Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author. SOCIAL INTERACTIONS IN NEW ZEALAND COMMON BOTTLENOSE DOLPHINS (TURSIOPS TRUNCATUS) ASSOCIATION DYNAMICS, SKIN DISEASES AND AGGRESSIVE INJURIES, AND VARIATIONS IN VOCAL SIGNALS

JESSICA PATIÑO-PÉREZ PhD thesis 2021

Social interactions in New Zealand common bottlenose dolphins (*Tursiops truncatus*); association dynamics, skin diseases and aggressive injuries, and variations in vocal signals.

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Thesis abstract

Social behaviour is described as a series of interactions between two or more members of the same or different species that usually benefits all the individuals involved. Individuals form strong bonds because of these interactions, which might be cooperative, hostile, mutualistic, or altruistic. Depending on the nature of the relationships and participants, social behaviour can lead to the establishment of distinct social systems. Although it is evident that social behaviour does not have to be selfless, the question of why and how social behaviours occur in animals is still being debated. According to Krause and Ruxton (2002), sociality emerges when the advantages of long-term social contact outweigh the drawbacks of such close relationships with conspecifics. Among the advantages of living in a group are increased oopportunities for food and mating, as well as protection from predators. This sociality, on the other hand, might have negative implications, such as increased rivalry for mates and resources or increased disease transmission risks. I investigated multiple aspects of the social lives of common bottlenose dolphins Tursiops truncatus (hereafter bottlenose dolphins) in New Zealand. Historically, the north-eastern North Island bottlenose dolphin population has been intensively studied at the Bay of Islands since it was the only place where dolphins are constantly sighted. A rapid decline in this population and high calf mortality raised concern about the viability of this population. The key objective of my research was to understand how different social aspects influence the population of bottlenose dolphins at Great Barrier Island (GBI), New Zealand, an area that was recently described as a 'social hub' for the species. Althouh, throughout my thesis I talk about the population of dolphins present in GBI, it is important to keep in mind that this is one part of the entire North Island population.

In the first part of my thesis, I describe the social structure of bottlenose dolphins in GBI using historical data from the Bay of Islands (BOI) and GBI, in addition to my own data. I analysed their social structure by examining: (1) preferred/avoided companions, (2) strength and distribution of associations, (3) temporal and spatial patterning of associations, and (4) residence times. The analysis of BOI-GBI showed two distinct social communities, each of which is made up primarily of members photographed only in their respective areas. Only a few individuals were identified in both areas. For GBI, two datasets were analysed: 2011-2013 and 2015-2019. During both time

periods, the population exhibited low levels of association, characteristic of fission-fusion societies like bottlenose dolphins, but the populations also showed some structure, with dolphins forming long-lasting bonds with some individual and avoiding others. Moreover, during 2015-2019, two social communities were identified in the population, exhibiting different ranging patterns and patterns of association within communities. The temporal analysis showed that during 2011-2013, the population exhibited a combination of stable associations among individuals and other individuals that associate, disassociate, and may reassociate again over extended periods of time. During 2015-2019, dolphins associate for short periods of times before breaking up, happening at two different times. Analysis of residency times during 2011-2013, showed that the models including emigration + reimmigration best described the population, while during 2015-2019, the best models also included emigration/mortality.

Bottlenose dolphins associate in groups that frequently change in size and composition, characteristic of fission-fusion societies. Skin lesions and tooth rakes can be used to assess natural and anthropogenic pressures within a population, which is useful information for better understanding population dynamics. In addition, tooth rake marks are a measure of the level of social contact within a population and are usually the outcome of inter- and intra-specific interactions. Gregariousness is a major component in disease transmission and increases the likelihood of aggressive confrontations. When it comes to diseases, animals with a high incidence of interactions with others will increase the chances to spread diseases, putting their populations at risk. In this thesis, I described for the first time the prevalence of skin lesions and tooth rakes for the north-eastern population of bottlenose dolphins. In addition, I described the skin lesions found in, and determined the location of, the skin lesions and tooth rakes on dolphins' bodies. I also proposed a protocol to assess skin lesions and what are the implications for future studies. Finally, I tested if there was an association between skin lesions and tooth rakes, and the strength of the dolphins in their social network. I wanted to know if the presence or absence of tooth rakes was defined by the strength in their social network and if dolphins with a higher coverage score of tooth rakes had a higher strength in their social network. In addition, I examined if tooth rake scores were different based on the presence and absence of skin lesions.

From the literature, I found 19 skin lesions with distinct and non-overlapping definitions. These lesions were the foundation of the protocol that I used to assess lesion presence in my population. Eight types of skin lesions were present in bottlenose dolphins at Great Barrier Island, with different prevalence in the population and varying distribution across different parts of the dolphin body. Pale lesions had the highest prevalence with 84.4% of the dolphins having this lesion and were found across four body parts, but mainly in the dorsal fin. Similarly, black lesions, whitefringe spots, nodules, and dark-fringe spot were found in four body parts but their prevalence in the population were lower (33.1%, 17.5%, 11.7%, and 15.6%, respectively). Finally, spotted lesions (10.4%), white fin fringe (5.84%), and tattoo-like disease (4.54%) had the lowest prevalence and were found in three, two, and one body region(s), respectively. Tooth rakes also had a high prevalence in the population (94%), and they were found mostly on the dorsal fin (100%, n = 150), followed by mid-flank (90.2%, n = 139), and anterior section (88.3%, n = 136). The mean coverage score did not change significantly over time (images were compared up to 20 months apart). From the 150 dolphins included in the tooth rake analysis, individuals sighted four or more times were included in the analysis of tooth rakes and strength of associations, giving a sample size of 50 dolphins. I found that the strength of the individual (i.e., it is the individual's gregariousness) in the social network does not affect the tooth rakes an individual has and having tooth rakes is not dependent on the strength of the associations. In addition, coverage score (a value obtained dividing the presence of skin lesions in 12 body parts by their visibility) did not change with the presence of skin lesions. In this chapter, I emphasised the need to determine the overall health of cetaceans in the North Island, as well as the need for more precise and systematic evaluations of the skin lesions of this population and other cetaceans in the region.

Cetaceans are highly vocals animal that depend on sound to communicate, navigate, and find food. Most dolphins can produce three different types of sound, from which whistles have been the most studied due to this type of vocalisation being within the human hearing range and more easily visualised in spectrograms for analysis. Whistles are narrowband, frequency modulated sounds with strong harmonic structure and are used in social interactions. Geographic variation in whistle characteristics has been reported in many populations of bottlenose dolphins around the world and the causes of this variation are diverse. For the first time in New Zealand, I have compared the variation in whistle characteristics of two isolated populations of bottlenose dolphins, GBI and Fiordland, using seven time-frequency variables. In addition, I compared the parameters between these isolated populations using Random Forests analysis (RF) and assessed the influence of location, group size, and presence of immatures on these characteristics. Finally, I compared the whistle characteristics of bottlenose dolphin populations from around the world with New Zealand populations using a hierarchical cluster analysis. Whistle characteristics of both populations were similar to other populations around the world, surprisingly, my populations were similar to other populations from the northern rather than the southern hemisphere regions. A comparison of whistle parameters between GBI and Fiordland, showed that the Fiordland population had longer whistles and more inflection points than whistles from the GBI population. Whistles from these two populations were distinct enough to be correctly allocated to one population-based on acoustic measures alone with a 90% of accuracy. The most important variables for classification were whistle type contour, duration, and end frequency. I obtained two principal components from the NIPALS PCA. The first principal component (PC1) explained 55.6% and the second component (PC2) explained 44.4% of the variance. Linear Mixed Models on PC1 and PC2 were used to assess whether whistles acoustic parameters were influenced by location, group size, and presence of immatures. I found that PC1 was not different between areas or with the presence of immatures. However, minimum frequency and duration differed between the two populations (location).

Overall, my research has produced significant new knowledge on the social structure, prevalence of skin lesions and tooth rakes, and geographic variation in vocalisations of bottlenose dolphins. My research provides better understanding of the high degree of social and acoustic plasticity of bottlenose dolphins by applying state-of-the-art approaches such as social network and random forests analyses to multiple temporally and spatially diverse datasets. In addition, I developed a useful tool for non-invasive categorisation of infectious skin diseases that can be used by researchers and conservation practitioners worldwide to assess the health of individuals and populations.

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Authors' Contributions

Chapter 2. The social structure of bottlenose dolphins at Great Barrier Island.

Jessica Patiño-Pérez: Study conception and design, data collection, analysis, and interpretation of results, and writing the thesis.

Professor Dianne H. Brunton: Study design and supervision.

Dr. Delphine Chabanne: Analysis and interpretation of results.

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Chapter 3. Prevalence of skin lesions and tooth rakes in an endangered population of common bottlenose dolphins in New Zealand.

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Chapter 4. Geographic variation of whistles in New Zealand's bottlenose dolphins.

Jessica Patiño-Pérez: Study conception and design, data collection, analysis, and interpretation of results, and writing the thesis.

Professor Dianne H. Brunton: Study design and supervision.

Dr. Heshani Edirisinghe: Statistical analysis and interpretation of results.

Dr. Marta Guerra: Data contribution. Dr. Guerra provided the recordings from Fiordland used for comparison between populations.

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INTRODUCTION



1. Introduction

1.1. Social structure

Social behaviour, also referred to as sociality, can be defined as a series of interactions that occur between two or more individuals from the same or different species that usually provides benefits for all participating individuals (Jasso del Toro & Nekaris, 2019). These interactions can be cooperative, aggressive, mutualistic, or altruistic, leading to strong relationships among individuals. Social behaviour can lead to the formation of various social systems based on the nature of the relationships and participants (Rubenstein & Rubenstein, 2013). Why and how social behaviours exist in animals is still a matter of extensive discussion, but it has been clear that for behaviour to be social, it does not need to be selfless (van Coeverden, 2017). According to Krause and Ruxton (2002), sociality evolves when the benefits of sustained social interactions are greater than the costs of these close associations with conspecifics. Some of the benefits of group living include enhanced opportunities to access food and mating and defence from predators (Majolo & Huang, 2018). However, sociality can have negative consequences such as increased competition for mates and resources or higher chances of disease transmission (Silk, 2007). In long-lived and highly social species, it has been shown that the quantity and the quality of the social relationships have direct consequences on fitness (Smith et al., 2016). For example, social integration between unrelated females increases both foal birth rates and survival in feral horses Equus caballus demonstrating that social integration has strong direct fitness consequences between nonrelatives (Cameron et al., 2009). In bottlenose dolphins, calving success has been shown to depend on both genetic inheritance and social bonds, and the interactions of these factors influence female fitness (Frère et al., 2010).

Social structure has been defined in several ways and from both ethological and behavioural ecological perspectives (Whitehead, 2008). One of the definitions more commonly used for social structure, and the one followed in this thesis, was proposed by Hinde (1976). From the ethological point of view, Hinde (1976) proposed a three-level framework for the analysis of animal societies (Figure 1). At the fundamental level, social structure is determined by the quality and nature of the interactions among individuals. These interactions occur when the presence or behaviour of

one individual affect another. At the second level are the relationships between individuals, and this comprises the content, quality, and patterning of such interactions. Lastly, the nature, quality, and patterns of relationships between individuals defined the social structure of a population (Whitehead, 2008). This bottom-up approach allows the study of the social structure of a population starting at the dyadic interactions up to a larger level of animal sociality (Whitehead, 2008).



Figure 1.1. Hinde's framework for the analysis of animal societies adapted from Whitehead, 2008.

