Andreia Filipa Figueiredo Pereira

Analysis of the social structure of bottlenose dolphins (*Tursiops truncatus*) in São Miguel island, Azores.

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Mestrado em Biologia Marinha

Supervisor:

Laura González García

Co-supervisor:

Rita Castilho

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Declaração de autoria de trabalho

Analysis of the social structure of bottlenose dolphins (*Tursiops truncatus*) in São Miguel island, Azores.

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

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Abstract

Studying social structure is a valuable technique to reveal the factors driving population processes, to understand the evolution of cooperation, the transmission of diseases, and patterns of social learning. Therefore, understanding social relationships between individuals and the differences in habitat use among social groups is critically important to ensure species management and conservation. Bottlenose dolphins are one of the most sighted cetacean species in the Azores archipelago. They are present year-round, frequently encountered close to the islands, as well as in offshore waters. This study aimed to update the existing bottlenose dolphin photo-identification catalogue of São Miguel (2014-2019) with photos taken in 2008, 2010, 2012 and 2020 on board Futurismo's whale watching vessels and analyse the social structure of the identified individuals. There were added to the catalogue 184 new individuals, having now the current catalogue of bottlenose dolphins in São Miguel, a total of 689 individuals identified. The social analyses have shown that associations between bottlenose dolphins identified in São Miguel are very dynamic and social bonds can be very flexible. The low association coefficients between pairs of individuals and consequently the low average coefficient of association for the population is in concordance with the typical fission-fusion society that characterizes this dolphin species. However, the higher association index of some individuals, suggest some long-term relationships. Some degree of structuring within the population of bottlenose dolphins in São Miguel with five groups identified was detected. Resident dolphins were sighted with migrants, individuals with more significant scale movements, contributing to an increase in genetic variability in oceanic dolphin communities. This study highlights the importance of long-term data series obtained from opportunistic platforms in Azores and provides a significant contribution to assess baselines conditions of the population and develop management strategies.

Keywords: Social structure, photo-id, *Tursiops truncatus*, bottlenose dolphins, Azores, SOCPROG

Resumo

Os golfinhos roazes (*Tursiops truncatus*) são mamíferos de vida longa que, no seu habitat natural, podem viver cerca de 50 anos. Encontram-se espalhados por todo o mundo, desde águas tropicais a temperadas, estando adaptados a vários habitats marinhos, estuários, ou mesmo a rios. Pequenos grupos de dois a quinze indivíduos são típicos desta espécie, no entanto, grupos maiores com mais de mil indivíduos já foram reportados. Tal como se verifica em outras espécies de golfinhos, os golfinhos roazes tendem a formar grupos maiores ao habitarem em mar aberto. Viver em grupo tem benefícios e custos, e para que esta vida coletiva seja sustentável, os benefícios individuais têm que exceder os custos. Benefícios estão geralmente relacionados com a proteção aos predadores, disponibilidade de alimento ou transferência de informação; enquanto os custos estão relacionados com competição por recursos, carga parasitária ou filopatria.

O estudo da estrutura social é uma técnica útil para revelar os fatores que impulsionam os processos populacionais, para compreender a evolução da cooperação, transmissão de doenças, e padrões de aprendizagem social. Assim sendo, a compreensão das relações sociais entre indivíduos e as diferenças na utilização do habitat entre grupos sociais é importante para assegurar a gestão e conservação da espécie.

Os Açores acolhem uma das maiores biodiversidades de cetáceos do mundo, com 28 espécies de cetáceos documentadas até à data. Os golfinhos roazes são uma das espécies mais avistadas no arquipélago, estando presentes durante todo o ano. Através da extensa base de dados recolhida ao longo dos anos em São Miguel, alguns indivíduos já são conhecidos pelas empresas de observação de baleias e golfinhos, sendo reavistados ao longo de vários anos, sugerindo associações entre eles e uma potencial fidelidade à ilha. Neste estudo, o nosso objetivo era atualizar o catálogo de foto-identificação de golfinhos roazes existentes em São Miguel (2014-2019) com fotografias tiradas em 2008, 2010, 2012 e 2020 a bordo dos barcos de observação de baleias e golfinhos da empresa *Futurismo Azores Adventures* em São Miguel e analisar a estrutura social dos indivíduos identificados. Nos Açores, a recolha de dados é hoje em dia uma tarefa comum para a maioria das empresas de observação de baleias e golfinhos. Estas empresas constroem a sua própria base de dados e utilizam-na para as suas próprias investigações, ou colaboram com organizações, investigadores ou plataformas existentes, tais como o MONICET (que visa recolher, organizar e divulgar dados sobre cetáceos recolhidos por empresas de

observação de baleias no arquipélago) para melhorar o conhecimento sobre os cetáceos na região.

Através da foto identificação conseguimos acrescentar ao catálogo mais 184 novos indivíduos, tendo agora o presente catálogo de golfinhos roazes em São Miguel 689 indivíduos identificados. A foto-identificação é um método não invasivo que desempenha um papel importante na nossa compreensão da biologia, ecologia e comportamento dos cetáceos, especialmente na investigação sobre o tamanho da população, migração, história de vida e estrutura social. Ser capaz de distinguir os indivíduos pode fornecer uma visão valiosa sobre questões básicas, biológicas e científicas, mas é também altamente relevante para a conservação baseada na ciência.

Uma população é definida como o número de indivíduos da mesma espécie, neste caso, golfinhos roazes, que ocorrem na zona de estudo, durante o período de amostragem. A curva de descoberta, ou seja, a taxa cumulativa de identificação de novos indivíduos durante o período de amostragem, revelou que a população de golfinhos roazes em São Miguel é considerada aberta, com um recrutamento contínuo de novos indivíduos para a população durante todo o período de estudo. Estes novos indivíduos podem representar nascimentos, imigração na população, marcar mudanças ou capturas nos anos subsequentes de indivíduos que anteriormente não tinham sido fotografados. O aumento contínuo do número de indivíduos e a elevada percentagem de indivíduos avistados apenas uma vez apoia a ideia de que a maioria dos indivíduos fotografados são apenas transitórios na área.

As populações de golfinhos roazes exibem diferentes padrões de residência em todo o mundo. Algumas exibem grandes movimentos e baixa fidelidade ao local, enquanto outras mostram movimentos de curto alcance e forte fidelidade ao local. Em São Miguel, os golfinhos identificados tendem a passar alguns dias na área antes de emigrarem permanentemente ou durante períodos maiores do que o período analisado, ou simplesmente morrem. A maior produtividade das águas dos Açores, em comparação com o mar aberto, parece ser a razão pela qual várias espécies de cetáceos são observadas na área. Golfinhos que aparecem em zonas oceânicas adjacentes podem sentir-se atraídos a utilizar os Açores como um local de alimentação temporária. Contudo, o facto de ser apenas temporário indica que não existem recursos alimentares suficientes para sustentar permanentemente uma população maior ou que os golfinhos não residentes têm diferentes estratégias de alimentação ou preferências alimentares, que são insustentáveis nos Açores.

A análise social demostrou que as associações entre golfinhos roazes identificados em São Miguel são muito dinâmicas e os laços sociais podem ser muito flexíveis. Este resultado é consistente com outros estudos, uma vez que as sociedades de golfinhos roazes são caracterizadas por uma dinâmica de fissão-fusão, onde os indivíduos se associam em grupos que mudam frequentemente de tamanho ou composição num período de tempo muito curto, levando a baixos coeficientes de associação entre pares de indivíduos e consequentemente a um baixo coeficiente médio de associação para a população. Apesar do baixo índice de associação encontrado neste estudo, houve alguns indivíduos que revelaram um índice superior à média geral, sugerindo relações de longo prazo.

O dendrograma produzido utilizando a análise hierárquica de agrupamento revelou certo grau de estruturação dentro da população de golfinhos roazes em São Miguel, com cinco grupos identificados. Também foi possível notar que golfinhos roazes residentes foram vistos com golfinhos migratórios, ou seja, estão ligados a golfinhos com movimentos de maior escala. Indivíduos que exibem extensos movimentos podem ter um papel fundamental, contribuindo para uma variabilidade genética nas comunidades de golfinhos oceânicos, que de outra forma estariam geneticamente isolados. Da mesma forma, a análise temporal também indicou que no período de estudo, não houve presença de associações aleatórias ao longo do tempo, entre os indivíduos analisados. No entanto, deve ter-se em consideração que esta é a tendência geral e nem sempre é possível prever o padrão de associação de todos os indivíduos. Este estudo destaca a importância do conjunto de dados de longo prazo obtidos através de plataformas oportunistas nos Açores e oferece uma contribuição significativa para desenvolver estratégias de gestão. No entanto, é necessário um maior esforço de investigação para fotografar repetidamente todos os indivíduos na área de estudo, avaliar a sazonalidade dos indivíduos transitórios e ter mais suporte de dados sobre os residentes observados durante todo o ano.

Palavras-chave: Estrutura social, foto identificação, *Tursiops truncatus*, golfinho roaz, Açores, SOCPROG

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List of Abbreviations:

Tt: *Tursiops truncatus*

LIR: Lagged Identification Rate

AIC: Akaike Information Criterion

QAIC: Quasi-Akaike Information Criterion

LIR: Lagged Identification Rate

HWI: Half-Weight-Index

SD: Standard Deviation

CV: Coefficient of Variation

SLAR: Standardized Lagged Association Rate

CCC: Cophenetic Correlation Coefficient

AI: Association Index

MSFD: Marine Strategy Framework Directive

Chapter 1: Introduction

1.1 Importance of studying cetacean’s biology and ecology

Cetaceans are an important part of the marine ecosystems as they affect the distribution and abundance of prey species and can have important effects on the structure and function of ecosystems. However, due to the difficulty of collecting data in offshore areas, their role in ecosystems’ functions and dynamics is still poorly understood (Bowen, 1997; Silva, 2007). They facilitate the vertical transport of nutrients by their vertical movements and consequent water mixing. Moreover, cetacean species that carry out extensive migrations, contribute to the horizontal movement of nutrients, trough urea, carcasses and even by placentas, enhancing productivity and abundance of prey in oligotrophic regions (Roman *et al*., 2014; González García, 2019).

When formulating a cetacean conservation strategy, a thorough understanding of cetaceans’ biology and ecology is needed. First, to identify key areas and to adapt conservation measures to the biological scales in which the population functions, it is essential to know the population's habitat preferences and requirements. Second, an understanding of the population parameters is important to assess its conservation status and population dynamics and identify its changes and trends. Lastly, to evaluate the potential impact of habitat changes it is crucial to understand the ecosystem of which a population is part (Silva, 2007; Augusto, 2017). In this context, to continuously implement appropriate conservation and management plans, the existing knowledge about cetaceans and their ecosystem must keep being expanded.

1.1.1 Opportunistic data

Collecting data from cetaceans is most of the times a demanding task since they can use a variety of habitats and are generally wide-ranging (Kiszka *et al*., 2004). Dedicated surveys follow strict scientific protocols and so, usually provide high quality data. However, due to their complex and expensive logistics they have limitations on their spatial and temporal extent (Evans & Hammond, 2004; Moura *et al.*, 2012; Gonzalez

García *et al*., 2018). As such, opportunistic data, like data collected from whale-watching platforms, comes up as an important and valuable solution to obtain low-cost information on species diversity and distribution in a given area, during long periods of time (Evans & Hammond, 2004; González García *et al*., 2018; Torreblanca *et al*., 2019).

