting a similar high r^2 value.

5.3.3 Temporal distribution

Effort was distributed throughout the year in both types of surveys. In systematic surveys April was the most surveyed month and August the month with less effort made. In non-systematic surveys effort was more concentrated in spring and summer (May to September), and there was relatively less effort in December (Figure 5.8)

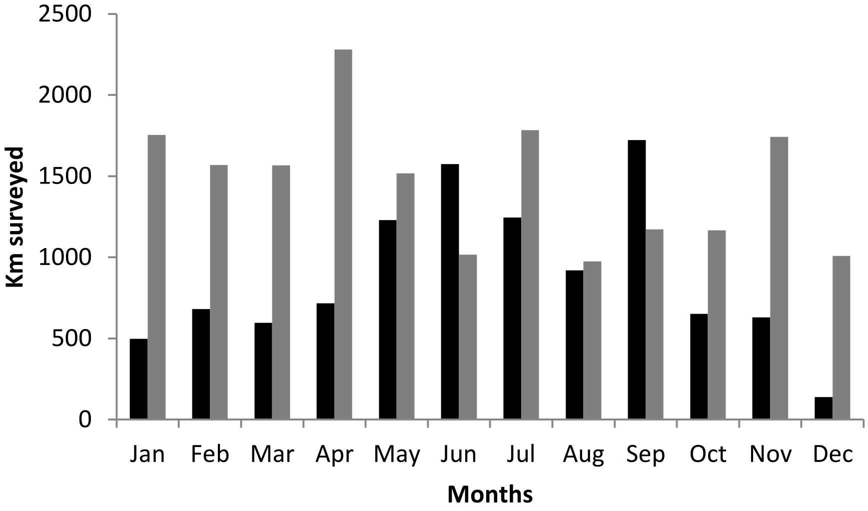

Figure 5.8 - Distribution of effort by month in systematic surveys (grey bars) and non-systematic surveys (black bars), based on the number of km surveyed.

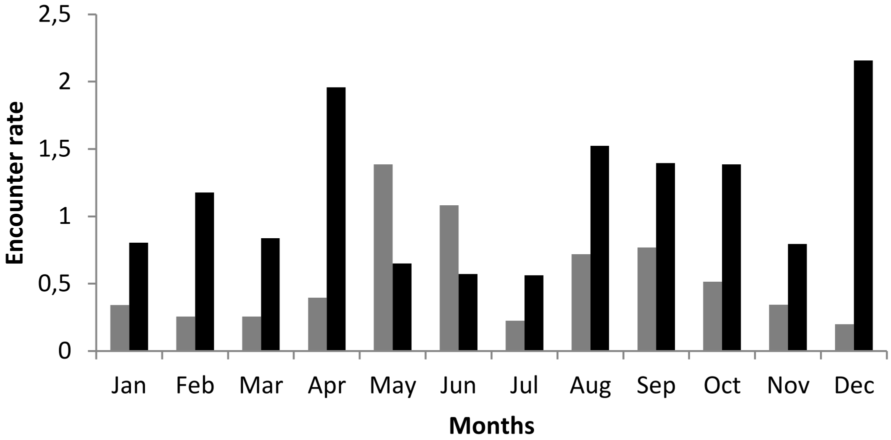

Figure 5.9 - Encounter rate per month from systematic surveys (grey bars) and non-systematic surveys (black bars).

In general, encounter rate seems to be higher in spring (May-Jun) and late summer (Aug-Oct) in systematic surveys. Non-systematic surveys had an overall higher encounter rate, but in May and June encounter rate was higher in systematic surveys (Figure 5.9).

Despite the heterogeneous results in encounter rate by moths, the Kruskal-Wallis ANOVA showed no significant differences in encounter rate between months (p=0.443) for systematic surveys, nor for non-systematic surveys (p= 0.172).

5.4 - DISCUSSION

5.4.1 Effort and sightings

Using a combination of long-term data collected throughout 11 years during dedicated surveys (systematic and non-systematic) this study provides new information on the spatial and temporal occurrence of bottlenose dolphins in Madeira archipelago. Transects used here during systematic surveys, were designed in a manner that every point in the study area has the same probability of being sampled. There are other factors known to affect cetacean detectability in conventional line transect sampling (Hammond 2010). The probability of detecting cetaceans is known to decline as a function of distance from the observation platform, and so perpendicular distance is used to fit a detection function which is then used to adjust the estimated encounter rate (Hammond 2010). In this study those distances were not considered, so encounter rate was not adjusted making it impossible to infer about the overall density of dolphins in the area. Factors influencing detectability were also likely to differ between types of survey, thus affecting the comparison of encounter rates of a given species across seasons or geographic area (Silva *et al.* 2014). By analysing data from each survey separately and restricting effort to Beaufort Sea state ≤3 bias introduced by the factors named above was reduced within and between surveys.