Social relationships are non-random and are motivated for different behaviours, phenotype, and/or ecological factors (Krause & Ruxton, 2002) and have been documented in a wide range of taxa from guppies *Poecilia reticulata* (Croft et al., 2004) to Australian humpback dolphins *Sousa sahulensis* (Hunt et al., 2019). Consequently, the interaction between individuals in a particular social structure will form distinctive patterns of social associations (Hinde, 1976). Social structure can affect or be affected by gene flow (Zonana et al., 2021), fitness (Dobson et al., 2012; Kusch & Lane, 2021), habitat use (Pirotta et al., 2020), information and disease transmission (Hamede et al., 2009; Lusseau & Newman, 2004; Silk et al., 2017; Wey et al., 2008), population density

(Watchorn & Whisson, 2020), and personality traits (Aplin et al., 2013), factors that are relevant to the conservation and management of animal populations (Watchorn and Whisson, 2020). Understanding the social structure of a population can reveal the role of individuals in a group. For example, Lusseau and Newman (2004) studied a population of bottlenose dolphin Tursiops truncatus where some dolphins act as 'social brokers' between communities; these brokers play an important role in maintaining the cohesion of the population. Also, social structures can help to identify and define subgroups in animal populations. Subgroups are biologically significant as interactions among individuals can be predicted under different scenarios. Wolf and collaborators (2018) found that giraffes Giraffa camelopardalis giraffa form subgroups (also known as clusters or social communities) and that the number of clusters changed between seasons, with more subgroups forming during winter (Wolf et al., 2018). Different factors can promote the presence of subgroups in a population such as predation risk (Heithaus & Dill, 2002), sex- and age-related homophily (Lusseau & Newman, 2004), association patterns among individuals (Lusseau et al., 2006), natal philopatry (Rako-Gospić et al., 2017), genetic relatedness (Connor et al., 1998), shared knowledge (Mann et al., 2012), behavioural strategies (Daura-Jorge et al., 2012; Díaz López & Bernal Shirai, 2008), and human activities (Ansmann et al., 2012). Deeper knowledge about why animals prefer to interact with specific members in the group will allow researchers better understanding of the evolution of social behaviour. Moreover, the understanding of the drivers of social structure can provide insights into how populations respond to anthropogenic, social, and environmental factors, especially if the subgroups are spatially segregated (Krause & Ruxton, 2002).

1.2. Social network analysis

In the last two decades, social network analysis has become a useful and powerful tool to quantify, compare and understand the social structure of many populations (e.g., Croft et al., 2008; Farine & Whitehead, 2015; Pinter-Wollman et al., 2014). A network can be described as 'any number of individuals (node) interconnected via social ties (edge) between them' (Croft et al., 2008). In a network, connections (ties) can be directed if the interaction has an initiator and a receiver (e.g., A grooming B), or undirected if there is no direction in the interaction. Ties also can be weighted,

indicating the strength or numbers of interactions, or unweighted (binary), if information about the strength is unknown (Wey et al., 2008). A social network analysis approach provides a solid framework to study the social structure of a population, and in turn, this social structure offers important evolutionary and ecological information at different levels of organisation (Krause et al., 2007). For example, at the population level, the structure of a network can affect the speed at which information is transmitted. At the individual level, it can show connections between individuals, and in turn, who interacts with whom and how diseases are transmitted (Krause et al., 2007; Newman, 2002).

With the application of social network methods to behavioural ecology, coupled with the use of mathematical models, more comprehensive information about the social structures of different populations has been documented. A variety of descriptive statistics are now available to refer to structural components of networks and the position of certain individuals in relation to others. Among the most widely used individual-based measures for the network are: degree - the number of immediate neighbours (James et al., 2009); strength - the sum of association indexes of each individual (Barrat et al., 2004); affinity - the strength of the associates an individual has (Whitehead, 2019); clustering coefficient - how well the associates of an individual are themselves associated (Whitehead, 2019); and node betweenness - the number of shortest paths between pairs of individuals (Croft et al., 2008). These statistics provide understanding of the local and global properties of the network (Krause et al., 2009). However, social networks can be used at different levels and have increased in applicability and complexity over the last 10 years. An example of the increasingly sophisticated approaches being taken by many researchers is the analysis of group-derived data to assess the temporal stability (over years) of relationships among individuals through Lagged Association Rates (LAR; Whitehead, 2008). Carter and collaborators (2013) found that female giraffes exhibited long-term relationships spanning six years, but this was not the case for males, and this difference may be explained by sex differences in ranging patterns and reproductive priorities. Similarly, Francesiaz and collaborators (2017) quantified the temporal stability of social bonds in slender-billed gull Larus genei, finding that associations were higher during two consecutive years, but no further evidence of stable association was observed

beyond this time. Similar to *LAR, Lagged Identification Rates* (*LIR*) have been widely used to assess residency time of many species. Chabanne and collaborators (2017) assessed the demographic processes within the four social communities identified in a population of Indo-Pacific bottlenose dolphin *Tursiops aduncus* using *LIR*. Emigration and mortality models best fitted the *LIR* of all four communities. Moreover, differences in residency times and community sizes were also observed, varying from five to 18 years and from 21 to 68 individuals, respectively. Lagged identification rates were used to assess the effect of major injuries on whale shark *Rhincodon typus* in the Maldives. Harvey-Carroll and collaborators (2021) found that sharks with major injuries are more likely to return to the study area, moreover, sharks with major injuries had a lower mean initial residency time than non-injured sharks

Social network analyses have helped to expand the knowledge of the social organisation of many animal populations, particularly, fission-fusion populations (Croft et al., 2004). Studies of social networks have been done for many species of toothed whales, including bottlenose dolphins (Augusto et al., 2012; Baker et al., 2018), Indo-Pacific bottlenose dolphins (Bonneville et al., 2021; Chabanne et al., 2017), Guiana dolphins *Sotalia* guianensis (Beirão-Campos et al., 2016), Indo-Pacific humpback dolphin *Sousa chinensis* (Cagnazzi et al., 2011; Dungan et al., 2012), Commerson's dolphins *Cephalorhynchus commersonii* (Coscarella et al., 2011), orcas *Orcinus orca* (Baird & Whitehead, 2000), sperm whales *Physeter macrocephalus* (Gero et al., 2014; Jaquet & Gendron, 2009), long-finned pilot whales *Globicephala melas* (Augusto et al., 2017), among others. Results of these studies have shown high variation among different populations of the same species. For example, bottlenose dolphins' social structure has been described as both random and non-random fission–fusion societies (Connor & Wells, 2000), some populations have a low level of association among its members (Pleslić et al., 2019; Dinis et al., 2018; Chabanne et al., 2017), as expected for fission-fusion societies, and others show high levels of association e.g., small, and isolated populations (Vermeulen, 2018; Augusto et al., 2012; Lusseau et al., 2003).

Multiple factors can influence dolphin social structure such as life history, food availability, predation risk, dispersal patterns, kin associations, and human activities (reviewed in Gowans et

al., 2007). For example, sex and kinship influence social network cohesion in Indo-Pacific bottlenose dolphins, and kinship have more influence on female than on male social relationships (Wiszniewski et al., 2010). Patterns of associations change among orcas in relation to food availability, with more interconnected networks occurring in years where salmon were more abundant (Foster et al., 2012). Williams and Lusseau (2006), using simulations of historic live captures of orcas, found that their network in the north-eastern Pacific broke into smaller, isolated units, raising concerns about the impact of targeted animals on matrilineal cetaceans. In addition, younger individuals have an influence in the social network of a population. For example, it has been reported that female juvenile orcas in this population play an important role in maintaining the cohesion in their social networks (Williams & Lusseau, 2006), and in social units of female and immature sperm whales in Dominica, calves seem to be important nodes in their networks (Gero et al., 2013).

1.3. Skin lesions and tooth rakes in cetaceans

The bottlenose dolphin is a socially complex species that lives in fission-fusion societies in which individuals associate in groups that often change in size and composition (Connor & Wells, 2000). Natural pressures within a population can be assessed using skin lesions and tooth rakes; information that is important to better understand the dynamics of the populations. Tooth rake marks usually are the result of inter- and intra-specific interactions and are an indicator of the level of social interactions within a population (Marley et al., 2013; Scott et al., 2005). In the case of skin lesions, animals that have high contact rates with others will have more opportunities to spread them, increasing vulnerability among their populations (Sah et al., 2018). In a social network, for example, animals occupying a more central position within the network will have more chances of transmitting information (Evans et al., 2020) or diseases in the population (Godfrey et al., 2009, 2010). Likewise, animals in such as position have more connections with other members of the population, consequently, they will have more opportunities for intra-specific interactions with other animals increasing their chances of contracting diseases and/or acquiring more tooth rakes.

The prevalence of skin lesions can reveal natural pressures or anthropogenic factors that represent a hazard to populations (Bearzi et al., 2009). Skin lesions have been assessed in many social domestic or captive animals such as pigs (Erhard et al., 1997; Tönepöhl et al., 2013; Turner et al., 2006), cattle (Brenner et al., 2009), and Southern sea lion *Otaria flavescens* (Alvarez-Pérez et al., 2010), usually focusing on the welfare of these species. Also, they have been assessed in wild populations of small ruminants (Chanie et al., 2010), lizards (Stöhr et al., 2013), and little brown bats *Myotis lucifugus* (Wibbelt et al., 2013), among other species. Relevant to my study of cetaceans, skin lesions in cetaceans have been described in numerous species and, specifically, in multiple population of bottlenose dolphins around the world (e.g., Félix et al., 2019; Ramos et al., 2018; Titcomb et al., 2020; Toms et al., 2018; Wilson et al., 2000). Due to their preference for coastal habitats, cetaceans are susceptible to anthropogenic pressures that degrade these habitats. It is these degraded habitats that have been shown to be associated with the occurrence of skin lesions in several populations of cetaceans (Rowe et al., 2010; Taylor et al., 2021; Wilson et al., 1997).

Skin lesions can be defined as a change in the gross appearance of the soft tissue (Lane et al., 2008). Several skin lesions in cetaceans have been described in the literature based on the shape, the colour, and the aspect of the lesion (Refer to chapter 3, table 3.1 for details). Although the aetiology of many of these lesions is usually unknown, good definitions based on appearance allow us to monitor the progress of such lesions and potentially prevent outbreaks if appropriate mitigation measures can be introduced. For example, disease transmission models can be implemented to assist wildlife managers in determining where and when to implement policies that reduce anthropogenic disturbances. Preventative measures and monitoring are critical since skin lesions cause stress in dolphins, lowering their immune function and making them more vulnerable to diseases. Skin lesions can have different origins such as virus, fungus, bacteria, helminth parasites and protozoa, with different consequences for cetaceans. Among the viruses are the *Poxviruses* responsible for the occurrence of 'tattoo' skin disease, a disease characterized by irregular, dark grey, black, or yellowish marks with a stippled pattern (Geraci et al., 1979; Van Bressem & Van Waerebeek, 1996). *Poxvirus* related diseases have been found in at least 12 species

of odontocetes and at least in one species of baleen whale (Fury & Reif, 2012; Kiszka et al., 2009; Powell et al., 2018; Van Bressem et al., 2003; Van Bressem et al., 2009). Their emergence has been associated to poor quality water and habitat degradation (Fury & Reif, 2012; Geraci et al., 1979). Other viruses found to be responsible for skin lesions and pathologies are herpesviruses (alpha herpesvirus), these are responsible for systematic infection in bottlenose dolphins (Burdett Hart et al., 2012; Cruz et al., 2014; Sacristán et al., 2019; Smolarek Benson et al., 2006). Caliciviruses produce vesicles that can turn rapidly into ulcers (Smith et al., 1983; Van Bressem et al., 1999b) and papillomaviruses have been associated to a high prevalence of tumours (Bossart et al., 2015; Cruz & Barrera, 2011; Van Bressem et al., 1999a,b). Immuno-compromised animals can be more vulnerable to the appearance of certain skin lesions. For example, several species of *Candida* sp. have been reported in cetaceans, usually present as mucocutaneous creamy plaques common in captive cetaceans and immuno-suppressed individuals (Dunn et al., 1982; Mouton & Both, 2012). Lacazia loboi, a fungus which produces white, elevated, crusty, nodular lesions on the dolphin's body, has been suggested as an opportunistic infection also in immuno-compromised animals (Murdoch et al., 2008; Reif et al., 2008). Finally, some bacteria such as Brucella ceti, Dermatophilus, Erysipelothrix rhusiopathiae, Mycobacterium, and Pseudomonas (Mouton & Both, 2012) tend to be opportunistic attacking immune-suppressed individuals (Van Bressem et al., 2008).