Many of the most important ecological and evolutionary processes affecting populations occur over several years or decades. Consequently, it is crucial to record the life history of identifiable individuals. Opportunistic data can provide these long-term datasets with a regular spatial cover, and although it has some limitations, lack of quantified effort or potential data bias, it can provide information that would otherwise be unavailable (Clutton-Brock & Sheldon, 2010; Moura *et al.*, 2012; González García *et al.*, 2018).

In the Azores, data collection is nowadays a common task for most whale watching companies. They build their own database and use it for their own research, or they collaborate with existing organizations, researchers or platforms, such as the MONICET (which aims to gather, organize and disseminate cetacean data collected by whale watching companies in the archipelago) to improve the knowledge about cetaceans in the region.

1.1.2 Photo identification

Photo identification is a non-invasive method which plays a major role in our understanding of the biology, ecology and behaviour of cetaceans, especially for research into population sizes, migration, life history and social structure (Whitehead, 2001). Several species of cetaceans possess natural marks, such as scarring, notches, pigmentation, and callosity patterns, as well as human-inflicted markings. These marks are unique for each individual and so, useful for photo identification. Being able to tell individuals apart can provide invaluable insight into basic, biological and scientific questions but is also highly relevant to science-based conservation (Genov *et al*., 2018).

Large photographic catalogues have been constructed for various species in several parts of the world (Beekmans *et al.*, 2005). Therefore, as more individuals within a population are identified, identification catalogues grow and the process of identifying individuals, matching photographs, becomes increasingly more complicated as each new photograph has to be compared with all previously identified individuals. This requires more time and skills, and increases the likelihood of misidentification (Whitehead, 1990). Given the importance of individual identification, and to try to reduce the labour and increase the accuracy of identification analysis, computer assisted matching techniques are increasingly important (Beekmans *et al*., 2005). *FinFindR*, an open source application, can help reducing the amount of effort needed to find matches. By using images to represent the trailing edge, rather than just information on the trailing edge angles, it allows researchers to quickly and accurately match dorsal fins in photos of unknown individuals with dorsal fins in a catalogue of known individuals (Thompson *et al*., 2021).

1.2 Why do some animals live in groups?

Most marine mammals live in groups where interactions between a set of conspecifics are more frequent than with members of other groups (Bouveroux & Mallefet, 2010). These repeated interactions between individuals in a population, defined here as a group of organisms of the same species occupying a particular space at a particular time (Silva, 2007), maintain cohesion and harmony among the group members. It also promotes the spread of information that are vital to the survival and fitness of the group members and allows a quick adaptation to a dynamic environment (López, 2020; Moreno & Acevedo-Gutiérrez, 2016).

Living in a group has benefits and costs. For collective life to be sustainable, individual benefits must exceed costs. For cetaceans, the benefits are related to the protection of predators, prey availability and transfer of information; while costs are related to travel, parasite load, competition for resources and philopatry (Louis *et al*., 2015; Augusto, 2017). In these social systems, the distribution of organisms is rarely random in space. Association of individuals is affected by different factors: the conspecifics involved, the environment, or even the basic needs (rest, feed and mate) of each individual (Whitehead, 2008; Augusto, 2017), being the social structure of a population determined by the content, quality, and temporal pattern of interaction among individuals (Danaher-Garcia *et al.*, 2020).

The availability of resources can be responsible for stabilizing social structure. If resources are stable and predictable over time, populations tend to remain in the area; while when resources are variable, they tend to expand their range. Living in groups might increase protection from predators, as larger groups means that each individual is less likely to be attacked (Augusto, 2017). Social structure is also affected by sex-biased dispersal. Being this influenced by two main selective pressures: mating systems, where males tend to disperse to avoid kin competition; and inbreeding avoidance strategies, where if one sex disperses for this purpose, the other sex tends to stay in the area (Augusto, 2017). Finally, allocare, defined as a non-parent who participates in the process of raising young, can also shape social structure by changing the way individuals interact with each other (Augusto, 2017).

1.3 The target species - Bottlenose dolphins, *Tursiops truncatus*

1.3.1 Life history

Bottlenose dolphins (*Tursiops truncatus*, Montagu 1821) (Fig. 1.1) are long-lived mammals. In their natural habitat, females can live more than 50 years and reach sexual maturity between 5 and 13 years old, while males can live around 40-50 years and reach sexual maturity between 9 and 14 years old. Oldest recorded was 67 years for female and 52 years for male (Connor *et al*., 2000; Silva, 2007; Carwardine, 2019). After the twelve-month gestation period, the female gives birth to a single calf that remains with the mother for at least 3 years. Number of births is usually higher in spring/early summer, and occasionally for some populations a second peak occurs in autumn (Connor *et al*., 2000; Louis *et al*., 2015; Carwardine, 2019).

Figure 1 Bottlenose dolphins, Tursiops truncatus, photographed during a whale watching tour with Futurismo Azores Adventures. Photo: Andreia Pereira

According to studies about the social structure and life history of bottlenose dolphins near Sarasota Bay, the separation of calves from their mothers may happen suddenly, as it usually occurs with the male offspring; or it may be gradual, slowly reducing the frequency and duration of interactions over several months, common with female calves (Connor *et al.*, 2000; Wells, 2014). The time that individuals take to become sexually mature is considered a period of social exploration with the juveniles interacting with large number of individuals of all age and sex classes (Wells, 2014). Social exploration appears to be important for the social development of young dolphins, since juveniles often engage in social interactions that will become more important in later life. Among these behaviours, copulations, affiliative behaviours, and agonistic behaviours are the most frequent. These associations may be maintained or recur throughout the life of the individual. Females mature earlier than males, and so they tend to leave the juvenile groups before males. With the birth of the first calf, female association patterns begin to change. Males, on the other hand, associate with juveniles until they develop a strong pair bond with another male of similar age (Connor *et al.*, 2000; Wells, 2014).

1.3.2 Distribution and ecology

The bottlenose dolphins are found widespread in tropical to temperate waters throughout the world. They are often seen in shallow coastal waters and around oceanic islands, but also in the continental shelf edge. They are adapted to various marine and estuarine habitats, even ranging into rivers. This versatility is also reflected in the diverse foraging behaviours and techniques employed by this species (Connor *et al*., 2000; Silva, 2007; Carwardine, 2019). Bottlenose dolphins are a generalist feeder, with specialisation within populations and among individuals. They feed on a wide variety of fish, especially croaker, mackerel and mullet, cephalopods and crustaceans (Carwardine, 2019).

1.3.3 Home range and migration

Most bottlenose dolphins studied to date have had clear habitat ranges, and behavioural, morphological, and biochemical information indicates discrete stocks in some areas (Shane *et al.*, 1986). There have also been reported worldwide huge changes in the distribution and scale of communities, with communities exhibiting residential patterns ranging from residents to migratory (i.e., exhibiting seasonal site fidelity) or transient (i.e., exhibiting no site fidelity).

The ranging patterns analysis is critical to understand the ecology, dynamics, social structure, and evolutionary trajectory of the population. Knowledge of individual patterns of space use can be used to identify residential areas and territoriality and can provide important insights into the temporal and spatial distribution of resources (Silva *et al.*, 2008). By providing opportunities for gene flow between different regions, individuals' movement also has a fundamental impact on the genetic structure of the population (Silva *et al*., 2008; Whitehead, 2009). Variations in home range size have been mainly explained as a function of body size/mass, diet, climate, competition, predation, and reproductive strategies. Among these, several studies reported a strong correlation between the movement patterns of common bottlenose dolphins and their prey distribution and abundance, being considered the most important factor (for example Shane *et al.*, 1986; and Silva *et al.*, 2008). In addition, one study in Sarasota Bay and another in South Carolina showed that dolphins in both places were year-round residents.

Still, in Sarasota Bay their home range was about 125 km^2, and they showed a strong site fidelity to the area. In South Carolina, they had smaller home ranges and showed moderate levels of mobility, never being encountered outside estuarine areas (Scott *et al.*, 1990 and Gubbins 2002, respectively). These authors suggest that the relatively abundant and predictable food resources in these areas may sustain a resident population throughout the year. On the other hand, in habitats with lower productivity, animals should maintain larger home ranges because they need to range further to find enough food (Scott *et al.*, 1990; Connor *et al*., 2000; Gubbins, 2002).

In Azores, estimates of home range size of bottlenose dolphins were considered wide (2–3 times greater than those previously reported for this specie) in response to the lower predation rate and the lower density and patchy distribution of food resources than other areas (Silva, 2007). Ultimately, the extensive ranging behaviour allows the interbreeding between dolphins associated with different islands and prevents genetic differentiation within the population of the Azores (Silva, 2007). The analysis of mitochondrial DNA and microsatellite DNA markers performed also in this previous study, supports this hypothesis, indicating a lack of genetic differentiation between dolphins sampled in different groups of islands. In summary, there is a single and open population of bottlenose dolphins in the pelagic waters of the Azores, composed of several geographical communities that maintain social interactions with neighbouring communities and groups from within and outside the archipelago (Silva, 2007).

1.3.4 Group size and social structure

Small groups of 2-15 individuals are typical for bottlenose dolphins, although groups of more than 1000 have been reported (Carwardine, 2019). As seen in other dolphin species, bottlenose dolphins tend to form larger groups when inhabiting offshore. Larger groups in open ocean present advantages against predators, and usually better adaptability to group foraging strategies to hunt schooling fish (Dinis, 2015).

Bottlenose dolphin society is categorized as fission–fusion, characterized by fluid relationships where individuals associate in groups that often change in both size and composition, mainly on a daily or hourly basis (Bouveroux & Mallefet, 2010; Moreno &

Acevedo-Gutiérrez, 2016;). This grouping pattern is thought to be an adaptive response to the dynamic interactions of ecological variables, for example, the requirement to spread out to reduce feeding competition (Blasi & Boitani, 2014). Studies on social structure shows that within the bottlenose dolphin community, relationships between individuals can be complex, with several levels of alliances. The strength and stability of these alliances may depend on social and ecological benefits of behavioural activities such as mating, foraging or predator defence (Bouveroux & Mallefet, 2010). Therefore, understanding the long-term association pattern of a population is the first step in interpreting its overall social structure and specific relationships between individuals of these highly social groups (Danaher-Garcia *et al.*, 2020).

In these dynamic societies, besides the mother-calf bonds, sexual segregation among adults is believed to be the basic social framework of some bottlenose dolphin populations. Grouping patterns reflect sex-specific behavioural strategies (Blasi & Boitani, 2014; Shane *et al*., 1986), perhaps due to differences in encounter rate and utilization time of the main reproductively limiting resource of each sex, food for females and mates for males (Moreno & Acevedo-Gutiérrez, 2016). As an example, in Golfo Dulce, Costa Rica, females have a larger network of associates than males and are connected to most other females in the group, even though they may have a subset of favourite female companions. Adult males form strongly bonded pairs or trios with other adult males and are more aggressive than females through intersexual competition and sexual coercion during the breeding season (Connor *et al.*, 1992; Moreno & Acevedo-Gutiérrez, 2016).

1.3.5 Status and conservation

The common bottlenose dolphin was the first species of cetaceans to be held in captivity and, since it is so highly adaptable and easily trained, is still the most commonly held species. They are live captured for public display, research and military use, existing currently 800-1000 captive individuals in at least 17 countries. They are also continuously hunted to shark bait and to reduce the competition with commercial fisheries (Carwardine, 2019). Although there are many threats to this species, such as pollution, fishing interaction, direct hunt, marine traffic, tourism and habitat degradation, bottlenose dolphins are classified globally as Least Concern since 2008, and Data Deficient in Europe since 2007, in the IUCN red list (Dinis, 2015; Carwardine, 2019; Wells *et al*., 2019).