5.4.2 Spatial distribution

Although sighted in every sector of the study area, with the exception of sector 2 (Madeira West), bottlenose dolphins showed an overall higher encounter rate in the East side of Madeira Island (especially in the Northeast) and also around Porto Santo. These areas were also previously considered areas of higher usage by the dolphins when analysing movement patterns probabilities (see Chapter 3), supporting the hypothesis that these are important areas for this population of dolphins. Furthermore, higher encounter rates in non-systematic surveys are probably due to the fact that effort was more intensely distributed in these areas (excluding Porto Santo).

The relation of the distribution of dolphins with some physiographic variables provided some important information. The majority of dolphins was found to be distributed in depths <1000m (for systematic surveys) and no more than 10 km offshore (for both surveys) indicating a preference for shallower waters. In Madeira archipelago, the absence of a continental shelf limits this kind of physiography to areas closer the coast and to the channel between Madeira and Desertas. This explains why the majority of sightings were closer to shore, despite the larger spatial coverage provided by the surveys. Nevertheless, there were sightings over deep bathymetries (2 000 - 3 000m). These sightings correspond to associations with short-finned pilot whale (*Globicephala macrorhynchus*) (see Chapter 3). Alves *et al.* (2013) reported that 1/3 of the sightings of short-finned pilot whale in the study area were in associations with bottlenose dolphins, and that these whales were distributed manly over bathymetries of 2000 to 2500m. All the regression curves revealed strong relations between the encounter rate and the static covariates. This confirms the non-linearity of the relations. As depth decreases rapidly with distance to coast it was expected that these two factors revealed the similar values. In addition the slope results from the regressions were very consistent indication a strong relation between the presence of dolphins and this physiographic variable. These findings are in conformity with Silva *et al.* (2014) in the neighbouring archipelago of Azores, and in the Hawaiian islands where bottlenose dolphins were typically found in areas <700m (Baird *et al.* 2013; Baird *et al.* 2009). The strong relationship between distance to shore, depth and slope and the presence of dolphins indicates that prey must play a fundamental role in dolphin distribution (Fortuna 2006). While bottlenose dolphins inhabiting inshore and coastal waters feed mainly on benthic and demersal fish species (Barros & Odell 1990; Cockroft & Ross 1990), dolphins occurring in offshore waters forage on a wide variety of prey but seem to rely more on epipelagic and mesopelagic schooling fish and cephalopods (Barros *et al.* 2000; González *et al.* 1994; Mead & Potter 1995). Bottlenose dolphins commonly associate with environmental features known to increase biological productivity and/or promote prey aggregation (Cañadas *et al.* 2002; Baumgartner *et al.* 2001), however a full understanding of the oceanographic processes influencing the Madeiran waters is still missing (Caldeira & Sangrà 2012). As mentioned before there is no information on the distribution of potential prey species of bottlenose dolphins in the study area, and habitat preferences of bottlenose dolphins in relation to oceanographic variables as well as other explanatory physiographic variables, that are known to influence biological productivity (and consequently prey distribution), should be further investigated.

5.4.3 Temporal distribution

No significant difference was found for any of the surveys in monthly encounter rate which seems to indicate that bottlenose dolphins use the research area similarly year-round, without an increase in the number of sightings. This corroborates the fact that transient dolphins, more present in the area during summer and autumn months (see Chapter 2), mixed with resident groups. This mixture is most likely to have mating purposes (see Chapter 2), as suggested by Quérouil *et al.* (2007) who referred that these associations might serve as a stimulus for gene flow.

While assessment of seasonality in this study was coarse, as only looking for complete absence during some seasons or significant differences between months, it seems to indicate that there is no strong seasonal fluctuation in the presence of bottlenose dolphins in Madeira archipelago waters.

6.4-Conclusions

Cetacean distribution is likely to be linked with a number of oceanographic features (Yen *et al.* 2004; Cañadas *et al.* 2002; Baumgartner *et al.* 2001). In this study, bottlenose dolphins were regularly found in shallow and closer to shore areas, suggesting the existence of biological processes influenced by bathymetry, as suggest by Silva (2007) in the archipelago of the Azores. These results advocate the existence of important areas of habitat for this species based on static bathymetric features. This should not be looked at as an isolated influence, as cetacean distribution ought to be affected also by hydrographic processes not dependent from local bathymetry. For that reason, understanding dolphin-habitat association patterns in relation with to bathymetric characteristics and oceanographic processes of their habitat is crucial to investigate possible critical areas for bottlenose dolphins that might exist in the study area. Despite this, the exposure of the near shore areas to anthropogenic activities like marine traffic or whale-watching and the results found here, should be seen as a warning sign towards bottlenose dolphin conservation in Madeira archipelago.