Skin lesions are often associated with external damage to the skin and since tooth rakes are an easy observable and identifiable trait of many cetaceans, these have been assessed in the same way as skin lesions. However, unlike skin lesions, tooth rakes are usually the result of a physical injury of an individual product of a predators, or inter- and intraspecific competition (Crespo-Picazo et al., 2021; Lockyer & Morris, 1990; Samarra et al., 2012). Due to their lack of hair to protect the skin, Odontocetes are more susceptible to cuts and abrasions than other mammals (MacLeod, 1998). These scars can be distinguishable among them thanks to their shape and size. In the case of tooth rakes, these are superficial wounds characterised by parallel lines of depigmentation or broken skin (Lee et al., 2019). The level of intraspecific scarring varies among Odontocetes species. For example, Risso's dolphins *Grampus griseus* usually are severely scarred, and the scars tend to be of a white colour (Mariani et al., 2016), making them very evident along

the body of the dolphins. On the other hand, bottlenose dolphins, have less unpigmented scars that tend to heal within five to 20 months, typically recovering they original skin colour (Lockyer & Morris, 1990).

Tooth rakes in odontocetes have been studied in a wide variety of social contexts such as aggression (Lee et al., 2019; Marley et al., 2013; Scott et al., 2005), to assess the reliability to use them to identify individuals (Mariani et al., 2016), or to determine healing times (Lee et al., 2019; Lockyer & Morris, 1990), among others. Comprehensive studies of scarring patterns in cetaceans can provide important information about their social behaviour, feeding, and swimming patterns (Lockyer and Morris, 1985). Aggressive encounters between conspecifics have been proposed as an important source of tooth rakes in dolphins (Lockyer & Morris, 1985). Indeed, MacLeod (1998) suggested that the accumulation of white scarring in some species can act as a 'quality' indicator (dominance and/or fitness) of males to others during aggressive social interactions. Aggression can occur in different context such as part of competition for resources or mates, dominance, or female access for copulation (Díaz López et al., 2018; Parsons et al., 2003; Scott et al., 2005). Tooth rake prevalence can differ between sexes, in several populations males usually have higher prevalence than females; this difference has even been used to determine the sex in certain species such as Cuvier's beaked whales Ziphius cavirostris (Coomber et al., 2016), bottlenose dolphins (Rowe & Dawson, 2009) and Indo-Pacific humpback dolphins (Wright et al., 2017). Rates of aggression also differ between females with different reproductive status. Scott and collaborators (2005) found that cycling females have a higher occurrence of new tooth rakes than non-cycling females (Scott et al., 2005).

1.4. Acoustic communication in social animals and geographic variation in acoustic signals

Underwater acoustic signals evolved to be the primary mode of information transmission for fully aquatic mammals and a predominant mode of communication for amphibious marine mammals due to the ease with which sound travels in water and the large area over which sound can be transmitted, as opposed to air (Dudzinski et al., 2009). Marine mammals often have complex social

lives and communication systems, and research has demonstrated that, for example, whistle complexity and social status are linked, implying that complex tonal sounds play a significant role in social communication (May-Collado et al., 2007a). The social system in odontocetes ranges from solitary (e.g., pink river dolphin *Inia geoffrensis*) to highly social (e.g., bottlenose dolphins or orcas). Odontocetes are highly vocal animals and use sound for communication, navigation, and to find food (Clark & Clark, 1980; King & Janik, 2015). Social groups can develop locally distinct components to their acoustic signals that, with isolation can result in geographic variation in acoustic 'repertories'. This geographic variation in acoustic signals has been reported in a wide range of species such as bottlenose dolphins (Boisseau, 2005; Hawkins, 2010; La Manna et al., 2017, 2020; May-Collado & Wartzok, 2008; Morisaka et al., 2005b), common dolphins Delphinus delphis (Ansmann et al., 2007), spinner dolphins Stenella longirostris (Bazúa-Durán & Au, 2004; Camargo et al., 2006); striped dolphin S. coeruleoalba (Azzolin et al., 2013), and Guiana dolphin (Azevedo & Van Sluys, 2005; Rossi-Santos & Podos, 2006), among others. In many animals, signal variation has been attributed to diverse factors such as environmental, genetic, or cultural differences (Janik & Slater, 2000). For example, in anurans, divergence in call parameters that affect call transmission through the environment might be caused by differences in the physical structure of particular habitats (Annibale et al., 2020). Genetic factors, for example, can directly affect the morphology of individuals causing variation in the acoustic signals. In cetaceans an inverse relationship has been shown between body size and frequency, where larger animals tend to have lower frequency sounds (May-Collado et al., 2007b). Lastly, acoustic disparities across divergent populations would result from the random drift in cultural evolution caused by the accumulation of copying errors in vocal learning (Janik, 2009; Xie et al., 2017). These variations can have a substantial impact on an individual's ability to recognize a conspecific having consequences for mating, reproductive isolation, and speciation (Slabbekoorn & Smith, 2002; Wilkins et al., 2013). These consequences have been widely explored in songbirds where it has been observed that geographic variation substantially affects breeding behaviour, particularly mate attraction and intra-sexual competition (Searcy et al., 2002).

Several hypotheses have been proposed to explain geographic variation in acoustic signals. One of them is the Acoustic Adaptation Hypothesis (AAH). This hypothesis states that animal acoustic signals are adapted to their environment to minimise degradation and maximise signal transmission and long-range communication (Morton, 1975). This hypothesis has been supported by evidence from several species of insects such as gomphocerine grasshopper *Chorthippus biguttulus* (Lang, 2000), and bladder grasshopper *Bullacris membracioides* (Van Staaden & Römer, 1997); birds such as Eurasian wren *Troglodytes troglodytes* (Holland et al., 1998); great tits *Parus major* (Blumenrath & Dabelsteen, 2004); dark-eyed junco *Junco hyemalis* (Slabbekoorn et al., 2007); also in frogs such as American bullfrog *Lithobates catesbeianus* (Boatright-Horowitz et al., 1999); and some species of primates such as Guizhou snub-nosed monkey *Rhinopithecus brelichi* (Riondato et al., 2021). An alternative hypothesis is the social complexity hypothesis that states that with increasingly complex social structure it is necessary to increase communication complexity (Freeberg et al., 2012). This has been seen in group living species such as marmots where it has shown that social complexity is responsible for the evolution of complex alarm communication (Blumstein, 2003).

1.5. Acoustic communication and geographic variation in acoustic signals in cetaceans

Cetaceans can produce both low and high frequency sound and the mechanisms related to sound production in these animals are, nowadays, well understood (Wei, 2021). In toothed whales, the sound is produced through the nasal air sacs located below the blowhole. This structure is responsible, at least, for producing two of three sounds made by most of the toothed whales: whistles and echolocation clicks. Toothed whales are capable of producing sounds classified into three structural categories: clicks or pulsed signals, burst-pulsed sounds, and whistles or tonal signals (Janik, 2009). Clicks are broadband, short sounds with frequencies between 10 and 200 kHz (ultrasonic range) used commonly for echolocation but also are used for communication (Janik, 2009). Click structure can vary in duration, waveform type, and frequency between different groups of toothed whales. Burst-pulsed sounds are broadband pulses consisting mainly in click trains, with most of their energy focused on the low frequencies (Janik, 2009). Sounds such

as the denominated bray calls, moans or rasps are in this category (Janik, 2009). It is believed that burst-pulsed sounds are used for general communication. Whistles are narrowband frequency modulated sounds with a harmonic structure (although some clicks are quite narrowband, e.g., from porpoises and *Cephalorhynchus* dolphins). Whistles can have frequencies between 3 and > 30 kHz (Gridley et al., 2012; Hiley et al., 2017), and a duration between 100 ms and 4s (Buckstaff, 2004). Almost all toothed whales can produce whistles except for the dolphin in the genera *Cephalorhynchus, Kogia, Neophocena, Phocoena, Phocoenoides* and *Physeter* (Au & Hastings, 2008). Whistles can be of two types: signature and non-signature whistles. Signature whistles are defined as whistles characterised by a distinctive frequency-modulated patterns and it is thought to convey information about the individual for recognition (Caldwell & Caldwell, 1979; Janik, 2013; King et al., 2018; Sayigh et al., 1995). Signature whistles are particular to individuals and have been suggested that they work similar to human names (Janik & Sayigh, 2013). Non-signature whistles or variant whistles are defined as other whistles without distinctive frequency-modulated patterns (Caldwell & Caldwell, 1979; Janik et al., 2013; Watwood et al., 2005).

Geographic variations in whistle parameters have been reported in several species of odontocetes such as common dolphins (Ansmann et al., 2007), bottlenose dolphins (Hawkins, 2010; Papale et al., 2014), and Guiana dolphins (Leão et al., 2016; Moron et al., 2019). Wang and collaborators (1995) found that bottlenose dolphins along the coast of the Gulf of Mexico, show a steady change in the acoustic parameters of their whistles. Morisaka and collaborators (2005b) studied three populations of Indo-Pacific bottlenose dolphins in Japan finding different whistle characteristics, mainly in frequency parameters that helped to discriminate among populations. Variation in whistle parameters has been attributed to ecological, social, and anthropogenic factors. Ecological factors, such as habitat preferences diminish dispersal between dolphin populations leading to differences in acoustic signal (Rossi-Santos & Podos, 2006). Social factors promoting variation in whistles have been attributed to certain group characteristics such as behaviour, size, and composition (Hawkins & Gartside, 2010; La Manna et al., 2013; Quick & Janik, 2008; Romeu et al., 2017). Lastly, it has been observed that bottlenose dolphins change their whistle parameters in

relation to the ambient noise (Morisaka et al., 2005a) and vessel traffic (Gospić & Picciulin, 2016; May-Collado, 2015; Pérez-Ortega et al., 2021).

1.6. Study system

Bottlenose dolphin (*Tursiops truncatus*, Montagu, 1821) IUCN Status: Least Concern (2012) New Zealand Status: Nationally Endangered (Baker et al., 2019)

Bottlenose dolphin (Figure 1.2) is one of the most well studied marine mammal species (Chilvers & Corkeron, 2002) and are widely distributed around the world. This species can be found in almost all warm temperate and tropical seas, both inshore and offshore (Rice, 1998; Wells & Scott, 2009). Bottlenose dolphins tend to be primarily coastal, but they can also be found in pelagic waters (Wells et al., 2019). Two ecotypes have been described; an inshore form that can be found in estuaries, bays, lagoons and other shallow coastal regions, and an offshore form that is apparently less restricted in range and movement (Wells et al., 2019). In New Zealand waters, researchers have reported four discontinuous populations in: the North Island, Marlborough Sounds, Fiordland, and Stewart Island (Baker et al., 2019; Bräger & Schneider, 1998; Brough et al., 2015; Constantine, 2002; Hartel et al., 2015; Johnston et al., 2017; Lusseau et al., 2003; Merriman et al., 2009; Rowe & Dawson, 2009; Tezanos-Pinto, 2009). The Fiordland population seems to be divided into three different units found around Milford, Doubtful, and Dusky Sounds based on observations and genetics data (Bräger & Schneider, 1998). This species has been reported to range from Cape Reinga to Tauranga in the North Island (Constantine, 2002), although its range may extend from Manukau Harbour on the west coast to Gisborne on the east coast (Tezanos-Pinto, 2009). The species has also been seen in the Hauraki Gulf (Berghan et al., 2008; Dwyer et al., 2014; O'Callaghan & Baker, 2002), Central Bay of Plenty (Meissner, 2015), and Bay of Islands (Constantine, 2002; Hamilton, 2013; Hartel et al., 2015; Mourão, 2006; Tezanos-Pinto, 2009). Recently, Dwyer and collaborators (2014b) reported sightings of bottlenose dolphins at Great Barrier Island and suggested this area as a social hub for the species in the region. The bottlenose dolphin is a medium sized dolphin with body lengths ranging from 220 cm to 410 cm depending

on the geographic location (Ross & Cockcroft, 1990). Dolphins from Fiordland appear to have longer bodies and relatively smaller appendages compared to dolphins in warmer locations (Schneider, 1999). This species can live up to 35-40 years, and females become sexually mature around 5-13 years, while males mature around 8-13 years (Sergeant et al., 1973).



Figure 1.2. Bottlenose dolphin JP068 bow riding at Great Barrier Island. Photo by J. Patiño-Pérez.