1.4 Theme justification

Studying social structure is a useful technique to reveal the factors driving population processes, to understand the evolution of cooperation, transmission of disease, and patterns of social learning (Madden *et al.*, 2009). Social development is a trade-off between the selective forces conferring benefits to group-living and the costs incurred in a group. Therefore, understanding social relationships between individuals and the differences in habitat use among social groups is critically important to ensure species management and conservation (Louis *et al*., 2015).

Azores hosts one of the highest cetacean biodiversity in the world, with 28 species of cetaceans documented so far (Silva et al., 2014). Bottlenose dolphins are one of the most sighted species in the archipelago, present year-round. Through the extensive long-term data series collected throughout the year in São Miguel, some individuals are already known by the whale watching companies, re-sighted over several years, suggesting associations between them and potential site fidelity to the island. However, this has not yet been proved. Studies on bottlenose dolphins from the Azores deal with ranging and residence patterns, occurrence and distribution, survival and abundance, and social structure, mainly focused on the central group of islands (Silva, 2007; Silva *et al*., 2008). Other studies overview cetacean occurrence in the Azores, with some insights about bottlenose dolphin occurrence and distribution in the archipelago (for example Silva *et al*. 2003; Silva *et al.*, 2014; and González García, 2019).

São Miguel island present great conditions for this type of research due to the fact that the species is very frequent in the area, and during the last years, more experienced biologists are successively recording all of the data. Thus, data is of enough quality, consistency and precision to be suitable for research on social structure, group composition and association patterns of this species.

By showing their constant companions, how they interact with other bottlenose dolphins' groups or communities and knowing the residence patterns, the conservation of the species in the area and the management plans can be improved.

1.5 Objectives

The main objectives of this study are:

1. To update and complete the photo-identification catalogue of *Tursiops truncatus* of São Miguel using whale watching data from Futurismo Azores Adventures.
2. To analyse the social structure of this population.
    a) Hypothesis: associations between bottlenose dolphins are non-random, with preferred and/or avoided companions.
    b) Expectation: previous data indicate that bottlenose dolphins have favourite or selected companions which are non-random, so we expect to detect privileged groupings.

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Chapter 2:

Analysis of the social structure of bottlenose dolphins (*Tursiops truncatus*) in São Miguel island, Azores

Pereira, A.[1, 2], González García, L.[1, 3], Castilho, R.[2, 4].

[1] Futurismo Azores Adventures, Ponta Delgada, São Miguel, Azores

[2] Universidade do Algarve, Campus de Gambelas, 8005-138 Faro, Portugal

[3] Azorean Biodiversity Group (University of the Azores), Centre for Ecology, Evolution and Environmental Changes (CE3C). Ponta Delgada, Azores

[4] Centre for Marine Sciences (CCMAR), Universidade do Algarve, Campus de Gambelas, 8005-138 Faro, Portugal

E-mail: affp.andreiapereira@hotmail.com

2.1 Abstract

Studying social structure is a valuable technique to reveal the factors driving population processes, to understand the evolution of cooperation, the transmission of diseases, and patterns of social learning. Therefore, understanding social relationships between individuals and the differences in habitat use among social groups is critically important to ensure species management and conservation. Bottlenose dolphins are one of the most sighted cetacean species in the Azores archipelago. They are present year-round, frequently encountered close to the islands, as well as in offshore waters. This study aimed to update the existing bottlenose dolphin photo-identification catalogue of São Miguel (2014-2019) with photos taken in 2008, 2010, 2012 and 2020 on board Futurismo's whale watching vessels and analyse the social structure of the identified individuals. There were added to the catalogue 184 new individuals, having now the current catalogue of bottlenose dolphins in São Miguel, a total of 689 individuals identified. The social analyses have shown that associations between bottlenose dolphins identified in São Miguel are very dynamic and social bonds can be very flexible. The low association coefficients between pairs of individuals and consequently the low average coefficient of association for the population is in concordance with the typical fission-fusion society that characterizes this dolphin species. However, the higher association index of some individuals, suggest some long-term relationships. Some degree of structuring within the population of bottlenose dolphins in São Miguel with five groups identified was detected. Resident dolphins were sighted with migrants, individuals with more significant scale movements, contributing to an increase in genetic variability in oceanic dolphin communities. This study highlights the importance of long-term data series obtained from opportunistic platforms in Azores and provides a significant contribution to assess baselines conditions of the population and develop management strategies.

Keywords: Social structure, *Tursiops truncatus*, bottlenose dolphins, Azores, SOCPROG

2.2 Introduction

Understanding of the behaviour, social organization, and ecology of bottlenose dolphins, especially in the wild, has received growing attention during the past years, promoting the research of animal social behaviour (Shane *et al.,* 1986). The interactions and associations between individuals, defined as social systems, are crucial for the success of the populations. They facilitate the transmission of information, allowing a quick adaptation to a dynamic environment (Moreno & Acevedo-Gutiérrez, 2016; Danaher-Garcia *et al*., 2020). However, these associations are usually non-random and can be related to the conspecifics involved, the resource availability, the environment or even the basic needs of each individual, like resting, foraging and mating (Menchaca *et al.,* 2019; Danaher-Garcia *et al.,* 2020). Groups stability has shown to be negatively correlated with body size. Larger cetacean's species form highly stable groups, while more fluid relationships are observed in smaller species (Hartman *et al.,* 2008). Long term research in several areas revealed that fission-fusion dynamics, composed of highly dynamic groups that change in size and composition at frequent intervals, are typical of some mammalian species, including bottlenose dolphins, *Tursiops truncatus* (Shane *et al*., 1986; Connor *et al*. 2000; Bouveroux & Mallefet, 2010; Moreno & Acevedo-Gutiérrez, 2016; Menchaca *et al.,* 2019).

Bottlenose dolphins are long-lived mammals that live ca. 45 years (Bouveroux & Mallefet, 2010). Because of this long lifespan and the possibility of observing individuals throughout their lives, we gain insights into their social structure and the ecological influences on their social patterns (Wells, 2014). Photo identification plays an essential role in these studies, by being a non-invasive method of identifying individuals (Whitehead, 2001; Bröker *et al.,* 2020). The trailing edge of a dolphin's dorsal fin is very thin, and the tissue does not regenerate (Würsig & Würsig, 1977). As a result, interactions with conspecifics, environmental or anthropogenic factors often lead to distinct and unique contours of the individuals' fins. The rear edge of the dolphins' dorsal fin may become irregular, resulting in a recognizable pattern of notches and scars. Because these scarring patterns can change over the years, individuals can typically be identified with some certainty as these patterns change slowly and most individuals identified are seen consistently over the years, providing a chronological photo record (Dinis *et al.,* 2018; Bröker *et al.,* 2020).

The Azores is considered an oasis in the middle of the Atlantic Ocean with 28 species of cetaceans documented so far (Silva *et al*., 2014). Opportunistic data collected by whale watching companies in the archipelago is becoming increasingly crucial for studying cetacean's species as it obtains low-cost and regular information on species distribution and diversity during long periods (Evans & Hammond, 2004; González García *et al*., 2018; Torreblanca *et al.,* 2019). Therefore, studies of social ecology can benefit from these long-term datasets, as they provide researchers with opportunities to distinguish the relative contributions of life history, demographics, and ecological pressures to the development of social patterns (Wells, 2014).

Bottlenose dolphins are one of the four species in Azores possible to see year-round. It is one of the most sighted species in the area and therefore it is an excellent model species to study its social network (Silva, 2007). Their preferential use of shallow areas, between 100 and 600 m, and their frequent presence along coastlines make them relatively accessible to study using opportunistic platforms (Moreno & Acevedo-Gutiérrez, 2016; Silva, 2007). In 2008, Silva *et al*. studied the ranging patterns of bottlenose dolphins living in oceanic waters, and the results were contrary to expectations. Bottlenose dolphins carried out long-distance movements of more than 100 km between the Azores islands. This suggests that bottlenose dolphins in the Azores constitute a single and open population, composed of several geographic communities that maintain social interactions with neighbouring communities and groups from the archipelago and beyond (Silva *et al*., 2008).

In this study, we aim to: (i) update and complete the photo-identification catalogue of *Tursiops truncatus* in São Miguel using photos taken during whale watching tours of Futurismo Azores Adventures from 2008-2013 and 2020; and (ii) analyse the social structure of the individuals identified around São Miguel. This information is needed to support potential conservation and management plans of the species in the area by showing their constant companions and how they interact with other bottlenose dolphin groups or communities.

2.3 Materials and Methods

2.3.1 Study area

The Azores archipelago is located about 1,500 km away from the nearest continental margin. It is composed of nine volcanic islands, divided into three groups: the Western group (Flores and Corvo), the Central group (Graciosa, São Jorge, Pico, Faial and Terceira) and the Eastern group (São Miguel and Santa Maria) (Figure 2.1a). This study focuses on the bottlenose dolphins of São Miguel island, Eastern group (Figure 2.1b).

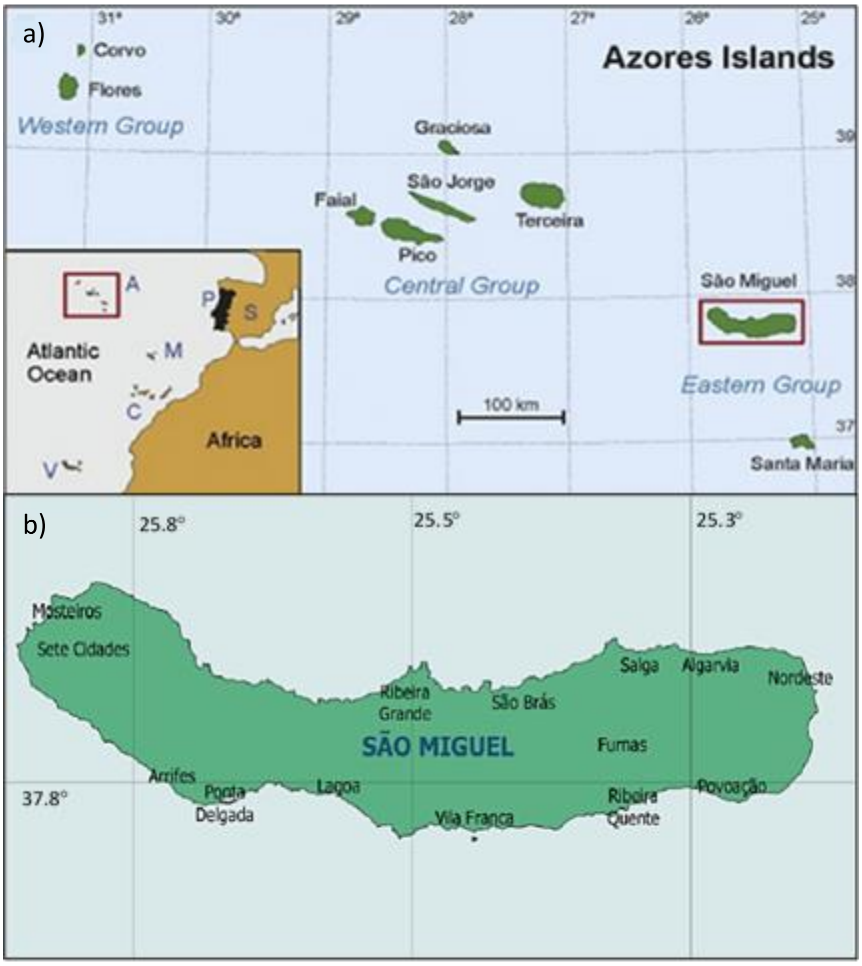

Figure 2.2 a) Map of the Azores archipelago and its relative location to mainland Portugal. b) São Miguel island

The bottom topography of the Azores is characterized by various habitat types, such as shallow seamounts, submarine canyons, steep island slopes, narrow island shelves and vast areas of abyssal plain (Silva *et al.*, 2008). The varying topography of the Azorean waters, the dynamic oceanography, the main currents (e.g. the North Atlantic Current and the Azores Current, both derived from the Gulf Stream), the latitudinal gradients of temperature (with colder waters usually towards the north) and the seasonal phytoplanktonic bloom (stronger in spring), generate higher levels of biological productivity and diversity than open waters, creating suitable hotspots for marine life (Silva *et al.*, 2008; Caldeira & Reis, 2017; González García *et al*., 2018).