References

Alves F. (2013) Population structure, Habitat use and Conservation of Short-finned Pilot Whale (*Globicephala macrorhynchus*) in the archipelago of Madeira. Doctoral Thesis, University of Madeira.

Alves F, Querouil S, Dinis A, Nicolau C, Ribeiro C, Freitas L, Kaufmann M, Fortuna C (2013). Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: implications for conservation. *Aquatic Conservation: Marine and freshwater ecosystems,* 5: 758-776.

Baird RW, Gorgone AM, McSweeney DJ, Ligon AD, Deakos MH, Webster DL, Schorr GS, Martien KK, Salden DR, Mahaffy SD (2009). Population structure of island associated dolphins: evidence from photo-identification of common bottlenose dolphins (*Tursiops truncatus*) in the main Hawaiin Islands. *Marine Mammal Science,* 25: 251-274.

Baird RW, Webster D, Aschettino J, Schorr G, McSweeney DJ (2013). Odontocete Cetaceans Around the Main Hawaiian Islands: Habitat Use and Relative Abundance from Small-Boat Sighting Surveys. *Aquatic Mammals*, 39(3): 253-269.

Baumgartner MF, Mullin KD, May LN, Leming TD (2001). Cetacean habitats in the northern Gulf of Mexico. *Fishery Bulletin*, 99: 219-239.

Barros NB, Odell DK (1990). Food habits of bottlenose dolphins in the Southeastern United States. Pp: 309-328. In: The Bottlenose Dolphin. (Eds. S. Leatherwood and R. R. Reeves). Academic Press, Inc. London

Barros NB, Parsons ECM, Jefferson TA (2000). Prey of offshore bottlenose dolphins from the South China Sea. *Aquatic Mammals*, 26: 2-6.

Caldeira R, Sangrá P (2012). Complex geophysical wake flows: Madeira Archipelago case study. *Ocean Dynamics,* 62: 683-700.

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

Cañadas A, Sagarminaga R, de Stephanis R, Urquiola E, Hammond PS (2005). Habitat preference modelling as a conservation tool: Proposals for marine protected areas for cetaceans in southern Spanish waters. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 15: 495-521

Cockcroft VG, Ross GJB (1990). Food and feeding of the Indian Ocean bottlenose dolphin off Southern Natal, South Africa. Pp: 295-308. In: The Bottlenose Dolphin. (Eds. S. Leatherwood and R. R. Reeves). Academic Press, Inc. London.

Croll DA, Tershy BR, Hewitt RP, Demer DA, Fiedler PC, Smith SE, Armstrong W, Popp JM, Kiekhefer T, Lopez VR, Urban J, Gendron D (1998). An integrated approach to the foraging ecology of marine birds and mammals. *Deep-Sea Research II*, 45: 1353-1371.

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

Dinis A, Ribeiro C, Nicolau C, Alves F, Carvalho A, Freitas L (2009). Common bottlenose dolphin (*Tursiops truncatus*) occurrence, distribution and conservation status in Madeira Archipelago (Portugal). SC/61/SM13, 61ª Annual meeting of the International Whaling Commission (IWC). Funchal.

Ferreira RB (2007). Monitorização da actividade de observação de cetáceos no Arquipélago da Madeira, Portugal. Master thesis, Universidade de Lisboa, Faculdade de Ciências, Portugal.

Forcada J, Gazo M, Aguilar A, Gonzalvo J, Fernández-Contreras M (2004). Bottlenose dolphin abundance in the NW Mediterranean: addressing heterogeneity in distribution. *Marine Ecology Progress Series*, 275. 275-287.

Fortuna CM (2006). Ecology and conservation of bottlenose dolphins (*Tursiops truncatus*) in the north-eastern Adriatic Sea. PhD dissertation, University of St. Andrews.

Freitas L, Dinis A, Alves F, Nóbrega F (2004). Cetáceos no Arquipélago da Madeira. Museu da Baleia, Machico, Madeira, Portugal.

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

Genin A (2004). Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *Journal of Marine Systems*, 50: 3–20.

González AF, López A, Guerra A, Barreiro A (1994). Diets of marine mammals stranded on the northwestern Spanish Atlantic coast with special reference to Cephalopoda. *Fisheries Research*, 21: 179-191.

Hammond PS (2010). Estimating the abundance of marine mammals. In: Boyd, I. Bowen, D. and Iverson, S. Eds. *Marine Mammal Ecology and Conservation*. *A handbook of techniques*. Oxford Press. 42-67.

Hoyt E (2011). Marine Protected Areas for Whales, Dolphins and Porpoises: a World Handbook for Cetacean Habitat Conservation and Planning, second ed. Earthscan, New York.