1.6.1. Social structure

Researchers have hypothesised that the relatively large brain size of cetaceans has evolved mostly as a response to social forces, i.e., the need for optimal functioning within a complex society marked by communication, collaboration, and group competitiveness (Marino et al., 2007). Evidence has shown that the large and complex brain of cetaceans allows them to process complex information and they have been shown to be capable of intelligent and rational behaviour (Marino et al., 2007). Bottlenose dolphins live in fission-fusion societies in which individuals associate in
groups that often change in size and composition (Connor & Wells, 2000; Würsig & Würsig, 1977). Populations of bottlenose dolphins show different patterns of associations that can vary in age and gender (Connor & Wells, 2000) and in response to environmental factors (Chilvers & Corkeron, 2002). For example, in Sarasota Bay females associate mainly with other females of similar reproductive stage and age, while juvenile dolphins tend to associate with other immature individuals rather than with adults. Likewise, males tend to form strong associations with other males (Wells, 1991) but not in all populations. For example, in the Moray Firth long-term associations in the population between males have not been detected (Wilson, 1995). In the case of Shark Bay, Western Australia, Connor, and collaborators (1992) described dolphins alliances where two or three dolphins form a group and these groups joined other dolphins to form what they called, second order alliances. These second order alliances functioned to consort females or attack other groups (Connor et al., 1992). In some populations of bottlenose dolphins, kinship can be essential to form alliances among males. Parsons and collaborators (2003) found that many males tended to spend more time paired with closely related males (Parsons et al., 2003). In contrast, kinship did not appear to be a determinant factor in the formation of alliances in Southern Australia (Möller et al., 2001).

In New Zealand, the social structures of populations of bottlenose dolphins have been studied, in varying detail, throughout its distribution range. However, in the North Island, the social structure of this species has only been studied in the Bay of Islands (Hamilton, 2013; Mourão, 2006). Bottlenose dolphins in the Bay of Islands inhabit a range of habitats within an enclosed embayment and open coastline (Mourão, 2006). The social organisation of bottlenose dolphins in this area ranges from flexible to high-ranking interactions, with some individuals showing preferred associations with other dolphins (Mourão, 2006). Three probably social communities were identified in the areas during 2000-2003 with individuals of the same community associating more frequently among them than with individuals from other communities. The best model describing the association among dolphins here was a short-term casual acquaintance and a constant long-term companion. Intra and inter-sexual associations were also observed in this population where females associate with a variable number of females linked at least indirectly, forming what has

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been denominated as female bands (Mourão, 2006). Associations among some females lasted at least two years. Males showed three different types of associations. Some males rarely interact with other males, others show weak associations with other males, while the last group of males formed moderate to high bonds with particular males (Mourão, 2006). Some of these associations lasted up to seven years. Associations between males and females also were observed and these also lasted approximately seven years (Mourão, 2006). Later, Hamilton (2013) described the social structure of bottlenose dolphins in the same area. Some similarities were found between the two time periods. The society was characterised by short-term acquaintances and long-term companionships. Also, long lasting associations were found across sexes (Hamilton, 2013). Changes in the social structure of this population were attributed to a decline in population size and a shift in habitat use (Hamilton, 2013).

The bottlenose dolphin population at Marlborough Sounds is a fission-fusion society exhibiting short- and long-term preferred associations, with long-term associates lasting over three years (Merriman, 2007). This population exhibits high levels of associations within large groups. The relationships among members are characterised by constant companions and casual acquaintances (Merriman, 2007). The population of bottlenose dolphins inhabiting Doubtful Sound, Fiordland, has distinct characteristics compared to the other New Zealand populations. This is a small, closed population whose members live in large, mixed-sex groups with low rates of emigration/immigration (Johnston et al., 2017; Lusseau et al., 2003). The association index in this population is one of the highest documented anywhere in the world for a bottlenose dolphin population, only comparable to other small and isolated populations such the one present at the Sado estuary in Portugal (Augusto et al., 2012).

1.6.2. Acoustic behaviour

Bottlenose dolphins are vocal animals, and their acoustic activity has been studied extensively (Boisseau, 2004). Geographic variation in bottlenose dolphins' whistles have received much

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attention worldwide, and whistle differences have been found in sympatric and adjacent populations of the species (e.g., Lima et al., 2020). Various factors such as ecological, genetic, and historical population changes can cause spatial variations in dolphins acoustic signals. Although well studied internationally, studies of acoustic behaviour of dolphins in New Zealand are scarce. The first description of the vocal repertoire of bottlenose dolphins was done in Fiordland, where 12 acoustic signals were broadly described and compared this repertoire between adjacent fiord's populations (Boisseau, 2005). Guerra et al., (2014) quantified the effects of tour boats and the research boat on the group structure and vocal behaviour of bottlenose dolphins in Doubtful Sound, Fiordland. Results showed that groups with mother-calf pairs vocalised more when the boats were nearby and while heading away. Moreover, when tour boats that were travelling and moving fast approach pods, the pods with calves tend to increase their whistle rate while groups without calves are quieter (Guerra et al., 2014). In the North Island, Snell (2000) described the whistle repertoire of bottlenose in the Bay of Islands in response to dolphin tourism. More recently, Peters (2018) compared the call rates of two bottlenose dolphin ecotypes and the influence of vessels. Her results suggested a call divergence based on the consistent differences in the social vocalisations of the ecotypes. Lastly, Outhwaite (2018) studied the whistle repertoire and the social and behavioural context of bottlenose whistles at Great Barrier Island.

1.7. Significance of research and gap knowledge

Although bottlenose dolphins have been studied throughout the distribution, little is known about their social behaviour in New Zealand, especially their social organisation, presence of skin lesion and acoustic behaviour. In addition, most studies have been concentrated in areas such as the Bay of Islands or Fiordland. Recently, a study of bottlenose dolphins, proposed that Great Barrier Island has become an important social hub for the species in the North Island (Dwyer et al., 2014). This offered a valuable opportunity to fill gaps in knowledge about the sociality of this species. My Ph.D. research aims to address this gap and provide better understanding about the social organisation of bottlenose dolphins in New Zealand. I assessed the prevalence of skin lesions and tooth rakes in the north-eastern population of bottlenose dolphin, contributing new knowledge of skin lesions and sociality of the species. In addition, my study will provide quantitative results on the acoustic

parameters of bottlenose dolphins and, for the first time, compare the whistle characteristics of two populations of bottlenose dolphins in New Zealand.

1.8. Thesis structure and aims

This thesis is comprised of five chapters, including an introductory and a concluding chapter. A description of each chapter and objectives are shown below:

Chapter one: This chapter presents an overview of what social structure is and the factors shaping it in a general context. I outline the key concepts, which form the foundation for the work undertaken in this thesis and how they apply to bottlenose dolphins. These include animal social networks, skin lesions, and vocal behaviour.

Chapter two: This chapter describes the social structure of bottlenose dolphins in waters around Great Barrier Island. The aim of this chapter was to compare the social organisation of this population at two different time periods and to other populations around the North Island. I assess the social structure of bottlenose dolphins by examining: (1) preferred/avoided companions, (2) strength and distribution of associations, (3) temporal and spatial patterning of associations, and (4) residence times. During 2015-2019, two social communities were identified in the population with different home ranges, and I aim to explain what the trends in the social organisation are when both communities are analysed both independently and together.

Chapter three: This chapter describes the diversity and prevalence of skin lesions and tooth rakes occurring within the endangered bottlenose dolphin population of north-eastern in the North Island of New Zealand. More specifically, I wanted to 1) describe the most common skin lesions present in bottlenose dolphins, 2) assess the prevalence of skin lesions and tooth rakes in the population, 3) determine the distribution of skin lesions and tooth rakes along the body of the dolphins, 4) develop a standardised protocol for skin lesion classification for bottlenose dolphins in New Zealand, and 5) describe the relationship between the presence of skin lesions and tooth rakes and tooth rakes with the strength of the dolphins in the social network.

Chapter four: In this chapter I describe the characteristics of whistle vocalisations of bottlenose dolphins at Great Barrier Island. Here, I compare the whistles characteristics of two populations in New Zealand. In addition, I use a Random Forest analysis to assess if dolphin whistles could be correctly allocated to their correct population based on these characteristics. Furthermore, I ask if the differences found in the whistle characteristics of these populations may be due to social variables such as groups size and/or the presence of immatures.

Chapter five: Finally, in the last chapter I summarise my main findings and explore my results in terms of sociality and conservation perspectives.

1.9. References

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SOCIAL NETWORKS

2. The social structure of bottlenose dolphins at Great Barrier Island.

2.1. Abstract

The social structure of a population has been described as the nature, quality, and patterning of relationships among individuals within a group. It is a synthesis of how individuals interact with each other and is an important determinant of the biology of any population, influencing fitness, gene flow, and spatial patterns. Dolphins are gregarious animals that form complex social structures, ranging from fission-fusion societies to social alliances. The north-eastern population of bottlenose dolphins in the North Island of New Zealand was thought to be restricted to a single location; an area where the dolphins have been intensively studied. However, recent studies have shown that Great Barrier Island in the Hauraki Gulf, south of this location, is an increasingly important area for these animals. For the first time, I examined the association patterns among individually identifiable bottlenose dolphins in the Hauraki Gulf and therefore the social network structure of the dolphins frequenting this area. I studied the social structure using three data sets, one from the Bay of Islands (BOI) and two from Great Barrier Island (GBI), during two time periods 2011-2013 and 2015-2019. I looked at the social structure of bottlenose dolphins in the region by examining: (1) preferred/avoided companions, (2) strength and distribution of associations, (3) temporal and spatial patterning of associations, and (4) residence times. All three datasets showed that the data were both of good quality and that the dolphins had well differentiated societies. The analysis of modularity yielded two communities in BOI-GBI dataset (Q = 0.307), one community formed mainly by dolphins only found in the Bay of Islands and the other formed by dolphins found either at both sites, BOI or GBI, or only at GBI. The dataset GBI-2015-2019 also showed two social clusters (Q = 0.361). One community was predominately formed by dolphins identified before 2015, and the other community was formed by dolphins identified between 2015-2019. An analysis of the spatial distribution of these two communities showed that while the core areas were similar between communities, home ranges differed between communities. Dolphins from one community had a range twice as large as the other community. Association patterns between BOI-GBI dolphins were low, but these associations were higher between

dolphins of the same community than different communities, indicating that dolphins tend to associate more with dolphins from the same community. In GBI, the population exhibited weak associations during both periods of time. At the community level, one community had moderate association, while the other presented low associations between dolphins. Long-term preferred companions and long-term avoidance were identified in the population during both periods at GBI. Within the communities, only one community presented both long-term companions and long-term avoidance, while in the other this pattern was not detected. During 2011-2013, the best model that described the temporal patterns of associations among dolphins was rapid dissociation + preferred companions + casual acquaintance, meaning that the population exhibited a combination between stable associations among individuals and those individuals that associate, disassociate, and may reassociate again over extended periods of time. On the other hand, during 2015-2019, the best model showed two levels of casual acquaintances, where dolphins associate for short periods of time before breaking up, happening at two different times. The residency models showed that the emigration + reimmigration were the best at describing the population during 2011-2013. The two models of emigration + reimmigration suggested that 73% of the dolphins remained in the study area for 142 days on average and spent around 53 days outside of it. Also, they suggested an emigration rate of 0.026/day and 73% of the population could be found in the area at any time. During 2015-2019, the models suggested high rates of emigration/mortality of individuals in the study area. The findings of my study highlight the relevance of studying bottlenose dolphins' local social structure. Examining the social structure of bottlenose dolphins at Great Barrier Island has provided new insights into the intricate nature of social interaction as well as providing baseline data for future studies in the area. My study population showed fission-fusion dynamics that are comparable to those seen in the Bay of Islands population and others around the world. This research confirms this species' widespread social flexibility, which allows it to thrive in a variety of contexts.