2.3.2 Data collection at sea

Data used for this research were collected between 2008 to 2020 during whale watching tours with *Futurismo Azores Adventures*, a whale watching company with the main base in Ponta Delgada, São Miguel, Azores. We only used data from encounters in the south of São Miguel, where each tour had an approximate duration of 3-hours and could be operated once or twice a day, depending on weather conditions and passenger availability. These sea surveys occur during the whole year but are more frequent during the spring and summer months.

During the tours, bottlenose dolphins were usually sighted by one or more experienced land-based lookouts located in strategic points around the coast, characterised by good visibility and good spatial cover, and equipped with powerful binoculars (Steiner 20 x 80). The help of these land-based lookouts is an essential and characteristic feature of the Azorean whale-watching. They gave radio guidance to direct the whale watching boats towards the animals present in the study area, managing the number of ships around the same animal.

Whale watching boats approached the animals respecting the current legislation (DLR 10/2003/A) and the guidelines of the World Cetacean Alliance for responsible whale watching, keeping at least 50 m between the boat and the animals and approaching the animals always from the back or the sides of the individual or group. Once the ship arrived in the area, biologists on board registered the sightings (time of sighting, species encountered, GPS coordinates, group size and composition) and, when possible, took photos of the animals for further identification.

2.3.3 Photo identification

The existing catalogue, recently updated by R. Catalão (Catalão, 2021) with data of 6 years (2014-2019), already had 723 photos of 505 individuals identified (dolphins with distinctive nicks/notches, marks/scars and/or extensive pigmentation on the dorsal fin): 218 with photos of the right and left side of the dorsal fin, and 287 with photos of only one side (Catalão, 2021). To complete the existing catalogue we analyse photos taken in 2008, 2010, 2012 and 2020 collected on board Futurismo's whale watching vessels.

All the photos were separated by year, month, and day in different folders, and then, pictures without enough quality (blurry, with a lot of water splashes, and/or in not a good angle) were deleted. Selected good photos were cropped to have one dorsal fin clipped per photo. A package for the R program called "FinFindR", that characterizes dorsal fins according to the trace of the fins photographed, was used to quantify an individual's unique fin characteristics and match them with the existing photograph catalogue (Thompson *et al.*, 2021). The program found the most similar fins, making the first selection of possible matches easier. After verifying them all, it was possible to add the new recapture dates to the matches found. If no matches were found, identification numbers were attributed to the new individuals, and then they were added to the catalogue. This last validation before adding new individuals to the catalogue is essential, therefore, the photos had to be checked carefully against much or all of the catalogue so that duplicates were not included. Only individuals with sufficiently distinctive marks and good quality photos to allow future recognition were included in the dataset (Figure 2.5).

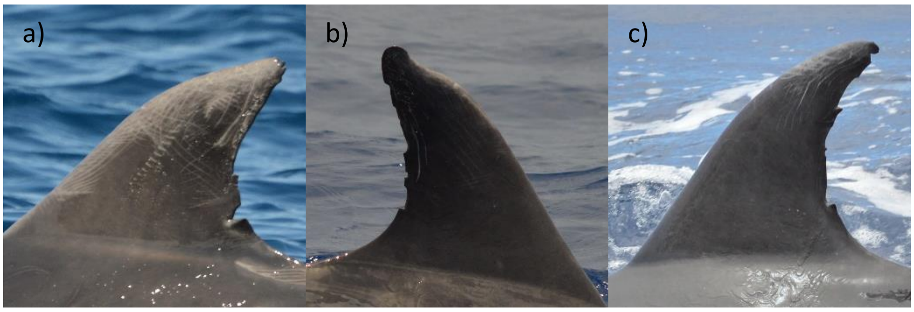

Figure 2.3 Examples of individuals present in the catalogue with distinctive marks. a) TT_022; b) TT_145; c) TT_023.

2.3.4 Population trend

A population is defined as the number of individuals of the same species, in this case, bottlenose dolphins, that occur in the study area during the sample period (Krebs, 1994; Silva, 2007). The discovery curve (cumulative rate of identification of new individuals during a sampling period) was plotted to assess the general trend of the population and investigate if the population of bottlenose dolphins in São Miguel is considered closed or open. Population trends were statistically analysed using the SOCPROG 2.9 (Whitehead, 2009).

Three models were fitted to the population estimates using the Akaike Information Criterion (AIC) to determine which model best described the population: (1) *Closed* (Schnabel), where the population has no mortality, birth, immigration or emigration; (2) *Mortality*, where the population remains the same with mortality balanced by birth; (3) *Mortality + trend*, where population grows or declines at a constant rate (Whitehead, 2015). The best-fitted model was selected by the lowest AIC (Whitehead, 2007; Whitehead, 2015).

2.3.*5* Site fidelity and residence patterns

Site fidelity or residence patterns can be described as the tendency of animals to stay in a specific area for a long time or to return to the previously occupied area (Baş *et al.*, 2019; Bröker *et al.*, 2020). Dolphins resighted during three seasons in one year and at least in two consecutive years are defined as residents. Dolphins resighted in less than three seasons for consecutive or non-consecutive years are considered migrants. Those only resighted a few times in one year are considered transients. And finally, the ones sighted only once are defined as non-residents.

The residence time for individuals within the study area, i.e., the amount of time that an individual spent in a particular area (Wells & Scott, 1990; Wells, 1991), was estimated by the Lagged Identification Rate (LIR) using the "movement analyses" component of SOCPROG 2.9. LIR is the probability that an individual identified in the study area at any time will be resighted again after a variable lag time (Pereira, 2012; Whitehead, 2015)

LIR plotted over time can provide a certain understanding of how individuals use the study area. Non-zero LIR values suggest that some individuals remain resident or that emigrated individuals reimmigration into the study area. If the population is closed and the identifications are independent, LIR remains constant over time. Due to immigration and mortality, LIR will decrease as the time lag increases (Bröker *et al.,* 2020). Posterior, the LIR was compared with different models. The selection for the best model fitted was based on the lowest Quasi-Akaike Information Criterion (QAIC) value.

2.3.*6* Social structure

To analyse the social structure of the identified individuals, we used the program SOCPROG (Whitehead, 2009) which provides flexible and fairly comprehensive analyses of social structure using data on the associations or interactions of identified individuals, and develops models of social structure, population structure and movement (Whitehead, 2009).

Following the general methodology applied in studies of the social structure of dolphins, we consider animals to be associated when they are photographed in the same group, i.e., animals moving in the same direction and/or interacting or engaged in similar activities within the same space-time. To increase confidence in the data set and avoid over/under estimation of the results, only individuals sighted on a minimum of 10 occasions were included in this analysis.

2.3.6.1 Analysing association indices

Association index estimates the proportion of time that dyads of individuals, i.e., pairs, spend together (Whitehead, 2009). To calculate these association rates and establish a matrix of association, we used the Half-Weight-Index (HWI), which evaluates the social unit composition and cohesion. Association values range from 0 to 1, where 0 indicates that the pair have never been observed together in the same group, and 1 indicates that the animals were consistently observed in the same group. This index is the most widely used in the analysis of cetaceans' social structure. As it is not always possible to photograph and identify all individuals within a group, this index presents the lowest bias when pairs are more likely to be seen separate than together (Cairns and Schwager, 1987).

To identify the best division of the data, a dendrogram of associations was plotted using different methods: simple, complete, average and ward. We used the cophenetic correlation coefficient to determine which linkage method gives the best and accurate representation of the data (highest coefficient). Since it indicates how well the dendrogram matches the matrix of association indices, if the cophenetic correlation coefficient is greater than 0.8, it means that it is a good match (Whitehead, 2015). The modularity, which is the difference between the proportion of the total association indices and the expected proportion within the clusters, was also analysed to investigate significant divisions within the population. Modularity greater than 0.3 indicates a useful division of the population (Newman, 2004; Whitehead, 2015).

To assess the significance of individual HWIs, it was important to determine whether the associations are random or not (Blasi & Boitani, 2014). We used permutation tests of SOCPROG to test for non-random associations in all data combined against the null hypotheses that dolphins associate randomly with no preferred/avoided associations. The method used was "Permute associations within samples", and the number of permutations was increased until the p-value obtained from the Monte Carlo simulation stabilized (Whitehead, 2015). Long-term preferred/avoided companionships are indicated by a significantly high standard deviation (S.D.) or coefficient of variation (CV) of the real association indices (Whitehead, 2015). Therefore, real S.D. and CV were taken as evidence to test if individuals have preferred or avoided companions.

2.3.6.2 Temporal stability of associations

To analyse the temporal variations in association values of the populations with time, Standardized Lagged Association Rate (SLAR) was calculated as the probability of two individuals that are associated will still be associated with various time lags (τ) later (Whitehead, 2015). SLAR was compared with theoretical models to determine the best one to fit the real data. The Quasi-Akaike's Information Criterion (QAIC) was applied, and the one with the minimum QAIC was selected as the best fit. The difference between the best fitted QAIC with the other models, ΔQAIC, indicated how well the data support the less favoured ones (ΔQAIC: 0-2 substantial support for the model; ΔQAIC: 4-7 considerably less support; ΔQAIC: >10 essentially no support) (Whitehead, 2015).

The null association rate represents the expected SLAR values if there are no preferred associations and is also included in the graph for reference. Therefore, if the lagged association rate is equal to the null association rate at some point, it means that dolphins associated randomly.

2.4 Results

2.4.1 Survey effort and photo identification

Effort was measured as the number of trips per month or year since the dolphins were often spotted by the lookouts on land that guided the boats directly to the area, so it is not an absolute measure. The results throughout the years showed that effort was not always the same, and 2016, 2017 and 2018 were the years with a higher number of trips (451, 452 and 447, respectively). The year with the lowest effort was 2020, with only 149 trips, due to the Covid-19 pandemic, followed by 2008, with only six months of data (May-September and December), with 227 trips (Figure 2.6).

Whale watching tours of Futurismo occurred year-round but in higher numbers during June, July and August, mainly due to favourable weather and sea conditions and the higher presence of tourists in the Azores (Figure 2.7). During the period analysed

(2008-2020), 4701 surveys were registered onboard Futurismo's vessels in São Miguel. Overall, 2586 bottlenose dolphins' sightings were recorded, with a higher number in June, July and August (Figure 2.7).