Mead JG, Potter CW (1995). Recognizing two populations of the bottlenose dolphin (*Tursiops truncatus*) off the Atlantic coast of North America: morphological and ecological considerations. IBI Reports, 5: 31-44.

Menezes D, Freitas I, Domingues M, Oliveira P (2011). Madeira Natural Paradise. Secretaria Regional do Ambiente e dos Recursos Naturais: Serviço do Parque Natural da Madeira.

Panigada S, di Sciara GN, Panigada MZ, Airoldi S, Borsani JF, Jahoda M (2005). Fin whales (*Balaenoptera physalus*) summering in the Ligurian Sea: Distribution, encounter rate, mean group size and relation to physiographic variables. Journal of Cetacean Research and Management 7: 137-145

Quérouil S, Silva MA, Freitas L, Prieto R, Magalhães S, Dinis A, Alves F, Matos JA, Mendonça D, Hammond PS, Santos RS (2007). High gene flow in oceanic bottlenose dolphins (*Tursiops truncatus*) of the North Atlantic. *Conservation Genetics,* 8: 1405-1419.

Redfern JV, Ferguson MC, Becker EA, Hyrenbach KD, Good C, Barlow J, Kaschner K, Baumgartner MF, Forney KA, Ballance LT, Fauchald P, Halpin P, Hamazaki T, Pershing AJ, Qian SS, Read A, Reilly SB, Torre L, Werner F (2006). Techniques for cetacean-habitat modeling. *Marine Ecology Progress Series*, 310: 271-295

Silva MA (2007). *Population Biology of bottlenose dolphins in the Azores archipelago,* University of St. Andrews: PhD Thesis.

Silva MA, Prieto R, Cascao I, Seabra MI, Machete M, Baumgartner MF, Santos RS (2014). Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. *Marine Biology Research*, 10(2): 123-137.

Silva MA, Prieto R, Magalhães S, Seabra MI, Machete M, Hammond P (2012). Incorporating information on bottlenose dolphin distribution into Marine Protected Area design. *Aquatic Conservation: Marine and Freshwater Ecosystems* 22: 122-133.

Vera AH (2012). Quantification of the exposure of cetacean individuals to whale-watching vessels through the photo-identification technique in the South coast of

Madeira Island (Portugal). Research Study for the Environmental Sciences Degree, Faculty of Biology, University of Murcia, Spain

Yen PPW, Sydeman WJ, Hyrenbach KD (2004). Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. *Journal of Marine Systems*, 50: 79–99.

CHAPTER 6

GENERAL DISCUSSION

Bottlenose dolphins are arguably the best known of all cetaceans (Wells and Scott 2009). Longitudinal studies of individual bottlenose dolphins began in the 1970s and with the development of photo-identification techniques studies of this species multiplied in an era of cetacean research (reviewed in Connor *et al.* 2000), but yet studies of bottlenose dolphins around oceanic islands are limited (Baird *et al.* 2009; Silva *et al.* 2008) even today. This thesis investigated some aspects of the ecology of bottlenose dolphins occurring in Madeira archipelago, one of the isolated oceanic archipelagos in the Northeast Atlantic Ocean. These included population structure, group dynamics, site fidelity, residency, movement patterns, survival, population size and temporal and spatial distribution with the influence of habitat physical features on the latter. The present work is based on data collected over 11 years resulting in a long-term study that hopefully will contribute to a better understanding of the ecology of the bottlenose dolphin in Madeira archipelago. Cetaceans living in offshore waters of the North Atlantic are under increasing pressure from many potential threats, like ship traffic, military exercises and seismic surveys for oil and gas exploration and for marine research, making information on biological and ecological parameters urgently needed for assessing the potential adverse effects of anthropogenic activities and to propose appropriate mitigation measures (Silva *et al.* 2014). The general objective of this work was to contribute to the conservation of the bottlenose dolphin in the Madeira archipelago through the investigation of aspects of the ecology and habitat use of the species in this region.

6.1 - Population Structure

One of the most important attributes of any animal population is its social structure, which plays a key role in many aspects of its ecology (Whitehead, 2009; Lusseau *et al.* 2006). Chapter2 aimed to examine individual photo-identification data of the bottlenose dolphin population in Madeira archipelago in order to investigate the type of association indices between pairs of identified individuals, the patterns of affiliation between individual dolphins and the probabilities of association between individuals over time.