2.2. Introduction

The social structure of a population has been described as the nature, quality, and patterning of relationships among individuals in a group (Hinde, 1976) and it integrates the behavioural interactions and ecological relationships between individuals in the group (Lusseau et al., 2006). In synthesis, the social structure of a population tries to explain how individuals interact with each other and is an important determinant of the biology of the population, influencing fitness, gene flow, and spatial pattern and scale (Whitehead, 2008a; 2019; Wilson, 1975). The social structure of populations is critical to our overall understanding of a species. This can create a feedback loop where the social structure can shape individual behaviour and, in turn, individual behaviour can impact a population's social structure (Augusto et al., 2017; Kappeler & Van Schaik, 2002). Using social networks to understand the social structure of a group can provide important evolutionary and ecological information at different levels of organisation (Krause et al., 2007). For example, at the population level, the structure of a network can affect the speed at which information is transmitted. Alternatively, at the individual level, it can show connections between individuals, and in turn, who interacts with whom and how (Dorning & Harris, 2019; Krause et al., 2007; Newman, 2002; Poulin & Filion, 2021). Additionally, researchers have suggested that network position can be related to individual fitness and might be heritable (McDonald, 2007; Ryder et al., 2008).

Social structure in group living cetaceans varies from stable, as in orcas *Orcinus orca* (Baird & Whitehead, 2000; Ivkovich et al., 2010; Tavares et al., 2017), to fluid societies, as in bottlenose dolphins *Tursiops* sp. (Baker et al., 2018; Chabanne et al., 2017; Pleslić et al., 2019). Bottlenose dolphins live in fission-fusion societies in which individuals associate in groups that often change in size and composition (Connor et al., 2001; Würsig & Würsig, 1977). Populations of bottlenose dolphins show different patterns of associations that can vary in sex, age (Baker et al., 2018; Connor et al., 2001), behavioural state (Gero et al., 2005) or in response to environmental factors (Brightwell et al., 2020). Multilevel alliances among males have been described in *Tursiops* sp. from Shark Bay, Australia (Connor et al., 2001; Connor et al., 2017; Gerber et al., 2021; Nishita et al., 2017; Wiszniewski et al., 2012) and Sarasota, Florida (Ermak et al., 2017) where dolphins can form

first and second order alliances. Furthermore, populations in Doubtful Sound (Lusseau et al., 2003) and the Shannon Estuary, Ireland (Baker et al., 2018) exhibit long-term associations between male and female dolphins. In addition, juveniles and adult bottlenose dolphins tend to form stronger associations within rather than between age classes (Baker et al., 2018). In Shark Bay, Australia, Indo-pacific bottlenose dolphins Tursiops aduncus exhibit behaviourally specific preferred associations where dolphins have approximately six behavioural associates in all behavioural states, i.e., behaviours that have appreciable durations (Altmann, 1974; Gero et al., 2005). Studies of social structure of many delphinid populations, including coastal bottlenose dolphins, have found what is defined as social communities, i.e., subgroups of individuals in a population simultaneously occupying the same space, hence having the opportunity to interact (Augusto et al., 2017; Chabanne et al., 2017; Lusseau et al., 2006; Pleslić et al., 2019; Urian et al., 2009). The social structure can vary among these social communities and seems to be affected by factors such as predation risk (Heithaus & Dill, 2002), association patterns among individuals (Lusseau et al., 2006), natal philopatry (Rako-Gospić et al., 2017), genetic relatedness (Connor et al., 1998), shared knowledge (Mann et al., 2012), behavioural strategies (Cantor et al., 2012; López & Shirai, 2008), and human activities (Ansmann et al., 2012). From a conservation perspective, this is an important factor to consider as different social communities may require different management plans (Baker et al., 2018; Dinis et al., 2017).

The New Zealand threat classification lists New Zealand bottlenose dolphin as *Nationally Endangered* due to its small population (250–1000 mature individuals, predicted decline 10–50%; Baker et al., 2019). Although the species is secure overseas, the populations of bottlenose dolphin in New Zealand are small and widely scattered and its status is likely to move to a higher threat category if there is not appropriated management. In New Zealand, coastal populations of bottlenose dolphins can be found in four regions: North-eastern coast of the North Island, Marlborough Sounds, Fiordland, and Stewart Island (Baker et al., 2019; Bräger & Schneider, 1998; Brough et al., 2015; Constantine, 2002; Tezanos-Pinto et al., 2009). These populations, based on genetic information, exhibit a high degree of isolation with low rates of female migration among populations (Tezanos-Pinto et al., 2009). Although the populations are relatively small and

isolated, they present relatively genetic diversity (Tezanos-Pinto et al., 2009). The population present in the North Island can be found from Doubtless Bay to Tauranga, covering an area of approximately 500 km (Constantine, 2002). Historically, this population has been well studied in the Bay of Islands, an area that has been considered the core centre of activities of this population (Constantine, 2002; Constantine & Baker, 1997; Dwyer, 2014). Bottlenose dolphins use the entire Bay of Islands area year-round with seasonal shift to deeper waters over the summer months (Constantine, 2002). This shift is related to water temperature, probably resulting in a shift in prey concentration or availability (Constantine, 2002). Peak in calving also occurs during the summer months with 41% of the neonates dying during the first year of life (Constantine, 2002). Group size in waters of the Bay of Islands range from one to 60 individuals with a median of 12 dolphins per group (Tezanos-Pinto et al., 2009). In the Bay of Islands, bottlenose dolphins show preferred/avoided associations, and two levels of association among dolphins, a short-term casual acquaintance, and a constant long-term companion (Mourão, 2006). Long-lasting companionships were observed to last between one and two years among females; and for males and female-male associations dolphins tend to form relationships lasting for up to seven years (Mourão, 2006). In addition, intra and inter-sexual associations were observed. Females were seen to associate with a variable number of females, mostly linked indirectly, creating a larger social network possibly forming female bands (Mourão, 2006). In this area, the population was estimated in 446 individuals in 2002 (Constantine, 2002) and an annual rate of 7.5% decline was calculated in the number of dolphins using the bay from 1997-1999 to 2003-2006 (Tezanos-Pinto et al., 2013). Between 2009 and 2012, the abundance of bottlenose dolphins in this area was estimated to be between 24 and 97 individuals, highlighting a significant decline in population size and seemed like fewer dolphins were using the bay more often (Hamilton, 2013; Tezanos-Pinto et al., 2013).

Few studies of the north-eastern bottlenose dolphin population have been conducted outside of the Bay of Islands. Berghan and collaborators (2008) did a preliminary photo-identification study of bottlenose dolphin in the Hauraki Gulf, approximately 100 km south of the Bay of Islands. They identified 162 bottlenose dolphins in this area; 70% of them sighted more than once showing an apparently seasonal pattern of sightings, with most of them occurring between April and June.

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Fifty-nine percent of these dolphins were sighted also in the Bay of Island (Berghan et al., 2008). Recent work conducted by Dwyer (2014) comparing the inner and the outer (Great Barrier Island; GBI) Hauraki Gulf, showed that bottlenose dolphins were infrequently sighted in the inner section of the gulf, but they were frequent at GBI being found all year around. Dwyer and collaborators (2014) argued that GBI is a potential hotspot for this species since dolphins consistently use this area all year around and there are relatively high levels of individual site fidelity to the area (Dwyer et al., 2014). Only two studies to date have investigated the social structure of bottlenose dolphins in the north island, both at the Bay of Islands (Hamilton, 2013; Mourão, 2006). Given the rapid decline of this population in the area, it is crucial to understand the population dynamics of this species in multiple locations across its range. Information on the social structure is important for local management and effective conservation plans, since the social structure can influence how a population responds to changes in its environment (Snijders et al., 2017).

Here, I describe and analyse the social structure of bottlenose dolphin for the first time at Great Barrier Island, New Zealand, making an advance in knowledge in this poorly study topic on a locally endangered species. I studied the social structure using two data sets for Great Barrier Island: 2011-2013 and 2015-2019; and comparing these results with the information available from Bay of Islands. I looked at the social structure of bottlenose dolphins by examining:

- 1- Preferred/avoided companions,
- 2- Strength and distribution of associations,
- 3- Temporal and spatial patterning of associations, and
- 4- Residence times.

I hypothesised that the social structure of bottlenose dolphin at Great Barrier Island will be similar to other populations inhabiting geographically and demographically open areas worldwide, i.e., areas without restrictions for movement and with possibilities of interaction with dolphins of other populations. In the context of New Zealand, I predict the associations to be more similar to the population in Bay of Islands than to the population in Fiordland. Also, I predict that during both time periods, to find dolphins having preferred/avoided companions in the population, more fluid association among individuals and the presence of social communities during the 2015-2019 period due to the large number of new individuals present during this period affecting the temporal and spatial patterning of associations, and the residence times in this population.

2.3. Methods

2.3.1. Study area

The Hauraki Gulf/Tikapa Moana (36°20'S 175°05'E; Figure 2.1) is a shallow semi-enclosed coastal sea situated in the north-east coast of the North Island, New Zealand (Black et al., 2000). Due to the nature of its bathymetry, the Hauraki Gulf presents semi-estuarine characteristics in the inner embayments, and the tidal and residual currents are variable along the Gulf (Black et al., 2000). Depth in the Gulf can reach up to 60 m and it is prone to thermal stratification (Black et al., 2000). The salinity in the Gulf ranges from 34.5 to 35.7 PSU in open water, diminishing to 33-34 PSU around the Firth of Thames and Auckland/Waitematā Harbour due to heavy rain after winter (Black et al., 2000). Mean sea surface temperature (SST) is 17.1 ± 3.3 °C, reaching an annual peak in February and are lowest during August. There is a high interannual variability in SST due to changes in summer solar radiation, wind, and oceanic processes that are linked to El Niño-Southern Oscillation (Black et al., 2000). The Hauraki Gulf is a highly productive region due to the influence of the East Auckland current (Booth & Sondergaard, 1989) making it an area with high biological diversity (Chang et al., 2003). The Hauraki Gulf presents a diverse range of habitats including shallow bays, inlets, and intertidal flats (Hauraki Gulf Forum, 2020) and supports several coastal fisheries, a marine reserve, sands for the building industry, sites for dredge-spoil disposal, an important port, marine farms and beaches for sport and leisure activities (Black et al., 2000).

The Hauraki Gulf can be divided between outer and inner regions (Figure 2.1). According to Wiseman et al., (2011), the inner Hauraki Gulf lies between Takatu Point and the tip of the Coromandel Peninsula. The outer part of the Gulf is an open shelf exposed to the ocean waves, however, sheltered by the headlands and islands to the south-east and north-east (Black et al., 2000). Great Barrier Island is situated in the outer Hauraki Gulf, approximately 80 km to the east

of the North Island. The island is approximately 28,500 ha (Nichol et al., 2003), making it the largest island in the Hauraki Gulf and the fourth largest island in New Zealand. Its coastline is characterised by numerous bays and a rocky shoreline, especially on the western coast where bays and inlets have received little sediment accumulation (Nichol et al., 2003). My study was restricted to the western side of the island between Miners Head and Ross Bay (Figure 2.1) following previous research in the area (Dwyer, 2014; Dwyer et al., 2014; Outhwaite, 2018).



Figure 2.1. Map of Hauraki Gulf showing the boundaries between the inner and outer Hauraki Gulf and the location of Great Barrier Island. Darker shades of blue represent deeper waters. Inset: The Hauraki Gulf in relation to the North Island, and to New Zealand.

2.3.2. Data collection

I collected data during boat-based surveys between December 2016 and May 2019. The surveys lasted between three to five days and were conducted under suitable weather conditions, i.e., good visibility, good light conditions and sea state Beaufort \leq 3 (Supplemental table 6.1). If the weather conditions deteriorated, the survey was cancelled. Due to bad weather conditions, surveys during the winter months (i.e., June, July, and August) were uncommon and were excluded from the analysis. I conducted these surveys on the Massey University research vessel Aronui Moana, a 5.5 m aluminium Stabicraft vessel powered by a four-stroke 100 hp outboard engine with maximum capacity for five people (Figure 2.2). I conducted non-systematic surveys, between Miners Head and Ross Bay and between 7 am. to 6 pm. at a speed of 15 knots, along the west coast of Great Barrier Island, in line with previous research done in the area (Dwyer, 2014; Dwyer et al., 2014; Outhwaite, 2018). A minimum of three observers were present during each survey and included the skipper, an intern, and the principal researcher. The observers scanned the horizon in an angle of 180° in front and to the sides of the vessel. Dolphins were detected either using binoculars (Bushnell, 10 x 50 magnification) or naked eyes. I defined a group of dolphins as individuals observed in apparent association, moving in the same direction, and often, not always, focused on the same activity (Shane, 1990) separated no more than 5 body lengths (10 m) between them. I monitored each focal group until all dolphins in the initial group were lost for a period of ten minutes or more, or the dolphins showed signs of avoidance. Once I sighted a group of dolphins, I approached the group parallel or from the rear at a speed of <5 knots or at the speed of the group (Tezanos-Pinto, 2009). I took photographs from a 90° angle or perpendicular to the body axis following Würsig and Jefferson (1990) methodology (see Photo-identification section). All individuals were photographed at least three times regardless of the presence of marks to avoid bias towards highly marked animals (Würsig and Jefferson 1990). At the end of each encounter, I took a 'blank' shot to differentiate between consecutive encounters (Tezanos-Pinto, 2009).