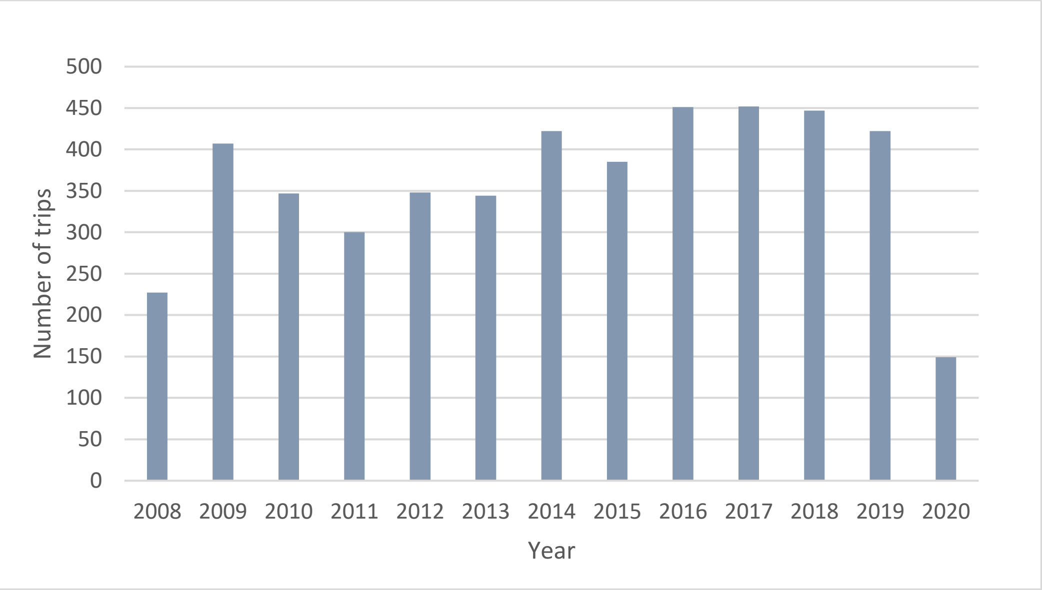

Figure 2.4 Number of whale watching trips during 2008-2020.

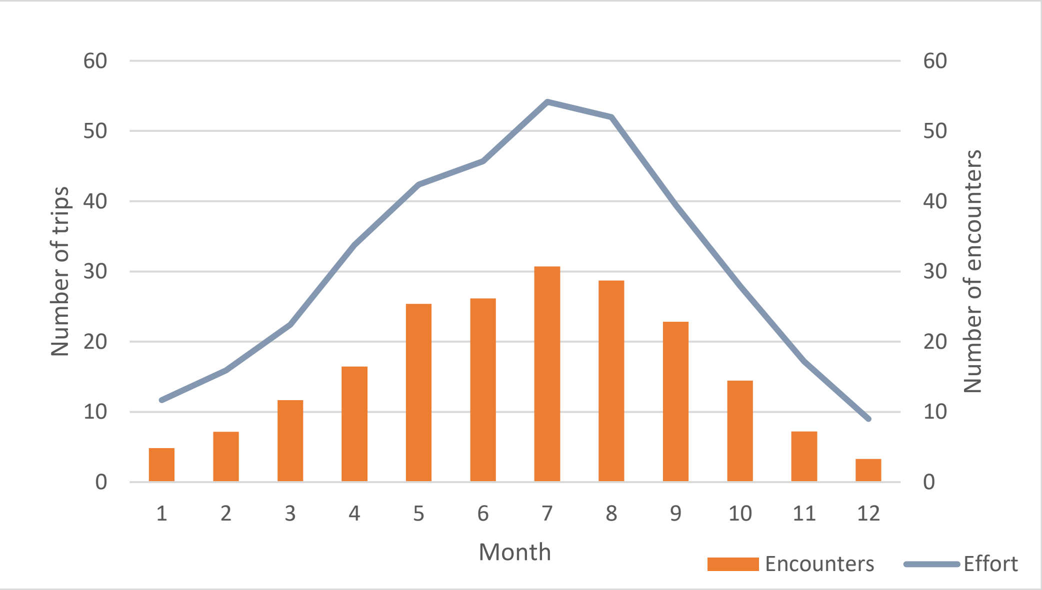

Figure 2.5 Average number of Futurismo whale watching trips (effort) and bottlenose dolphins encounters by month, between 2008 and 2020.

A total of 4323 photos were analysed from the years 2008, 2010, 2012 and 2020 to complete the catalogue of 2014-2019 (with already 505 individuals identified by R. Catalão). The year with a higher number of photos analysed was 2020, with 3628 images (Figure 2.8). In 2008, the number of pictures analysed was the lowest, with 72 images. There were added to the catalogue 184 new individuals, having now the current catalogue of bottlenose dolphins in São Miguel, a total of 689 individuals identified. Two hundred sixty-nine individuals with photos of both sides of the dorsal fin, and 420 individuals, with only one side of the dorsal fin.

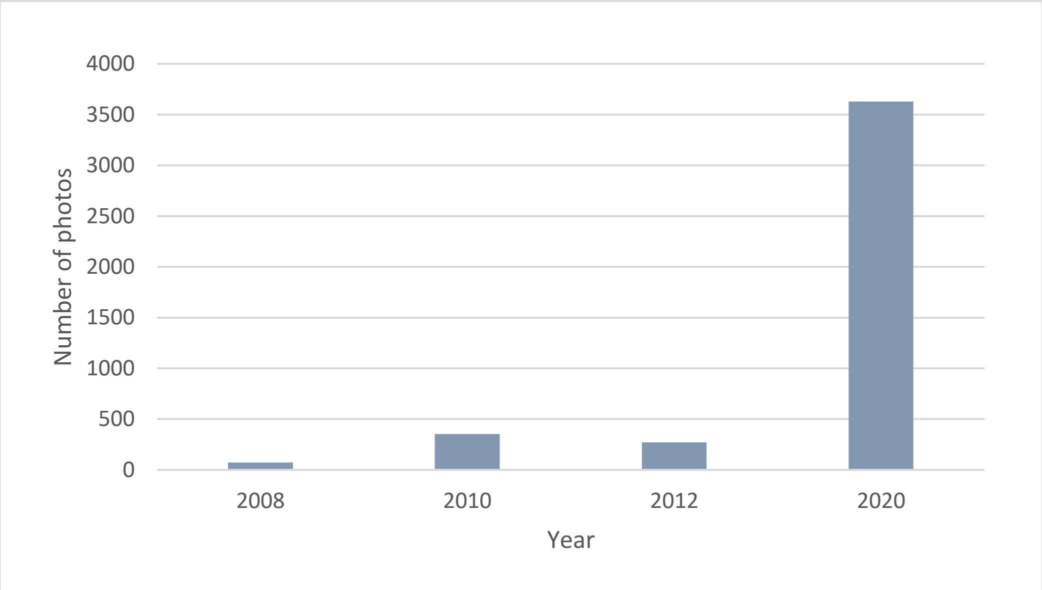

Figure 2.6 Number of photos analysed of the years added to the catalogue.

By gathering all the years of data available, a total of 2843 identifications were possible to obtain in the 530 encounters where at least one individual was identified. The average number of identifications per encounter was 5,36 (SD = ± 5,62). The year with more identifications was 2014, with a total of 972 identifications. No identification was made in 2008 due to the low quantity and poor-quality photos available, and in 2009, 2011 and 2013 due to the lack of photos (Figure 2.9). The maximum number of individuals identified in one encounter was 39 on July 20th, 2020.

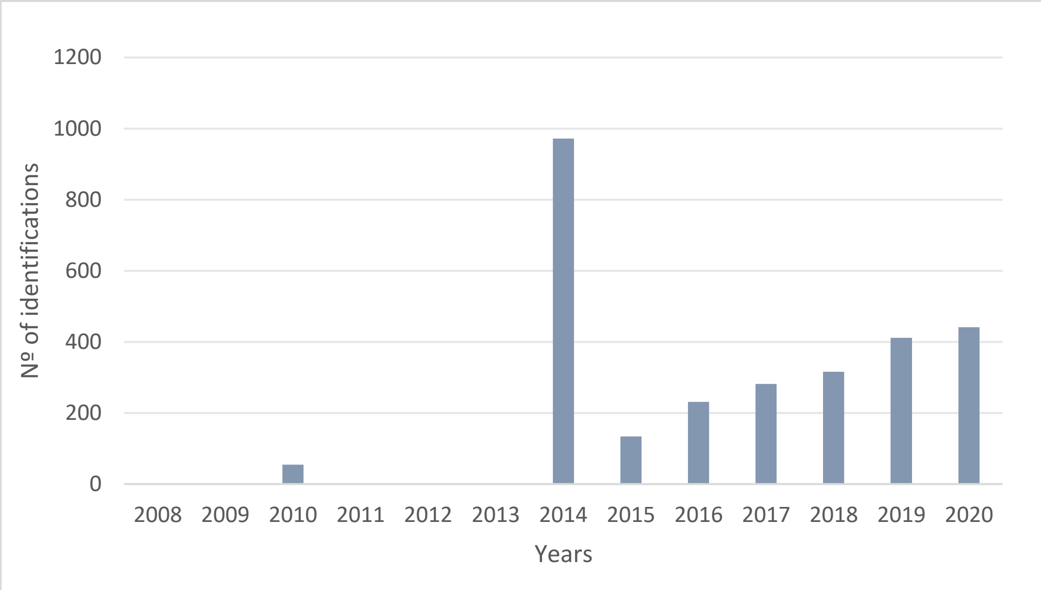

Figure 2.7 Number of identifications per year of bottlenose dolphins in São Miguel during whale watching tours with Futurismo Azores Adventures between 2008 and 2020.

Of all the identified individuals, 325 were sighted only once in the study area, 110 were sighted twice, and 55, three times. Only one individual was encountered in 100 days (TT_002). Thus, the number of times the individuals identified were encountered in the study area varied from 1 to 100 (Figure 2.10). The number of individuals sighted on ten or more occasions was 73.

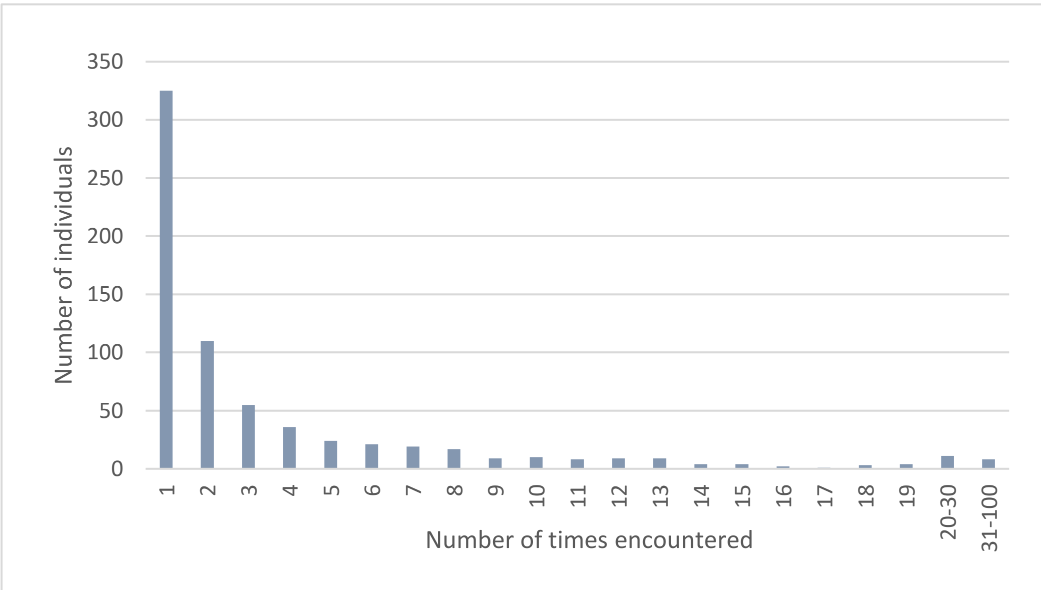

Figure 2.8 Sighting frequency of the individuals identified in São Miguel for the study period, 2008-2020.