There is strong evidence that the Madeira bottlenose dolphins' population is an open population with regular recruitment of new animals to the area. The variations in time between many of the re-sightings of identified individuals in the study area suggested that Madeira archipelago represents part of a larger home range within the Northeast Atlantic Ocean. This is in agreement with previous studies that found no genetic structure among the several populations of bottlenose dolphins within the Northeast Atlantic (Louis *et al.* 2014; Querouil *et al.* 2007). When analysing the social structure of the frequent users of the study area, the dolphins presented a dynamic and fluid social structure, with no clear architecture or division of groups, except for dyads and triads. Almost none long-term fidelity between individuals was found, indicating that random associations prevail in this population. The temporal analysis also indicated that this pattern persists over the time scale. Quantifying the social structure of an animal society is difficult, because it represents a complex agglomerate of individuals in which relationships change in time and space (Lusseau *et al.* 2006). The bottlenose dolphin population of Madeira archipelago appears to be typical of this species, exhibiting a highly social and rapidly changing fission-fusion society. In an open ocean habitat like Madeira this is not unexpected, as there are neither geographic boundaries nor enclosed environments, such as estuaries, bays and fjords where stable and long-lasting associations are more likely to occur. This lack of community structure is challenging for managers due to the difficulty to distinguish more vulnerable units, if they exist. Consequently, the population of bottlenose dolphins occurring in Madeira should be considered in future conservation efforts, as one large community, where individuals associate, disassociate and reassociate with each other over short periods of time. Also, future research on this population should look further into sex-related associations as they seem to have an important role in this species sociality (Connor *et al.* 2000).

6.2 - Group dynamics, Site fidelity, Residency and Movement patterns

Chapter 3, tried to determine group dynamics, to assess the level of residency and site fidelity, and to investigate movements patterns within and out of the study area.

Group sizes of bottlenose dolphins in Madeiran waters seem to be skewed towards small groups although large groups were observed in summer and autumn, likely due to the presence of pelagic bottlenose dolphins observed during the summer months. Groups with calves were recorded more often in late summer/early autumn coinciding with the presence of pelagic offshore dolphins. As bottlenose dolphin females give birth to a single calve after a 12 month gestation (Wells & Scott 2009), this suggests that they mix and mate when the transient dolphins visit the island.

Bottlenose dolphins associated with several species, being the most common the short-finned pilot whale. All these associations are expected to be related to feeding as this species is known to feed on a variety of fish and cephalopods and have a variety of foraging strategies (Connor *et al.* 2000). These associations are also thought to be the main reason for the presence of these dolphins in deeper waters (>2000m; see Chapter 5). By associating with the whales it is likely that opportunistic feeding on preys that are out of range for the dolphins occurs. Also, these associations are not permanent, as two individuals captured with the whales were recaptured later within a group exclusively of dolphins (own observations).

Only a small number of dolphins, of the total identified in the catalogue showed long-term site fidelity, with a great deal of dissimilar types of occurrence from the majority of the individuals. Bottlenose dolphins of Madeira archipelago exhibit different degrees of site fidelity to the islands indicating various patterns of occurrence. This seems to be corroborated by the social network diagram and by the LIR analysis. Both showed strong evidences of different patterns of occurrence that associate with each other (residents, transients and migrants). This mixture of different patterns of occurrence was reported also in other bottlenose dolphin population's worldwide (Baird *et al.* 2009, Silva *et al.* 2008, Connor *et al.* 2000) and also in other cetacean's species in Madeira archipelago (Alves *et al.* 2013). Similarly to the findings of Silva (2007) in the Azores, Madeira archipelago seems to have an open population of bottlenose dolphins with only a small number of individuals showing residency to the area.

Movement patterns indicate that dolphins move rapidly between sectors being the north of Madeira and Porto Santo the areas more used by the dolphins and both correspond to shallower sides of the islands. These findings are in agreement with the spatial distribution investigated in Chapter 5, in which a strong relation between the presence of dolphins and shallow waters (<1000m) was found. These areas might provide a suitable habitat for these dolphins compared to more open pelagic waters that surround the islands.

6.3 - Population Parameters

In order to understand the structure and dynamics of a wild population it is essential to have knowledge about the population size and vital rates, such as survival (Seber 1982). The aim of the analysis in Chapter 4 was to estimate apparent survival and the seasonal abundance of the bottlenose dolphin population in Madeira archipelago, for the first time. This was made taking into account heterogeneity of capture probabilities by applying distinctive approaches on capture-recapture records of naturally marked individuals.

A key issue in capture-recapture analyses is the fulfilment of the main assumptions, as violation of these assumptions may cause severe bias in parameter estimates (Seber 1982). Perhaps the most difficult assumption to assure in this study was equal capture probability. As seen in the previous chapters the population of bottlenose dolphins of Madeira exhibits a variety of ranging and occurrence patterns, which may affect their sighting probability, as they were not always available for sampling in the study area. Also, by reducing the area to the south of Madeira, because the restrictions imposed by the utilization of the opportunistic data, this potential violation was aggravated due to possible individual preferences for certain areas. Despite this, the apparent survival results are within the expected for a long-lived mammal (0.95). Unfortunately, it was not an accurate estimation, and this can indicate that there were problems with the data that were not completely eliminated. Nonetheless, there is no obvious reason for considering that survival rates of this population are lower than the ones found here.