Figure 2.2. Research vessel *Aronui Moana* used during this study. Photo courtesy of Dr. Emma Betty.

I defined an encounter as the time spent photographing dolphins. For each encounter, I used two data sheets to record environmental and sighting data (Supplemental figure 6.1 and 6.2). I recorded date, time, and position (at the beginning and at the end of each encounter using the depth sounder on board) in both data sheets. Additionally, in the environmental sheet I recorded: effort (on/off), swell, Beaufort Sea state, cloud cover, visibility, weather, and glare. I graded each variable from one, for excellent conditions, to four for bad conditions. In the sighting sheet I recorded: sea surface temperature and depth from the depth sounder in the boat, estimated distance from the shore (± 5m), cue type, direction of travel, cohesion, detection, composition of the group, size of the group (census), and initial behavioural state (foraging, resting, travelling, socialising, and milling). I assessed group composition based on the size of the dolphins as adult, juveniles, calf, and neonate. An adult was a fully grown individual that can reach up to 3-3.5 m in length. A juvenile does not surpass 2/3 the size of adults and may swim in association with other dolphin but not in infant position (calf in proximity underneath its mother's tailstock; Noren and Edwards, 2011). A calf is defined as an individual half of the size of the largest adult in the group, swims in infant position and has lighter body coloration. Finally, a neonate is an individual with obvious foetal folds and has darker pigmentation on the head and the back (Constantine, 2002). To study the social structure of bottlenose dolphins, I used three different datasets. First, I used

the data from the Bay of Island collected by O. Hamilton during 2011-2013. Second, I collated the information from the Hauraki Gulf Bottlenose Dolphin Catalogue (HGBDC) to create a dataset of sightings occurring from 2011 to 2013 at Great Barrier Island. Finally, I also collated sightings from B. Outhwaite personal database from 2015 to early 2016 at Great Barrier Island, which I added to my own data, creating the 2015-2019 dataset (for details about the data collection see Hamilton, 2012; Dwyer, 2014; and Outhwaite, 2018).

2.3.3. Photo-identification

Photo-identification is a technique that aims to use certain characteristic features of an animal that are consistent over long time periods such as nicks, notches or patterns in the skin or fur, to identified individual animals (Hammond et al., 1990; Urian et al., 2015; Würsig & Jefferson, 1990). This tool has been used in a wide range of species such as toads Melanophryniscus montevidensis (Elgue et al., 2014), leatherback turtles Dermochelys coriacea (Gatto et al., 2018), whale sharks Rhincodon typus (Brooks et al., 2010), and grey seals Halichoerus grypus (Vincent et al., 2001) to obtain ecological information on animal populations. Photo-identification has been commonly used to study home rage, dispersal, migration, and social structure of different taxa (Brusa et al., 2016; Chabanne et al., 2017; Passadore et al., 2018; Zanardo et al., 2016). In dolphins, individual identification is done through photographs of the dorsal fin of the animal that usually contains nicks and notches as primary source of identification. Other characteristics such as deformities, tooth rakes and scars can also be used to distinguish individuals. In this study, I focused on nicks and notches on the trailing edge of the dorsal fin of bottlenose dolphins to identified individuals. During each survey, I took photos of the dorsal fin of the dolphins using a Nikon D90 and a Canon EOS 7D Mark II SLR cameras fitted with a Nikon 100-300 mm and a Canon 100-400 mm zoom lenses respectively. I sorted the photographs using a quality and nick distinctiveness scale proposed by Tezanos-Pinto (2009). This scale includes an assessment of the quality of the photo considering focus, size, contrast, angle, and the information contained in each photo (Tezanos-Pinto, 2009; Table 2.1 and 2.2). In addition, I scored each photo from 1 to 3 depending on nick/notch distinctiveness: 1 was given to dolphins with small marks, 2 medium marks and 3 large marks (Tezanos-Pinto, 2009; Table 2.3). To avoid false positives or false negatives errors, only photographs catalogued as photo quality > 2 and a nick distinctiveness of 2 or 3 were considered in the analysis (Table 2.2 and 2.3). Identified individuals were compared to the HGBDC, and new dolphins will be added to this catalogue after a curatorial process. The process involves three researchers confirming, independently, that the dolphin is indeed a new individual. In case of not finding a match, I assigned a temporal number in my provisional catalogue (e.g., JP001) until the dolphin can be added to the main catalogue.

Attribute	Description
	1- Blurred
Focus	2- Partially blurred: outline of fin visible
	3- In focus
	1- Dorsal fin occupies < 25% of the frame
Size	2- Dorsal fin occupied 25-50% of the frame
	3- Dorsal fin occupies > 50% of the frame
	1- Dorsal fin over or under-exposed only outline is visible
Exposure	2- Some over or under exposure but details and outline are visible
	3- All details are visible
	1- Dorsal fin is perpendicular or > 45°
Angle	2- Dorsal fin is ~45°
	3- Dorsal fin is parallel

Table 2.1. Criteria used to assess the photographic quality. Modified from Tezanos-Pinto, 2009.

Table 2.2. Scale of quality and attributes used to assess photographs taken during the 2016-2019 surveys at Great Barrier Island. Modified from Tezanos-Pinto, 2009.

Scale	Rank	Attributes	Examples
1	Poor photographs	Three or more attributes failed to comply, or one or more attributes were significantly affecting nick visualisation. Information content is compromised by poor photographic quality.	
2	Fair photographs	Two attributes failed to comply; however, information content is not compromised by photographic quality.	
3	Good photographs	One attribute failed to comply. Information content is retained.	
4	Excellent photograph	All attributes complied.	

Table 2.3. Scale of nick distinctiveness used to assess photographs taken during the 2016-2019 surveys at Great Barrier Island. Modified from Tezanos-Pinto, 2009.

Scale	Rank	Attributes	Examples
1	Small marks	One or more very small nicks towards the tip and/or the base of fin.	
2	Medium marks	One or more small to medium size notches of unusual shape and/or fin of unusual shape.	
3	Large marks	One or more medium to large size notches of very distinctive shape.	
2.3.4. Association patterns

In aquatic organisms, the study of patterns of association can be logistically challenging due to observational limitations (Chilvers & Corkeron, 2002). In cetaceans, it is common to assess associations through spatial proximity of individuals, and the number of times that a pair is sighted or not, will generate valuable information of the nature of their associations (Chilvers & Corkeron, 2002). In this study, for two dolphins to be considered as associated, they must be sighted in the same group (Smolker et al., 1992; Whitehead, 2008). As a result, I used the 'gambit of the group' definition that states that all the individuals sighted in the same area are associated. To assess associations between dolphins I used the Half-weight Index (HWI), as this accounts for observation bias during sightings where not all individuals can be identified, as it is usually the case with dolphins (Cairns & Schwager, 1987), besides it allows direct comparison with other dolphins' studies.

$$HWI = \frac{X}{X + 0.5 (Ya + Yb)}$$
 Eq. 2.1

HWI is calculated using the equation 1, where *X* is the number of times that both individuals *a*, and *b*, are sighted in the same group. *Ya* is the number of times individual *a* is seen without b. Finally, *Yb* is the number of times individual *b* is seen without *a* (Smith & White, 2007). This index varies between 0, where two individuals are never seen together, to 1 where two individuals are always seen together (Herzing & Brunnick, 1997). Following Quintana-Rizzo (2001), I grouped these indexes into five association categories: very low (0.01–0.20), low (0.21–0.40), moderate (0.41–0.60), high (0.61–0.80), and very high (0.81–1.00). To estimate the association patterns, I only included well-marked adult dolphins sighted during three or more times (Numsamp>2). For the Great Barrier Island databases, I confirmed this approach after running both datasets using different sighting thresholds and found that this threshold could be used on both datasets based on the r and S values (explained below). In addition, I only included groups where at least 50% of the dolphins were identified (Zanardo et al., 2016). I set the sampling period to '*day*' (Chabanne pers. comm.) for this analysis matching the temporal patterns in which my colleagues and I collected the data. I carried out a Mantel test to examine whether there is difference in

associations between communities (two-tailed 0.05, P = 0.05). I did these tests using the uncompiled version of SOCPROG 2.9 (Whitehead, 2009) and I draw the network using UCINET version 6 (Borgatti et al., 2002) where dyads with stronger bonds were positioned closer together by spring-embedding (Dorning & Harris, 2019).

2.3.5. Social differentiation and power

To assess the accuracy and the quality of the social representation of this population, I calculated a Pearson's correlation coefficient (r) between the true association indexes (AIs) and the observed AIs (Whitehead, 2008b). Values of r of approximately 0.4 indicates that the data shows a moderate representative pattern; 0.8 a good representation; and 1 an excellent representation (Whitehead, 2008b). I used social differentiation (S) measures that estimate the variability in the probability of dyadic association indexes within the population, to indicate how complex a society is (Whitehead, 2008a; 2008b). Consequently, I calculated the social differentiation as the coefficient of variation of the proportion of time the dyads were associated (Whitehead, 2008a; 2008b). Values of S < 0.3 indicate homogenous, values > 0.5 indicate well differentiated, and values > 2 extremely well differentiated societies (Whitehead, 2008a; 2008b). Additionally, I used S and the mean number of associations per individual (H) to test the power to reject the null hypothesis of no preference for social partners. When the product of S²H > 5, the null hypothesis can be rejected (Whitehead, 2008a; 2008b). I calculated the values of r and S using the maximum likelihood method with 1000 bootstrap replicates at a resolution of integration of 0.001.

2.3.6. Network properties

To assess the structure of the bottlenose dolphins' social network at Great Barrier Island, I measured the following network properties for all the individuals between periods and within communities: strength, affinity, and cluster coefficient. The **strength** is the sum of associations indexes of each individual (Barrat et al., 2004); **affinity** is the strength of the associates an individual has (Whitehead, 2019); and **clustering coefficient** tells how well the associates of an individual are themselves associated (Whitehead, 2019).

2.3.7. Community detection

I used the definition proposed by Croft and collaborators (2008) stating that a community is a group of individuals more associated amongst themselves than with the rest of the society. Following this definition, I assessed the possibility that this population might be divided into social clusters/communities using modularity (Q). Modularity is defined as the difference between the proportion of total associations observed within communities and the expected proportion if the individual associated at random (Newman, 2004; Whitehead, 2019). I used the eigenvector-based community detection method since this method controls for individual differences in gregariousness and subdivide the population into communities or social clusters and optimises modularity over all possible divisions. If Q is higher than 0.3, this is considered a useful division of the population (Newman, 2004; Whitehead, 2019). I also calculated a cophenetic correlation coefficient (CCC) using an average linkage hierarchical cluster analysis to see how well the dendrogram matched the matrix of AIs (Whitehead, 2019). A CCC higher than 0.8 indicates a good match between the degree of association between individuals and the association matrix (Bridge, 1993; Chabanne et al., 2017; Whitehead, 2019).

2.3.8. Spatial distribution of communities

I calculated the kernel density estimation (KDE) using ArcMap 10.7.1 (Environmental Systems Research Institute [ESRI], 2012) for the two social communities found during 2015-2019. I calculated the probability of contours of 50%, the core range, and 95% the home range of the dolphins at Great Barrier Island. Since the home and core ranges were restricted to this area, these measurements were considered more the area where the dolphins are sighted rather than the complete home or core range of the whole population (Magileviciute, 2006). I calculated KDE using MacLeod (2013) protocols for an environment with barriers. The output grid cell size was set at 100 x 100, and the bandwidth was fixed to 4000. I transformed the coordinates to NZGD 2000 New Zealand Universal Transverse Mercator (UTM) Zone 50 South projection using the coordinate system World Geodetic System (WGS) 1984 datum.