2.4.2 Population trend

According to the discovery curve (Figure 2.11), the number of individuals identified increased day by day throughout the study period; thus the cumulative curve of new individuals never reaches the plateau, indicating a larger or an open population. A population is defined here as a group of bottlenose dolphins that occupy a specific area at a specific time (Silva, 2007). It is also possible to notice in the curve the higher number of individuals identified in 2014 and 2020 compared to the other years.

Regarding the AIC values, the best-fitted model for population size estimative, given by the SOCPROG program, was the open model "Mortality + trend". This model assumes a population growing or declining at a constant rate (Whitehead, 2015). In this study, the population is growing, which means we have not yet identified all bottlenose dolphins around São Miguel (Table 2.1).

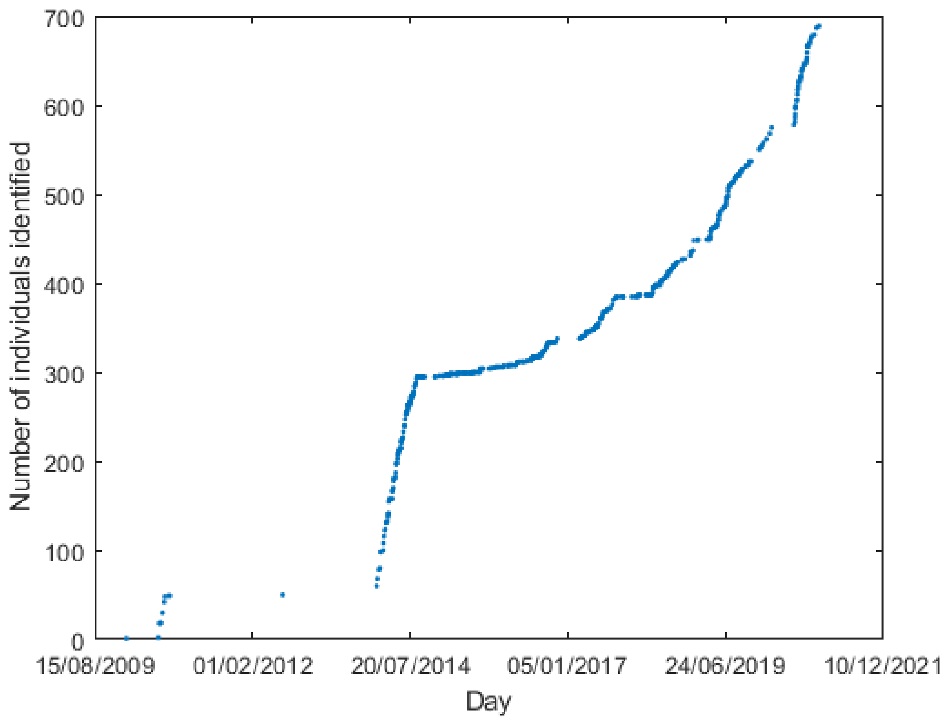

Figure 2.9 Discovery curve. The cumulative rate of identification of new individuals during the sampling period, day.

Table 2.1 SOCPROG fit of population models for bottlenose dolphins in São Miguel, Azores, in 2014-2020. Bold value indicates the best fit model.

Model	***AIC***
Closed (Schnabel)	21728.3144
Mortality	20173.1183
Mortality + Trend	**20105.5195**

2.4.3 Site fidelity and Residence patterns

The high values of LIR in the first days reveals that it is more likely to resight an individual previously identified within approximately 10 to 100 days than later (Figure 2.12). This suggests that bottlenose dolphins might spend a few days inside the study area before leaving. The decrease of the LIR with time, indicates that individuals tend to emigrate from this area permanently or during a period longer than the study period and/or simply die. The model which best adjusts to data is the "Emigration + Reimmigration + mortality" model (Table 2.2).

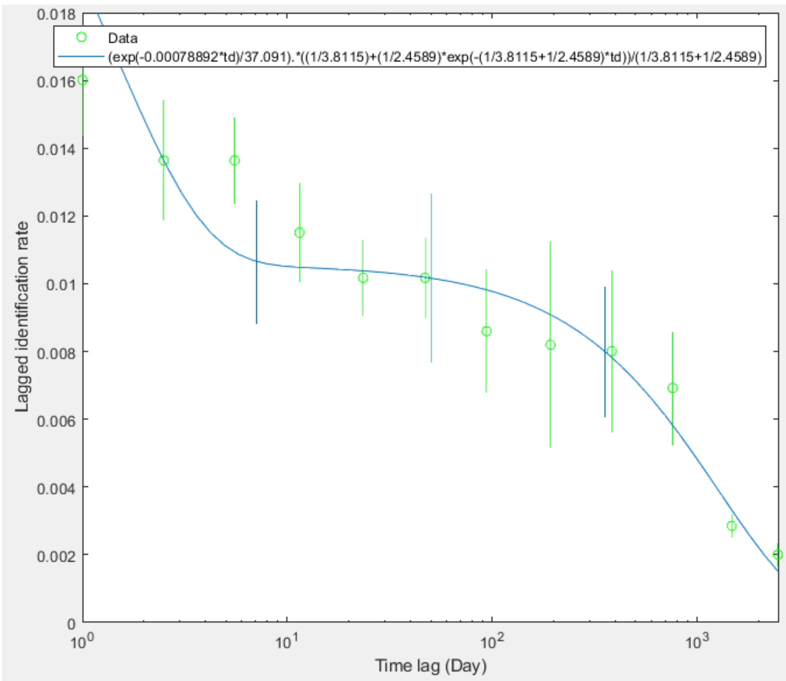

Figure 2.10 Lagged Identification Rate. The probability that identified individuals be reidentified various time lags (days) later. The best fitted models are represented with a line. Error bars were estimated with 100 bootstrap replications.

Table 2.1 Model fitting results to the lagged identification rate (LIR) for bottlenose dolphins in São Miguel between 2008 and 2020 given by the SOCPROG program. Bold value indicates the best fitted model for LIR values.

Explanation	*Model type*	*QAIC*
Closed	*a1*	148824.4
Closed	1/a1	148824.4
Emigration/mortality	*a2 * exp (-a1 * td)*	145196.5
Emigration/mortality	(1/*a1*) * exp (-*td*/*a2*)	145196.5
Emigration + reimmigration	*a2 + a3 * exp (-a1 * td)*	145194.4
Emigration + reimmigration	(1/*a1*) * ((1/*a3*) + (1/*a2*) * exp (-(1/*a3* + 1/*a2*) * *td*)) / (1/*a3* + 1/*a2*)	145194.4
Emigration + reimmigration + mortality	*a3* * exp (-*a1* * *td*) + *a4* * exp (-*a2* * *td*)	148547.3
Emigration + reimmigration + mortality	**(exp (-*4* * *td*) / *a1*) * ((1/*a3*) + (1/*a2*) * exp (-(1/*a3* + 1/*a2*) * *td*)) / (1/*a3* + 1/*a2*)**	**145182.0**

2.4.4 Social Structure

2.4.4.1 Analysing Association Indices

As mentioned before, only the individuals resighted ten or more times were considered for social structure analysis, resulting in 73 individuals. The overall mean association index was 0.07 (SD ± 0.03), suggesting that, in general, associations within the population were low. In addition, the maximum association index for each individual had a low average of 0.49 (SD ± 0.15). Only two individuals (TT_155 and TT_154) had a maximum association index of 0.78 (Fig. 12).

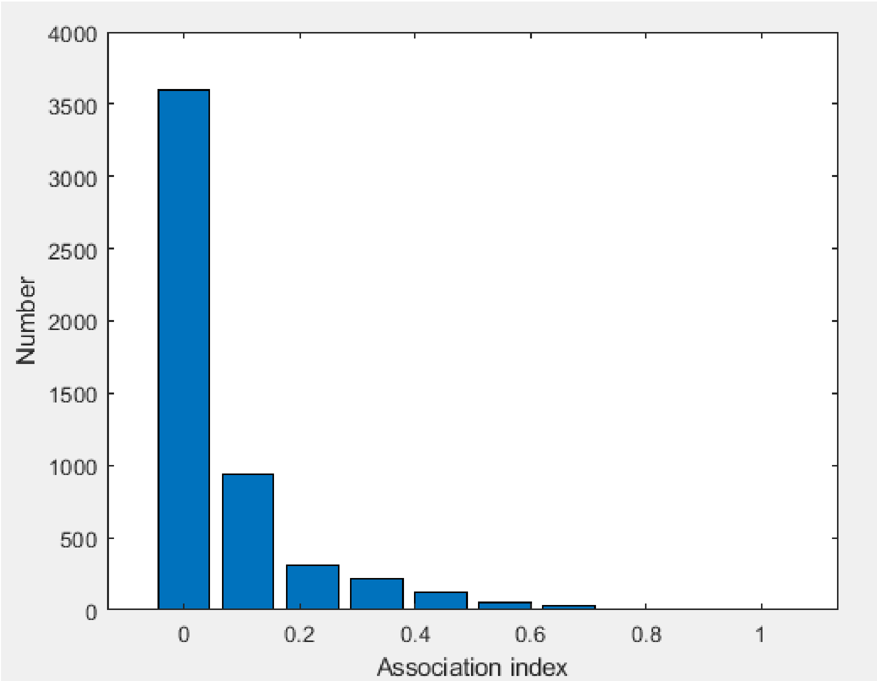

Figure 2.11 Coefficient of association plot for individuals identified in São Miguel during the study period, 2008-2020. Y-axis represents the number of dyads, pairs of individuals.

The linkage method that had the highest value of the cophenetic correlation coefficient was the average one (CCC= 0.90537) (Table 2.3) and so was the one used to give the best representation of the data. The dendrogram produced using the hierarchical cluster analysis revealed some structuring within the population of bottlenose dolphins in São Miguel, with five groups identified (Figure 2.14). The threshold for stable associations used by the program for the division was an association index (A.I.) of 0.071. It was considered the best representation for the division of the population as the values of the modularity were greater than 0.3 (Modularity = 0.47667).

Table 2.2 Results of cophenetic correlation coefficient given by the SOCPROG program for each Linkage method. Bold value indicates the highest cophenetic correlation coefficient and so the most appropriate linkage type for our data.