This study estimated through the Arnason-Schwarz model that 183 resident dolphins (95% CI= 155 to 218) used the south of Madeira Island during the study period.. The differences in seasonal abundance from resident dolphins and the total number of dolphins, given by the Chapman estimator, indicate that there is an influx of transients and seasonal residents during spring until autumn. The low number of resident dolphins during this period suggests that either they move out of the area or, as they are mixed with the transient dolphins, their capture probability decreases. The existence of a population of resident dolphins and a super-population is, perhaps one of the main contributions of this study, as this would imply that bottlenose dolphins not only visit this area, but also use it for their daily activities. This also indicates that Madeira archipelago is an area of importance for this species.

Studies for estimating population size using data from photo-identification studies of cetaceans that initially began without this objective are particularly prone to violation of assumptions, and even tough analysis can help to minimize those problems (Hammond 2010), a well-designed study should be considered for future estimations of demographic parameters.

6.4 Spatial and temporal distribution

The first step to understand the relationship between populations and their habitat is to determine which habitats they use more frequently (Cañadas *et al.* 2005). In Chapter 5, bottlenose dolphin sighting and survey effort data were used to investigate temporal occurrence and spatial distribution of bottlenose dolphin around Madeira, Desertas and Porto Santo islands. Using a combination of long-term data collected throughout 11 years during dedicated surveys (systematic and non-systematic) this study provides new information on the spatial and temporal occurrence of bottlenose dolphins in Madeira archipelago.

Bottlenose dolphins showed an overall higher encounter rate in the East side of Madeira Island (especially in the Northeast) and also around Porto Santo. The relation of the distribution of the dolphins with depth and distance to coast provided some important information, with most dolphins being distributed in depths <1000m and no more than 10 km offshore indicating a preference for shallow waters. The results of the present study reflect the year-round occurrence of bottlenose dolphins in Madeira archipelago waters, indicating that there is no strong seasonal fluctuation in the presence of the species in the region.

This chapter presents important results that strongly support the existence of important areas of habitat for this species that should be taken into account in future conservation plans in the region.

6.5 Implications for conservation of bottlenose dolphins in Madeira archipelago

With a widespread distribution and high public profile, bottlenose dolphins is one of the most well suited cetacean to play a role as an environmental flagship (Connor *et al.* 2000). However, their proximity to humans exposes them to numerous threats like pollution, boat traffic, interaction with fisheries, habitat loss and tourism (Mann *et al.* 1995; Wells & Scott 2009).

The data presented here represent the first long-term study of bottlenose dolphins in the waters of Madeira archipelago and illustrate the importance of the region for bottlenose dolphins that occur in the Northeast Atlantic. This study has made an important contribution to the future conservation of this species in the region. All the resulting information from the different chapters provided a scientific basis for the definition and implementation of protected areas, and to assess mitigation measures for potential impacting activities like whale-watching.

As mentioned in Chapter 1, bottlenose dolphins are listed under the Annex II of the EU Habitats Directive, which requires the designation of Special Areas of Conservation (SACs). Chapter 5, discussed that no MPAs targeting cetaceans, exist in Madeira archipelago, however the Madeira Whale Museum has an ongoing proposal of a Site of Community Importance (pSCI) for bottlenose dolphins, to be delivered to the Regional Government of Madeira as a result of the LIFE+ project CETACEOSMADEIRA II (see Declarations). In protecting a specific population, the optimal protected area would cover that population's year-round distribution (Reeves, 2000). As pointed out in Chapter 3, movements of bottlenose dolphins in Madeira archipelago extend from Madeira to Porto Santo and any designated area should have, at least the same coverage. For example, the SAC boundaries in the Moray Firth (Scotland) were later considered insufficient due to the range expansion of the resident dolphin population (Wilson *et al.* 2004). The important lessons from other previously established protected areas, should be considered for this proposed SIC, and a wider area that extends, at least, from the East of Madeira to Porto Santo should be included.

After the long and difficult process of implementing an SAC, comes also the complicated procedure of developing management plans. For this, I recommend that the research presented here should be extended in the future. It would be especially useful to investigate any trend of the population size, any major threats that could possibly arise and a possible displacement of the areas of distribution presented here. A permanent monitoring plan (Freitas & Alves 2004), targeting the conservation of cetaceans in the study area, was delivered to the Madeira Regional Government, as a result from the previous LIFE project CETACEOSMADEIRA (see Declarations). Like other cetaceans, bottlenose dolphins have long life spans and low reproductive rates (Wells 1991), and extensive periods of monitoring may be required to detect a trend in any demographic parameter (Wilson *et al.* 1999). Maintaining long-term research effort in these designated areas is valuable (Cheney *et al.* 2013), but yet substantial resources are required to maintain this long-term studies, and monitoring plans of this kind are only expected to be sustainable if they are integrated into wider research projects, education programmes or ecotourism operations.