2.3.9. Preferred and avoided companionships

I conducted permutation tests to determine whether the variation in associations between individuals was due to preferred or avoided associations or a result of chance alone (Bejder et al., 1998; Whitehead, 2019). To test for preferred or avoided associations between sampling periods (long-term), I ran the 'permute associations within samples' test. The null hypothesis for this test is that there were no preferred or avoided companions between sampling periods, i.e., between days (Whitehead, 2019). This test controls for demographic effects over the study period and differences in gregariousness between individuals (Whitehead, 2019). If the coefficient of variation (CV) of the real association indexes is higher than those of the randomly permuted data, this indicates the presence of preferred long-term companions in the studied population (Whitehead, 1999). Also, I used the proportion of non-zero elements to test avoidance among individuals in the population. Lower values in the real data meant that there is avoidance between dolphins in the population. I ran this test using 4000 permutations and 1000 trials. Also, I wanted to test for differences in sociality among dolphins (i.e., gregariousness). For this, I ran the test 'permute groups within samples' and use the 'SD of typical group size' (i.e., the group size typically experienced by a member of the population; Whitehead, 2008) as test statistic. High values of this test compared to those from the random data sets indicate that some animals are found consistently in large or small groups. I ran this test using 5000 permutations and 1000 trials. Moreover, I used the permutation test to calculate which dyads had significantly higher (i.e., a preferred associations) or lower associations than their random values in the population using a two-tailed test (p-value = 0.05). A preferred association can be considered when the association index value is at least twice higher than the mean (Whitehead, 2008b). In addition, if the observed number is close to or less than the expected value, the observed significant dyads should be regarded with caution. If the observed number is higher than the expected value, those dyads can be described separately.

2.3.10. Temporal patterns of associations

To measure the stability of the association over time, I calculated lagged association rates (*LAR*) and the null lagged association rates (*NLAR*). *LAR* analysis estimates the probability that two animals seen together now would be seen again at some time lags later (Whitehead, 2008a). *LAR* can be calculated using equation 2, where $g(\tau)$ is the lagged association rate, $\sum_{j}(A, j, d)$ represents the total number of repeat associations after time lag τ , and $\sum_{A} \sum_{j} N(A, \tau, j, d)$ represents the expected number of repeat associations after time lag τ (Whitehead, 1997; 1999; Henderson, 2004).

$$g(\tau) = \frac{\sum A \sum j (A, j, d)}{\sum A \sum j N (A, \tau, j, d)} Eq. 2.2$$

Conversely, the NLAR is the expected value of the LAR if there is no preferred association, i.e., if associations are random. When LAR reaches NLAR, the associations in the population are random at that point (Whitehead, 2008a). I used LAR and NLAR instead of SLAR and NLAR because these needed high moving averages resulting in significant loss of information. When running both, LAR and SLAR, the models were the same, but the value of the parameters where different. I fitted seven exponential decay models to describe the temporal patterns of associations of dolphins at Great Barrier Island, during 2011-2013 and 2015-2019. The models are based on three main models and a combination of them. The three main models are: (1) Rapid dissociation: associations are very short, within one period; (2) preferred companions: some individuals have a preferred associate constant over time; (3) casual acquaintances: individuals associate for some time, dissociate, and may reassociate again or not. As suggested by Whitehead (2007), I used the quasi-Akaike information criterion (QAIC) for model selection which corrects for over-dispersion in the count data. The model with the lowest QAIC is the best model. However, if there are fewer than two units of difference between the best and any other model(s), both models are taken into consideration (Whitehead, 2008a). In addition, I used a jack-knife method to obtain estimates of the precision of the LAR (Efron & Stein, 1981). For this analysis, I included all the dolphins sighted more than three time and chose 'day' as a sampling period. I used SOCPROG version 2.9 for the calculations (for MATLAB2015A; Whitehead, 2019).

2.3.11. Residency time

To analyse dolphin movements, I looked at their residence times at Great Barrier Island during 2011-2013 and 2015-2019, using lagged identification rates (*LIR*). *LIR* is the probability of reidentification of an individual in the study area after τ times later (Whitehead, 2001). This method allows estimation of the amount of time that individuals spend in and out of the study area and how many individuals are present in the area at any given time (Whitehead, 2001). There are four pairs of models that can be fitted to the data and are explained in table 2.4; each pair of models is structurally identical but parameterised differently. These models are used to test for a closed population or a combination of emigration, reimmigration and mortality (Araujo et al., 2014). If the population is closed, the *LIR* should remain constant at the inverse of the population size. On the other hand, if there is emigration or death within the population, then the *LIR* should fall with an increasing time lag (Whitehead, 2001). I included all dolphins in this analysis regardless of the number of times sighted and chose 'day' as the sampling period. I ran all models simultaneously and used *QAIC* to choose the best model (model with the lowest *QAIC*) since the data showed overdispersion (Whitehead 2007). Finally, I used 1000 bootstrap replications to determine the standard error of the *LIR* (Whitehead 2001; Whitehead, 2007).

Table 2.4. Description of the models available to fit LIR and their equations and their descriptions. A1, a2 and a3 are model parameters; N is population size; and td is time lag (Whitehead, 2019. Program users' manual).

Model	Equation	Model description	
A	21	Closed	
	al	1/a1 = N	
B	1/21	Closed	
	1/ 01	a1 = N	
		Emigration/mortality	
С	a2*exp(-a1*td)	a1 = emigration rate	
		1/a2 = N	
		Emigration/mortality	
D	(1/a1)*exp(-td/a2)	a1 = N	
		a2 = Mean residence time	
E		Emigration + reimmigration	
	a2+a3*exp(-a1*td)	a1 = Emigration rate	
		a2/(a2+a3) = Proportion of population in	
		study area at any time	
F		Emigration + reimmigration	
	(1/a1)*((1/a3)+(1/a2)*	a1 = N	
	exp(-(1/a3+1/a2)*td)) /(1/a3+1/a2)	a2 = Mean time in study area	
		a3 = Mean time out of study area	
G		Emigration + reimmigration + mortality	
	a3*exp(-a1*td)+a4*exp(-a2*td)	a1 = N; a2 = Mean time in study area;	
		a3 = Mean time out of study area;	
		a4 = Mortality rate	
Н		Emigration + reimmigration + mortality	
	(exp(-a4*td)/a1)*((1/a3)+(1/a2)*	$a \perp = N; a \perp = Mean time in study area;$	
	exp(-(1/a3+1/a2)*td))/(1/a3+1/a2)	a3 = Mean time out of study area;	
		a4 = Mortality rate	

2.4. Results

When analysing the datasets from the Bay of Islands and Great Barrier Island (BOI-GBI) together during 2011-2013, there were 142 dolphins sighted more than three times during 48 sampling periods (days), with a mean of 27.63 dolphins identified during each sampling period. Likewise, analysing the Great Barrier Island dataset during the same period, 138 dolphins were identified through 27 sampling periods with a mean of 37.15 dolphins identified per sampling period. From 2016 to 2019, a total of 204 bottlenose dolphins were identified during 33 sampling periods. A

mean of 20.79 dolphins were identified per sampling period. After restricted both Great Barrier Island datasets to only dolphins sighted three or more times, I had 93 and 90 individuals in each dataset.

2.4.1. Social differentiation and power and community detection

The BOI-GBI dataset showed that the data are both of good quality and showed a well differentiated society ($r = 0.782 \pm 0.016$; $S = 1.057 \pm 0.011$). The analysis of modularity, using the eigenvector method, yielded a result of Q = 0.317 and split the community into four social communities. In contrast, the clustering using average linkage (controlled for gregariousness) determined five social communities at a modularity of 0.303 at a HWI of 0.181. The cophenetic correlation coefficient (CCC) was 0.928, indicating a good match between the association matrix and the degree of association between individuals (Chabanne et al., 2017). Since both methods produced different results and some of the communities obtained were very small (e.g., three individuals), I exported the matrix to UCINET where I could run the same modularity analysis but have the option to specify the number of partitions for analysis. I chose to analyse two to 10 community divisions and I got similar results for all Q values. Hence, I chose to keep the modularity value for two communities (Q = 0.307), community Y with 50 dolphins and community P with 92 (Figure 2.3a). Here, there was a segregation between individuals, with one community formed mainly by dolphins only found in the Bay of Islands and the other formed by dolphins found either in both sites, Bay of Islands or Great Barrier Island, or only in Great Barrier Island. Unlike the previous results, in the network GBI-2011-2013, dolphins were identified forming one social network (Q = 0.097; Figure 2.3b). The data for this period show a moderate representation of the social pattern ($r = 0.840 \pm 0.024$ SE) and a well differentiated society ($S = 0.614 \pm 0.033$ SE). The dataset GBI-2015-2019 had good representation of the true social system ($r = 0.762 \pm 0.036$ SE) and also exhibited a well differentiated society ($S = 0.899 \pm 0.038$ SE). The eigenvector method indicated a community division with a Q = 0.363 and determined three social clusters. Similarly, the clustering using average linkage (controlled for gregariousness) determined two social clusters at a modularity of 0.361 at an HWI of 0.134. The CCC was 0.881, which indicates a good match between the association matrix and the degree of association between individuals (Chabanne et

al., 2017; Figure 2.4). Therefore, dolphins were assigned to two communities, community B with 49 dolphins and community R with 41 dolphins. Similarly, to what I found in the BOI-GBI network, community B were predominately formed by dolphins identified before 2015, while community R was formed by 'new' dolphins (i.e., identified between 2015-2019; Figure 2.3c). Regarding the hypothesis of no preferences for social partners, the mean number of associations per individual varied between the two periods. During 2011-2013, this number was 424 individuals, while for 2015-2019 it was 134 individuals. Given that S²H was 159 and 134, respectively, I can reject the null hypothesis of no preferences for social partners (Whitehead, 2008a; 2008b).





Figure 2.3. Social network diagrams of bottlenose dolphins sighted three or more times at: a) Bay of Islands and Great Barrier Island 2011-2013 (n = 142), different colour nodes represent two distinct communities: community Y (yellow) and community P (purple), b) Great Barrier 2011-2013 (n = 93) and c) Great Barrier 2015-2019 (n = 90), community R (red) and community B (blue) circles represent two different social communities. Nodes (circles) represent individual dolphins with their corresponding catalogue number.



Figure 2.4. Dendrogram showing average linkage cluster analysis of the matrix of HWIs of bottlenose dolphins sighted at least three times during 2015-2019 at Great Barrier Island, New Zealand (n = 90). Two communities (B and R) plus a solitary animal were defined at a HWI of 0.134 (dashed line) at a maximum modularity of 0.363.

2.4.2. Spatial distribution of communities in Great Barrier Island

I estimated the core areas and home ranges of the two social clusters that were identified during the 2015-2019 period at Great Barrier Island. Core areas were similar between communities, with community B occupying an area of 11 km² while community R occupied an area of 15 km². Unlike the core areas, home ranges differed between communities. Dolphins from community B ranged in an area of 100 km², while community R covered only half of this (approximately 48 km²; Figure 2.5). The core and home ranges were not mutually exclusive, since dolphins from both communities ranged the same area at different extensions.



Figure 2.5. Home range (KDE 95%; light shades) and core area (KDE 50%; dark shades) for the two social communities found at Great Barrier Island during 2015-2019.