Method	***Cophenetic correlation coefficient (CCC)***
Single	0.85139
Complete	0.77024
Average	**0.90537**
Ward	0.63999

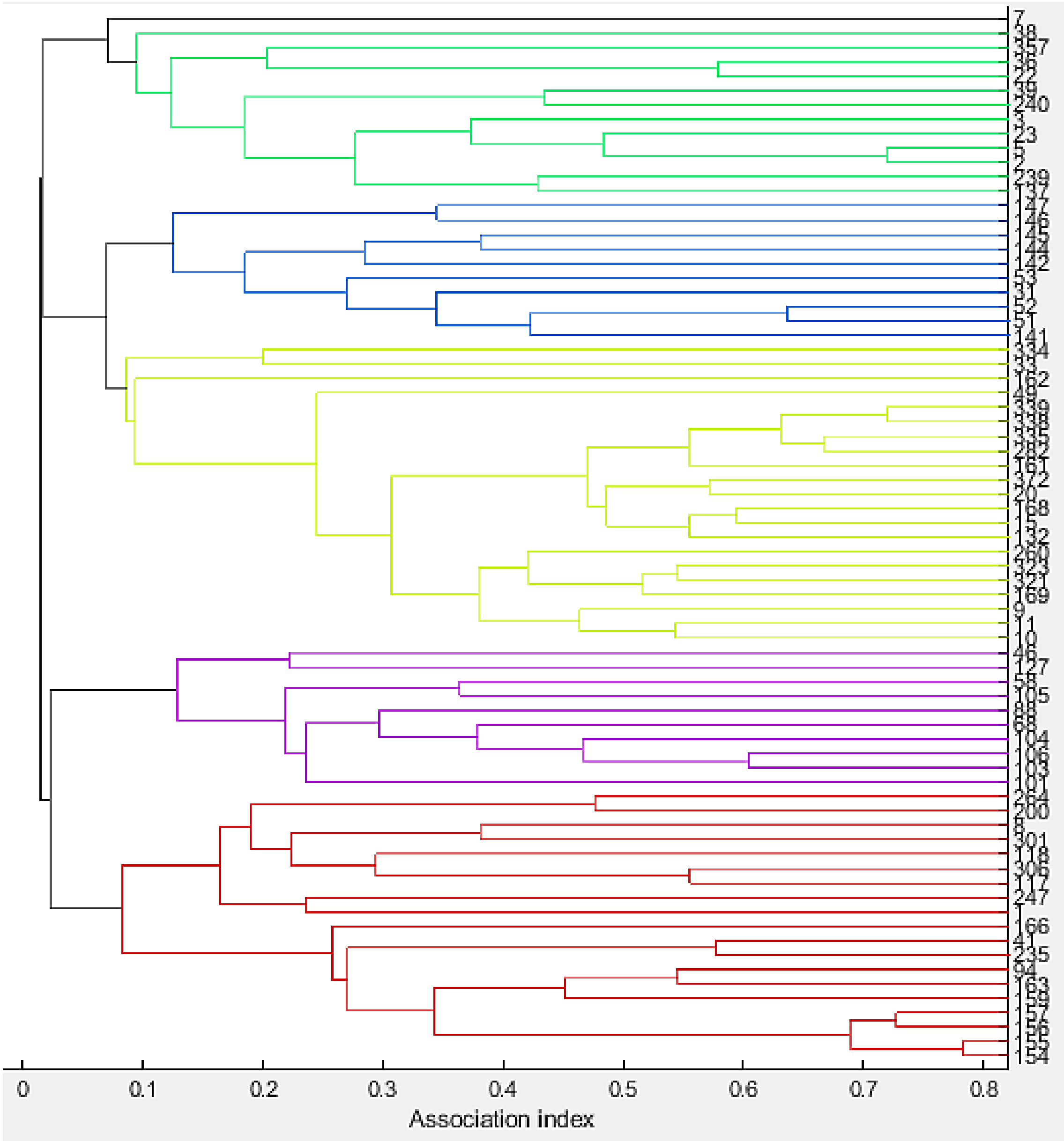

Figure 2.12 Dendrogram of associations between individuals identified at least 10 times in São Miguel from 2008 to 2020. Cluster division was obtained using maximum modularity controlling for gregariousness.

To understand the composition of the potential groups, at least one "key-individual" (resident individual already known and named by Futurismo) (Figure 2.15) and/or the individual most sighted was selected. The green group, with 12 individuals, included one well known resident individual named "Bubblemaker" (TT_002) sighted 100 times in the area, together with the second most sighted individual (66 times), the TT_005, also resident. The most sighted individual of the blue group, within these ten individuals was the TT_145, photographed 29 times. The yellow group, the bigger one, with 21 individuals, TT_011 and TT_010, both residents, stood out with a total of 45 and 42 times sighted, respectively. The purple group, composed of ten individuals, has a key individual named "Max" (TT_046), sighted 20 times. Lastly, in the red group, from the 19 individuals there are two already known residents, "Egípcio" (TT_041), and "Submarine" (TT_235), sighted 36 and 26 times, respectively.

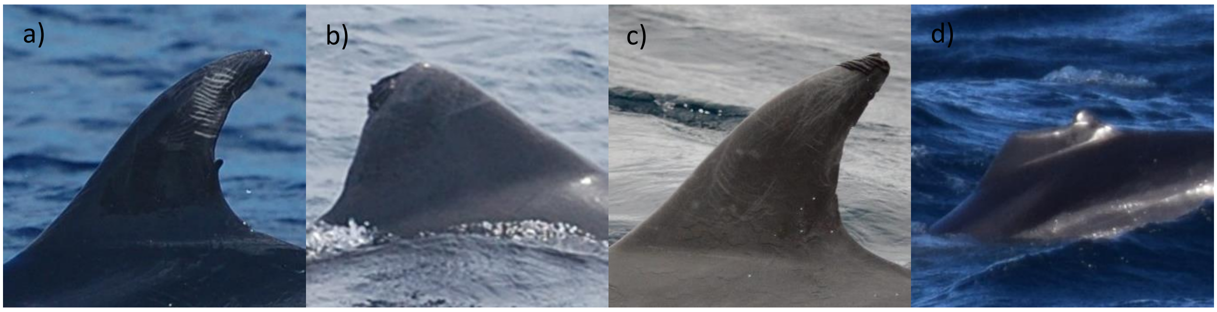

Figure 2.13 Examples of individuals regularly seen in São Miguel and already known by the people working in Futurismo. a) TT_002 "Bubblemaker"; b) TT041 "Egípcio"; c) TT_046 "Max"; and d) TT_235 "Submarine".

The results of permutation tests for long-term preferred/avoided associations showed significant higher S.D. and CV values of the real data over the permuted data ($p< 0.0001$) (Table 2.4). Therefore, the null hypothesis that individuals associate randomly can be rejected. In general, bottlenose dolphins identified in this study do not associate randomly and have long-term preferred/avoided associations with other individuals.

Table 2.3 Results of the preferred/avoided associations test of the resighted bottlenose dolphins in São Miguel, given by the SOCPROG program. Real values represent observed data and random values represent the generated values from 10,000 permutations.

	Real	***Random***	***P-value***
Mean	0.06571	0.06566	-
SD	0.12374	0.12191	0.0001
CV	1.88317	1.85678	0.0001

2.4.4.2 Temporal stability of associations

The model of temporal patterning off associations that best explain the SLAR data was the “casual acquaintances”, which means that individuals associate for some time, disassociate, and may re-associate (Whitehead, 2015) (Table 2.5; Figure 2.16). There was also considerable support for the “two levels of casual acquaintances” model (ΔQAIC = 2.1) that suggest two levels of acquaintance: a short casual level of association and a longer-term, as described by Whitehead (2008). Both models show that the associations between individuals are stable for approximately 100 days before they begin to dissociate. The level of null association was never reached, confirming the existence of some stable relationships, at least during the study period.

Table 2.4 Model fitting results to the standardized lagged association rate (SLAR) for bottlenose dolphins in São Miguel between 2008 and 2020 given by SOCPROG program. Bold value indicates the best fitted model for SLAR values.

Explanation	***Model type***	***QAIC***	***Δ QAIC***
Preferred companions	a1	35689.3	427,7
Casual acquaintances	**a2 * exp (-a1 * td)**	**35261.6**	**-**
Pref. comps. + casual acqs	a2 + a3 * exp (-a1 * td)	35690.7	429,1
Two levels of casual acqs	a3 * exp (-a1*td) + a4*exp (-a2 * td)	35263.7	2,1

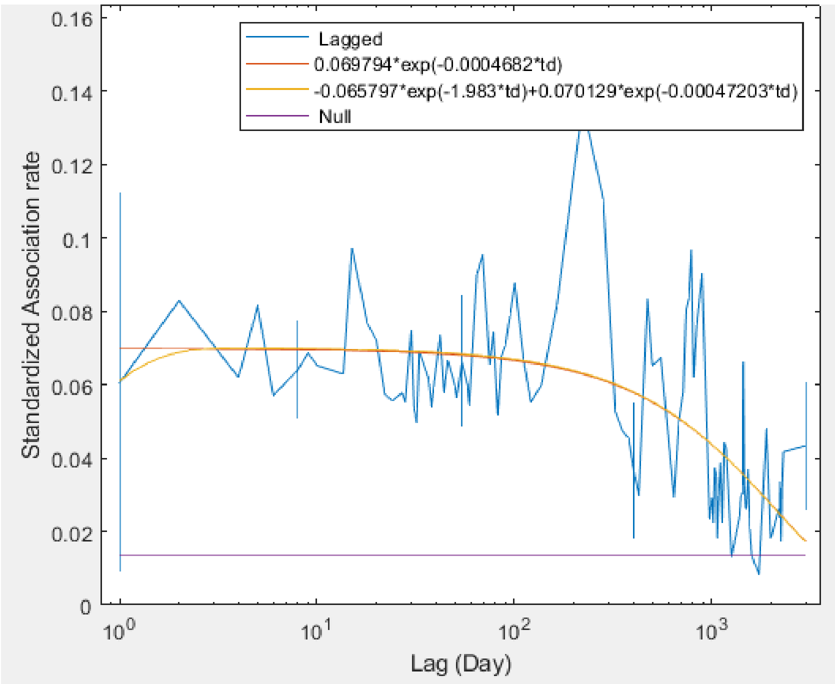

Figure 2.14 Standardized Lagged Association rate (SLAR) of bottlenose dolphins in São Miguel during 2008 and 2020. The best fitted model was the Casual Acquaintances model that is represented in red. Two levels of casual acqs model showed substantial support for the model and is also represented in the graph in orange. Null association rate is represented in purple. Jack-knife techniques were used to calculate 95% confidence interval error bars.

2.5 Discussion

2.5.1 Population trend

The discovery curve for bottlenose dolphins in São Miguel revealed an open population with a continuum recruitment of new individuals throughout the study period. These new individuals may represent births, immigration into the population, mark changes or captures in subsequent years of individuals who had been previously unphotographed or unidentified due to the absence of distinctive marks (Pereira, 2012; Gowans *et al*., 2000). The continuous increase in the number of individuals and the high percentage of individuals sighted just once supports the idea that the most individuals photographed are only transients to the area.

The curve does not seem to stabilize, at least in the study period, and thus more new individuals are expected to be identified in the area in the following years. As seen by the curve and with the number of photos analysed, in the first six years (2008-2013), the effort made for photo identification was low, due to the lack of emphasis on photo-identification and the absence of suitable equipment for collecting photos. In 2014, the year with the highest effort registered for photo identification, was also the highest number of images analysed (11592) and consequently more identifications (Catalão, 2021). Nevertheless, from 2015 to 2020, it can be noted that the number of photographs taken is increasing, and their quality is improving. This reveals a greater interest in studying cetacean species, greater knowledge of the biologists on board, better cameras, and especially since 2018, Futurismo has protocols that standardise data collection and storage so that they are available when needed. Notwithstanding, the effort to collect viable photos of every individual in each group must be improved to increase the confidence of the results.