The conservation status of bottlenose dolphins for Madeira is given as 'Least Concern' (Cabral *et al.* 2005). The estimated population size and the high survival rates reported in Chapter 4 seem to give no reasons for concern about the status of this population. However, because these are primary estimates and relate only to a small number of years, care should be taken when looking into these values. Additionally, without previous information about demographic parameters of this population, there is no way of knowing if the population is increasing, declining or stable. At the present time, the main threat for this species in Madeira archipelago seems to be the growing whale-watching industry (Vera 2012; Ferreira 2008; Dinis *et al.* 2006). Apart from the whale-watching activity, the absence of any other major threats to this species in the waters of Madeira archipelago and the high genetic diversity displayed (Querouil *et al.* 2007), leads to think that the viability of this population at present is of no concern.

6.6 Directions of Future work

The present study provides a broad foundation for future studies on the ecology of bottlenose dolphins in Madeira archipelago; following these results there are some aspects that researchers and managers should take into consideration. Future studies on sex specific data may provide additional insights into the social interactions, occurrence of mixed sex groups and the relatedness of this population. Further dedicated photo-identification effort is required in order to evaluate any trend in the abundance of this population, specially the resident number of animals. Additionally, comparison with catalogues of the neighbouring archipelagos of Azores and the Canary Islands could provide a better picture of the full extent of the movements and home range for this population.

Research on spatial and temporal patterns of prey species in the study area and relations with other variables, namely environmental may provide further insight into causal factors in bottlenose dolphin distribution and habitat use within this region. Moreover, inter-specific relationships should be investigated, especially with the short-finned pilot whales, to better understand the reasons for this association. Individual identification of the animals will allow investigating if there are animals that associate more preferentially than others.

Finally, monitoring the fast growing whale-watching industry is crucial in order to assess any potential threat deriving from this activity on this population.

Cetaceans have a huge educational, scientific and economic value (Augustowsky & Palazzo 2003; Agardy 1997; Hoyt 1992). Among other cetacean species, bottlenose dolphins may provide the key to protecting ocean habitats and to the establishment of large marine areas under conservation management.

References

Agardy T (1997). *Marine Protected Areas and Ocean Conservation*. Academic Press, London.

Alves F, Querouil S, Dinis A, Nicolau C, Ribeiro C, Freitas L, Kaufmann M, Fortuna C (2013). Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: implications for conservation. *Aquatic Conservation: Marine and freshwater ecosystems,* 5: 758-776.

Augustowsky M, Palazzo JT (2003). Building a marine protected areas network to protect endangered species: Whale conservation as a tool for integrated management in South America. V Word Parks Congress, IUCN, Durban, South Africa.

Baird RW, Gorgone AM, McSweeney DJ, Ligon AD, Deakos MH, Webster DL, Schorr GS, Martien KK, Salden DR, Mahaffy SD (2009). Population structure of island associated dolphins: evidence from photo-identification of common bottlenose dolphins (*Tursiops truncatus*) in the main Hawaiin Islands. *Marine Mammal Science,* 25: 251-274.

Cabral MJ (coord), Almeida J, Almeida PR, Dellinger T, Almeida NF, Oliveira ME, Palmeirim JM, Queiroz AL, Rogado L, Santos-Reis M, editors (2005). Livro Vermelho dos Vertebrados de Portugal. Instituto de Conservação da Natureza, Lisboa.

Cañadas A, Sagarminaga R, de Stephanis R, Urquiola E, Hammond PS (2005). Habitat preference modelling as a conservation tool: Proposals for marine protected areas for cetaceans in southern Spanish waters. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 15: 495-521

Cheney B, Thompson PM, Ingram SN, Hammond PS, Stevick PT, Durban JW, Culloch RM, Elwen SH, Mandleberg L, Janik VM, Quick NJ, ISLAS-Villanueva V, Robinson KP, Costa M, Eisfeld SM, Walters A, Phillips C, Weir CR, Evans PGH, Anderwald P, Reid RJ, Reid JB, Wilson B (2013), Integrating multiple data sources to assess the distribution and abundance of bottlenose dolphins *Tursiops truncatus* in Scottish waters. *Mammal Review*, 43: 71–88.

Connor R, Wells R, Mann J, Read A (2000). The Bottlenose Dolphin: Social Relationships in a Fission-Fusion Society. In: J. Mann, R. Connor, P. L. Tyack & H. Whitehead, eds. *Cetacean Societies: Field Studies of Dolphins and Whales.* Chicago: University of Chicago Press, pp. 91-126.

Dinis A, Alves F, Freitas L (2006). Assessment of cetacean threats in Madeira archipelago: an approach to conservation measures. 20th Conference of the European Cetacean Society, 2-7 April, Gdynia, Poland.

Ferreira RB (2007). Monitorização da actividade de observação de cetáceos no Arquipélago da Madeira, Portugal. Master thesis, Universidade de Lisboa, Faculdade de Ciências, Portugal.

Freitas L, Alves F (2004). Plano de monitorização permanente. Documento H do Projecto CETACEOSMADEIRA (LIFE 99NAT/P/6432), Museu da Baleia da Madeira.

Hammond P (2010). Estimating the abundance of marine mammals. In: Boyd, I. Bowen, D. and Iverson, S. Eds. *Marine Mammal Ecology and Conservation*. *A handbook of techniques*. Oxford Press. 42-67.

Hoyt E (1992). Designing marine reserves around whales and dolphins: Three case studies. IV Word Parks Congress, Caracas, Venezuela.

Louis M, Viricel A, Luca T, Peltier H, Alfonsi E, Berrow S, Brownlow A, Covelo P, Dabin W, Deaville R, de Stephanis R, Gally F, Gauffier P, Penrose R, Silva MA, Guinet C, Simon-Bouhet B (2014). Habitat-driven population structure of bottlenose dolphins, *Tursiops truncatus*, in the North-East Atlantic. Molecular Ecology, 23(4): 857-874

Lusseau D, Wilson B, Hammond PS, Grellier K, Durban JW, Parsons KM, Barton TR, Thompson PM (2006). Quantifying the influence of sociality on population structure in bottlenose dolphins. *Journal of Animal Ecology,* Volume 75, pp. 14-24.

Mann J, Smolker RA, Smuts BB (1995). Responses to calf entanglement in free-ranging bottlenose dolphins. *Marine Mammal Science*, 11:168-175.

Quérouil S, Silva MA, Freitas L, Prieto R, Magalhães S, Dinis A, Alves F, Matos JA, Mendonça D, Hammond P, Santos RS (2007). High gene flow in oceanic bottlenose dolphins (*Tursiops truncatus*) of the North Atlantic. *Conservation Genetics,* 8: 1405-1419.

Reeves RS (2000). The value of Sanctuaries, Parks, and Reserves (Protected Areas) as tools for conserving marine mammals. Final Report to the Marine Mammal Commission, Contract Number T74465385. Marine Mammal Commission, Bethesda, MD, 50p.

Seber GAF (1982). The Estimation of Animal Abundance and Related Parameters. 2nd ed. Arnold, London, UK.

Silva M, (2007). Population Biology of bottlenose dolphins in the Azores archipelago*,* University of St. Andrews: PhD Thesis.

Silva MA, Prieto R, Cascao I, Seabra MI, Machete M, Baumgartner MF, Santos RS (2014). Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. *Marine Biology Research*, 10(2): 123-137.

Silva MA, Prieto R, Magalhães S, Seabra MI, Santos RS, Hammond P (2008). Ranging patterns of bottlenose dolphins living in oceanic waters: implications for population structure. *Marine. Biology* 156: 179-192

Vera AH (2012). Quantification of the exposure of cetacean individuals to whale-watching vessels through the photo-identification technique in the South coast of Madeira Island (Portugal). Research Study for the Environmental Sciences Degree, Faculty of Biology, University of Murcia, Spain

Wells RS (1991). The role of long-term study in understanding the social structure of a bottlenose dolphin community. In: Pryor, K., Norris K.S.(Eds), Dolphin societies: discoveries and puzzles. University of California Press, Oxford, California, pp. 199-225.

Wells RS, Scott MD (2009). Common Bottlenose dolphin (*Tursiops trucatus*). In: Perrin, W.F., Würsig, B., Thewissen, J.G.M. (Eds.), Encyclopedia of marine mammals, second ed. Academic Press, Amsterdam, pp. 361-364.

Whitehead H (2009). SOCPROG programs: analysing animal social structures. *Behaviour Ecology Sociobiology,* Volume 63, pp. 765-778.

Wilson B, Reid RJ, Grellier K, Thompson PM, Hammond PS (2004). Considering the temporal when managing the spatial: a population range expansion impacts protected areas-based management of bottlenose dolphins. *Animal Conservation*, 7:331-338.

Wilson B, Hammond PS, Thompson PM (1999). Estimating size and Assessing Trends in a Coastal Bottlenose Dolphin Population. *Ecological Applications,* 9:288-300.

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