2.5.2 Site fidelity and residence patterns

Although the population of bottlenose dolphins in São Miguel appeared to be larger than the individuals identified, and with most of the individuals migrants and transients, some individuals seem to use the area regularly and are already known by the people working in Futurismo (for example, TT_002, known as "Bubblemaker"; TT041 "Egípcio"; TT_046 "Max" and TT_235 "Submarine"). Catalão (2021) identified fifty-two bottlenose dolphins as residents in São Miguel, 182 as migrants, 81 as transients, and 200 as non-residents. This fidelity pattern, a mixture of residents, migrants, transients and non-resident animals in São Miguel, was also found previously for Azores islands by Silva (2007). It seems to be a similar feature to what is found among other populations of bottlenose dolphins (for example, for Madeira island by Dinis *et al.*, 2018; in Argentine coast by Würsig & Würsig, 1977; in the western coast of Florida by Wells *et al*. 1987 and Shane, 2004; in São Tomé and Príncipe by Pereira, 2012; and the coastal Setubal Bay, Portugal mainland, by Martinho, 2012).

Bottlenose dolphin populations exhibit different patterns of residency around the world. Some display large movements and low site fidelity (Defran & Weller, 1999;

Shane, 2004; Dinis, 2015), while others show short-range patterns and strong site fidelity (Passadore *et al*., 2018; Wells, 2014). Low-level site fidelity is typical of individuals living in oceanic zones or areas characterized by low productivity and unpredictable prey availability. In contrast, bottlenose dolphins, often higher-level site fidelity in protected coastal areas, where prey biomass is more recurrent and foreseeable in distribution (Passadore *et al*., 2018; Pace *et al*, 2021).

In comparison to open waters, the higher productivity of the seas of the Azores seems to be why several cetacean species are observed in the area (Silva *et al.*, 2008; González García *et al*., 2018). Therefore, dolphins that appear in adjacent ocean areas may feel attracted to use the Azores as a temporary feeding ground. However, the fact that it is only temporary indicates that there might not be enough food resources to sustain permanently a larger population (Silva *et al*., 2008). In the neighbouring archipelago of the Madeira, a similar situation appears to occur, as the population of bottlenose dolphins is also open with different degrees of site fidelity, and only a small number of dolphins showed high fidelity to the area (Dinis *et al*., 2016; Dinis *et al*., 2021). The values of LIR obtained in this study suggested that some bottlenose dolphins might spend between 10 to 100 days inside the study area before leaving. This is in concordance with the previous results found by Catalão (2021) that there is a decrease in the number of sightings during winter and autumn in São Miguel, explained by the seasonal changes in the conditions might not be favourable for all individuals. However, a complete data series would be valuable to provide more confident results about residency patterns and site fidelity of the individuals sighted around São Miguel.

2.5.3 Social Structure

The social analyses have shown that, associations between bottlenose dolphins identified in São Miguel are very dynamic and social bonds can be very flexible. This result is consistent with other studies, as bottlenose dolphins' societies are characterized by a fission–fusion dynamic, with group membership varying within a very short time frame, leading to low association coefficients between pairs of individuals and consequently to a low average coefficient of association for the population (Connor *et al*., 2000; Augusto *et al*. 2011; Louis *et al*., 2015; Pereira, 2012; Dinis, 2015). High levels of association seem to be a characteristic feature of bottlenose dolphins' populations that occur in more enclosed environments, such as estuaries, bays and fjords, rather than in open oceanic habitat, as the population in this study. These high levels of association might be, in partly, due to the topographic features that may increase the difficulty for neighbouring communities to meet (Lusseau *et al*. 2003; Merriman, 2007).

Despite the low association index (A.I.) found in this study, there were some individuals that revealed a higher A.I. than the overall mean, suggesting long-term relationships. Some stable associations among pairs or even trios of individuals have been documented in various populations of bottlenose dolphins (Wells *et al*., 1987; Connor *et al.*, 1992; Wells, 2014). These associations are usually alliance between males and/or mother-calf bonds that can be extended beyond the nursing period (as calves are known to stay with their mother for 3–6 years after birth) (Shane *et al*., 1986; Greiller *et al*. 2003; Wells, 2014 Louis *et al*., 2015). Nevertheless, there appears to be considerable variability among populations in the types and degree of such stable associations (Connor *et al*., 2000).

The permutation test results led to rejection of the null hypothesis, suggesting that the bottlenose dolphins in São Miguel do not associate randomly within the population. Other studies also described long-term preferred associations (for example, Blasi and Boitani, 2014; Wells *et al.*, 1987; Connor *et al*. 1992; Lusseau *et al*. 2003; Merriman, 2007). Again, these long-term associations may indicate male-male bonds, or it was also documented that females in similar reproductive states, particularly during the first year of post-parturition, had higher association coefficients than with other females (Möller & Harcourt, 2008). These female associations may be related to predation risks, feeding competition costs, or reducing infanticide risks (Almeida, 2017). Sex seems to be a vital feature driving these kinds of associations (Shane *et al*., 1986; Connor *et al*. 2000; Dinis, 2015), and so it would be valuable and interesting to examine if different groups of the population have different patterns of interactions, like sex-related relationships. However, due to the lack of dimorphism in adult bottlenose dolphins and because the ventral genitalia and mammary slits are usually hidden from researchers, sex determination in the field is complex and can be considered a limitation to the study.

Similarly, the temporal analysis also indicated that in the study period, and within the analysed individuals, there was no presence of random associations over time. The decline of the SLAR curve after approximately 100 days suggests disassociation over that time period which can be explained by demographic events such as mortality or emigration (Whitehead, 2008). Nevertheless, it should be taken into consideration that this is the general trend, and it is not always possible to forecast the association pattern of all individuals.

Bottlenose dolphins' social structure vary between locations, and even individuals from the same community may behave differently among them (Gowans, 2019; Genov *et al*., 2019). Our dendrogram revealed that resident bottlenose dolphins were seen with migrants, i.e., they are connected with dolphins with larger-scale movements. Individuals exhibiting extended home ranges can have a fundamental role, contributing to an increased genetic variability in oceanic dolphin communities, which otherwise would be genetically isolated (Silva *et al*., 2008; Louis *et al*., 2014; Dinis *et al*., 2012). Nonetheless, more data and photographic evidence is needed to confirm this hypothesis, as the time between resights of migrants and/or transients does not necessarily mean that the individuals were not present in the area during that period, but that they were not identified within the available photographs or encountered during whale-watching tours.

Previous analysis of mitochondrial DNA and microsatellite DNA markers done with the bottlenose dolphin identified in the Azores concluded there is a single and open population composed of several geographic communities (Silva *et al*., 2008). These communities maintain social interactions with neighbouring communities and groups from within and outside the archipelago (Silva *et al*., 2008; Quérouil *et al*., 2009; Dinis *et al*., 2021). These interactions are facilitated by some individuals and/or groups' extensive ranging behaviour in response to the lower density and patchy distribution of food resources (Silva *et al*., 2008; Pereira, 2012). As long-lived animals, bottlenose dolphins benefit from these associations to transmit knowledge and develop social skills, which are essential to successfully perform in their environment (Lusseau *et al*., 2003; Rendell & Whitehead, 2001; Pereira, 2012).

It is necessary to emphasize that there may be negative biases in the correlation coefficients estimates reported here, mainly due to the inherent difficulties of the methodology applied (Dinis, 2015). These difficulties stem from opportunistic data where it is not always possible to photograph all the groups encountered or even all the individuals in each group. Furthermore, as the study was limited to only well-marked individuals, potential associations between unmarked individuals, like calves and juveniles, and the rest of the population are not being accounted for. Nonetheless, opportunistic data generally provides long-term datasets with a regular spatial cover that would otherwise be inaccessible (Evans & Hammond, 2004; González García et al., 2018).

2.6 Final considerations

The photo identification study presented here was based on opportunistic data from whale watching trips in São Miguel. Potential biases and limitations of this kind of data have been extensively argued, however, it was also proven their great value in cetacean research that supports its use. With the increased interest in understanding the occurrence, distribution and behaviour patterns of cetacean species present in Azores waters, the collection of data from platforms of opportunity, such as whale watching operations, is nowadays a common task in most companies in the region and, as it is now generally recorded by experienced biologists. The quality of the data collected has also increased, leading to a more consistent and accurate species identification, and resulted in a number of studies in the Azores in the past decade (for example: Olio, 2017; De Soto *et al*., 2017; González García *et al*., 2018; González García, 2019, Negulescu, 2020; Van der Linde & Eriksson, 2020; and Ernesto, 2021). The growth of these companies led to an increase in the availability of opportunistic data, as the data collection during whale watching trips does not interfere with the tours but can also increase its value (González García, 2019). However, the limitations are inherent to these data sources, as the major goal of touristic activities is satisfying the tourist. First of all, lookouts search for all the cetacean species rather than just the target species; and as they guide the boats directly to the animals, there is a lack of real effort, as search is done both from land and from ship. However, the time spent consistently at sea each year or month, although not an absolute effort measurement, gave an approximation of the different effort between years, seasons or months (González García, 2019). Then, there is a general preference for emblematic species (for example baleen whales, sperm whales, orcas) over resident dolphins. Finally, shorter distances are usually preferred over longer ones as there is a limited time per trip. Despite the limitations, there are also advantages such as: (1) opportunistic surveys are a comparatively inexpensive way to conduct surveys on cetaceans; (2) can cover regions where little information is known, i.e., can provide data that is otherwise inaccessible; and (3) can provide spatial and temporal cover regularly (Hupman *et al.*, 2015; González García, 2019).

Bottlenose dolphins are key components of the inshore and coastal marine biodiversity worldwide (Pace *et al*., 2021). With their widespread distribution and high public profile, they are well suited to environmental sentinels for coastal habitats. They are considered an indicator for Species Status Assessment mentioned in the Marine Strategy Framework Directive (MSFD) (Palialexis *et al*., 2019). Long-term studies are able to monitor the trend in population dynamics and health, providing an important indicator of the overall health of their habitat and the ecosystem it supports (Connor *et al*., 2000). They can provide an opportunity to extrapolate knowledge and understanding to other marine mammal species and/or other areas of the world (Barratclough *et al*., 2019). Coastal bottlenose dolphins are being monitored along the Atlantic coast of Europe from Scotland in the north to Spain in the south, where the majority of populations for which there are sufficient data to estimate trends show little change, except the Sado Estuary population in Portugal, which continues to decline (OSPAR, 2018c). Changes in abundance and distribution provide essential information on the state of the population, and it is indicator of environmental health, such as food web integrity and pollutant load. Therefore, understanding the population abundance and its tendencies, site fidelity and group composition are necessary to assess baselines conditions and develop management strategies. This study offers a significant contribution, but further research is needed to repeatedly photograph all animals in the study area, assess the seasonality of the transient individuals, and have more support for the year-round residents. Besides that, more sightings would provide more individual information in order to make more reliable estimations of the population over time.

2.7 Conclusions

- Photo identification revealed more 184 new individuals present around São Miguel, making 689 individuals identified between 2008 and 2020.

- Bottlenose dolphins identified in São Miguel belong to a larger or an open population, where individuals stay in the area only for a few days before leaving.

- The social structure analysis of the identified individuals revealed five potential groups within individuals sighted at least ten times, and the permutation tests led to the rejection of the null hypothesis, suggesting that the bottlenose dolphins in São Miguel do not associate randomly within the population, having preferred and/or avoided companions.

- SLAR values showed that the associations between individuals are stable for a period of approximately 100 days before they begin to dissociate.

- Opportunistic platforms, such as whale watching companies, can provide long-term datasets with a regular spatial cover valuable for scientific research on cetacean's populations.

2.8 References

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