2.4.3. Association patterns

The analysis of association patterns between BOI-GBI dolphins was low (mean HWI = 0.20, SD = 0.11). This associations were higher between dolphins of the same community than different communities as supported by the Mantel test (HWI_{meanWithin} = 0.36 ± 0.15 ; HWI_{meanBetween} = $0.01 \pm$ 0.01, Matrix correlation = 0.6587, p < 0.000), indicating that dolphins tend to associate more with dolphins from the same community. During the period 2011-2013, the population showed an overall mean HWI of 0.38 (SD = 0.16) and a maximum association of 0.86 (SD = 0.12; Figure 2.6a). In 2015-2019, the overall mean decreased to 0.23 (SD = 0.08), and the maximum HWI reached 0.84 (SD = 0.13) similar to the previous period (Figure 2.6b). This indicates that the population overall had weak associations during both periods. Although, some dolphins can form strong bonds with a certain individual, reaching a maximum association index of 1 (For example, individuals HG292 and HG296 during 2011-2013. See supplemental table 6.2). At community level, community B had moderate association among its individuals, while community R presented low associations between dolphins (HWI_{mean} = 0.47, HWI_{max}. = 0.88; HWI_{mean} = 0.32, HWI_{max}. = 0.80, respectively; Figure 2.6c-d). Mantel test showed that associations were stronger within than between communities (HWI_{meanWithin} = 0.40 ± 0.14 ; HWI_{meanBetween} = 0.05 ± 0.05 , Matrix correlation = 0.6811, p < 0.000) meaning that dolphins tend to associate more with dolphins from the same community than among dolphins assigned to different communities.



Figure 2.6. Mean (blue) and maximum (orange) distribution of the association index (HWI) for bottlenose dolphin sighted three or more times at Great Barrier Island during a) 2011-2013; b) 2015-2019; c) 2015-2019 community B and d) 2015-2019 community R. Y axis is proportion of individuals and X axis is association index.

2.4.4. Preferred/avoided associations

The tests for preferred/avoided associations showed that the coefficients of variation (CV) were higher in the real data than in random datasets, indicating the presence of long-term preferred companions during both periods. Conversely, the proportion of non-zero elements was lower in the real than in the random data suggesting long-term avoidance among members of the population (Table 2.5). During 2011-2013 there were 65 out of 213 expected dyads, stronger than expected by chance. Of these 65, eight dyads had HWIs above 0.76 that were stronger than by chance alone. These dyads were formed by 14 different dolphins, individuals HG248 and HG205 formed significant dyads with 2 different dolphins (Supplemental table 6.2). From these dolphins, only the sex of HG205 was known and has been identified as a female. Three dyads had an HWI value of 1, meaning that these pairs were sighted together every time. During 2015-2019 there were 61 out of 200 expected dyads stronger than expected by chance, of these, 29 had a HWIs > 0.46 (Supplemental table 6.2). These significant dyads were formed by 15 different dolphins, six dyads were a mix of dolphins from both periods involving only three dolphins form the first period HG258, HG287 and HG288 and five new dolphins (Supplemental table 6.2). The rest of the dyads were formed exclusively by dolphins from the second period. However, the number of observed significant dyads was lower than the expected number for both periods and the results should be interpreted with caution. When compared at community level, the tests for preferred/avoided associations showed that community B presented both long-term companions and long-term avoidance, while in community R these did not show neither long-term companions nor long-term avoidance among individuals. I ran the test of gregariousness only at population level, during both time periods, some dolphins were found in consistently smaller or larger groups than other (2011-2013 SD(typical group size)_{Real} = $11.08 > SD(typical group size)_{Random} = 9.60$, p < 0.05; 2015-2019 SD(typical group size)_{Real} = $7.09 > SD(typical group size)_{Random} = 6.20 p < 0.05)$.

Period	Test statistic	Real data	Random data	P-value	Timeframe of associations
2011-2013 BOI-GBI	CV*	1.35229	1.34175	0.0000	Long-term companions
	Proportion non- zero*	0.45190	0.45861	0.0003	Long-term avoidance
2011-2013	CV	0.73129	0.72213	0.0002	Long-term companions
	Proportion non- zero	0.80902	0.81727	0.0003	Long-term avoidance
2015-2019	CV	1.18008	1.15790	0.0000	Long-term companions
	Proportion non- zero	0.52484	0.54122	0.0003	Long-term avoidance
	CV	0.52607	0.52380	0.0000	Long-term companions
2015-2019 Community B	Proportion non- zero	0.89711	0.89930	0.0210	Long-term avoidance
2015-2019 Community R	CV	0.77708	0.00078	1.0000	No long-term companions
	Proportion non- zero	0.75976	0.00076	0.0000	No long-term avoidance

Table 2.5. Permute associations within samples test for preferred/avoided association in bottlenose dolphins at Great Barrier Island during two periods.

*3000 permutations were used in these tests.

2.4.5. Network properties

I found significant differences in the network metrics between both periods (Mann-Whitney test, p < 0.001 for all metrics; Supplemental table 6.3). There was a higher affinity, clustering coefficient, and strength during 2011-2013, suggesting that a denser, more connected network was formed during this time (Table 2.6). During both periods, there was no significant difference between the strength and clustering coefficient from the real and the expected data networks, but there was a significantly lower affinity than expected by chance. I found that during both periods of time, dolphins with high strength also had higher affinity (2011-2013: r = 0.7972; p < 0.001; 2015-2019: r = 0.7331; p < 0.001) and clustering coefficient (2011-2013: r = 0.8276; p < 0.001; 2015-2019: r = 0.4131; p < 0.001). This is called assortative mixing, where dolphins preferentially associate with others with

similar numbers of associates. At community level, community B showed a similar pattern to the population during 2011-2013: higher values in all the metrics, indicating a denser and more connected network among dolphins of this community. Community R had lower values in all the metrics indicating weaker associations among its members. Clustering coefficient was relatively high for both periods and for both communities, indicating that individuals were strongly associated with their neighbours and these, in turn, associated with each other.

Table 2.6. Overall mean values for network measures (SD) for bottlenose dolphins sighted at least three times at Great Barrier Island during two periods.

Period	Affinity	Clustering coefficient	Strength
2011-2013	39.00 (6.69)	0.52 (0.09)	35.40 (14.31)
2015-2019	21.74 (4.21)	0.44 (0.09)	20.18 (7.40)
2015-2019 Community B	25.31 (1.00)	0.50 (0.07)	24.48 (6.47)
2015-2019 Community R	17.48 (2.00)	0.37 (0.07)	15.03 (4.67)

2.4.6. Temporal patterns of associations

The lagged association rate (*LAR*) of bottlenose dolphins at Great Barrier Island during 2011-2013, sharply declined during the first 100 days. After this, the *LAR* stayed fairly constant well above the null lagged association rate (*NLAR*) indicating the presence of non-random associations at this point (Figure 2.7a). The best model for this period was rapid dissociation + preferred companions + casual acquaintance, which had the lowest *QAIC* among the models fitted (Table 2.7; Supplemental table 6.4). This model, explains a combination between stable associations among individuals and those individuals that associate, disassociate, and may reassociate again over extended periods of time. In the population, 64% of the individuals spent most of their time with the same dolphins; 22% stayed associated with the same individual for about 54 days and the rest (14% of the individuals) were only sporadically associated with other dolphins. During 2015-2019, the *LAR* fell constantly for 200 days and then increased again for about 100 days, until it fell yet again. Like the pattern during 2011-2013, the *LAR* stayed well above *NLAR* indicating the presence

of non-random associations during this period as well (Figure 2.7b). The best model was two level of casual acquaintances (Supplemental table 6.5), that explains a social system where dolphins associate for short periods of times before breaking up, happening at two different times and dolphins may reassociate or not (Table 2.7). During this period, 48% of the individuals showed associations lasting for approximately seven days and the rest of the dolphins for about 1683 days (equivalent to about 4 and a half years).

The best model for community B was two levels of casual acquaintances (Table 2.7; Supplemental table 6.5), where dolphins associate for short periods of times before breaking up and can be seen in the graph with a peak in the associations at around 80 days and the decreasing, and the other peak at around 280 days (Figure 2.7c). After this, the association kept decreasing until the end of the study period. In this community, 40% of the dolphins showed association that lasted around 14 days and among the rest of the dolphins the associations lasted approximately 2141 days (~ six years). For community R, I only ran three models since the others did not match the data (i.e., I got negative values for some parameters). From the three models, rapid dissociation + preferred companions had the lowest QAIC value (Table 2.7; Supplemental table 6.7). This model explains a rapid decay in the associations happening for about 250 days, showing non-random and ephemeral associations among dolphins, in this case, due to a dyadic preference. Here, 46% of the community had preferred companions. The model stayed above the NLAR indicating that the association were non-random (Figure 2.7d). Another model that showed some support was preferred companionship + casual acquaintance ($\Delta QAIC = 2$; Supplemental table 6.6). In this community, 54% of the dolphins formed casual relationships that lasted less than 0.034 days (as calculated by this programme).

Table 2.7. Description of the models fitted to the lagged association rates (LAR) for bottlenose dolphins at Great Barrier Island.

Period	Model	Model equation	Maximum-likelihood for parameters (SE)
2011-2013	Rapid dis. + Pref. comps + Casual acquaintance	$g(\tau) = a2 + a3e^{(-a1\tau)}$	a1 = 0.018406 (0.0094861) a2 = 0.64451 (0.038057) a3 = 0.22758 (0.074854)
2015-2019	Two levels of casual acquaintance	$g(\tau) = a3e^{(-a1\tau d)} + (1-a3)e^{(-a2\tau d)}$	a1 = 0.13972 (1.17) a2 = 0.00059417 (0.00065805) a3 = 0.4818 (0.21552)
2015-2019 Community B	Two levels of casual acquaintance	$g(\tau) = a3e^{(-a1\tau d)} + (1-a3)e^{(-a2\tau d)}$	a1 = 0.072602 (0.0802) a2 = 0.00046702 (0.00045327) a3 = 0.4013 (0.17822)
2015-2019 Community R	Rapid dis. + Pref. comps	g(t) = a1	a1 = 0.45996 (0.020285)





Figure 2.7. Lagged association rates (LAR) for bottlenose dolphins at Great Barrier Island. Orange lines indicate LAR and vertical bars indicate approximate standard errors calculated using the jackknife method. Blue lines indicate the NLAR. Yellow lines represent the best fitted models for this population: a) 2011-2013 rapid dissociation + constant companions + casual acquaintance; b) 2015-2019 Two levels of casual acquaintance; c) 2015-2019 Community B Two levels of casual acquaintance and d) 2015-2019 Community R Rapid dissociation + preferred companions.

2.4.7. Residency time

Residence patterns were analysed including all individuals regardless the number of times the dolphins were sighted in each period. After analysis, two models were identified during both periods: emigration + reimmigration and emigration/mortality. During 2011-2013, the lagged identification rate (*LIR*) sharply falls for 100 days meaning constant emigration of the dolphins

from the area. The curve stabilises after this time, suggesting dolphins stayed longer in the area or higher rates of reimmigration (Figure 2.8a). Both models of emigration + reimmigration (Supplemental table 6.8) suggested that 73% of the dolphins remained in the study area for 142 days on average and spent around 53 days outside of it. Also, they suggested an emigration rate of 0.025825/day and 73% of the population could be found in the area at any time. For the period 2015-2019, *LIR* fell constantly in the study area almost reaching 0 (Figure 2.8b). This suggested high rates of emigration/mortality of individuals in the study area. The lowest $\Delta QAIC$ was for the two models of emigration/mortality (Supplemental table 6.9). These models suggested a population size of 79 individuals that spent around 950 days in the study area and have an emigration rate of 0.0010514/day or 0.384/year. The other model showing support was emigration + reimmigration + mortality ($\Delta QAIC = 1$), suggesting that a small portion of dolphins (n = 12) spent around 0.456 days in the study area, and 2.82 days outside of it. The mortality rate was calculated to be 0.000957/day (approximately 0.349/year; Table 2.8).

In Community B, *LIR* fell constantly throughout the study periods indicating constant emigration or mortality of the dolphins from the area (Figure 2.8c). The best models describing this were both models of emigration/mortality (Supplemental table 6.10) and suggested that dolphins emigrate from the area at a rate of 0.00047378/day and have a mean residence time of 2113 days. Both models suggested a community size of 36 individuals (Table 2.8). Another model that showed support was emigration + reimmigration ($\Delta QAIC = 1.74$). According to this model, the dolphins that form the community spend a mean time of 1745 days in the study area and 2647 days outside of it. For Community R, *LIR* fell sharply for the first few days, meaning a high rate of emigration/mortality during this time; after this, the rate of emigration/mortality decreased considerably, meaning longer permanence of dolphins in the area (Figure 2.8d). Five models showed strong support for this community. The model emigration + reimmigration + mortality had the lowest *QAIC* (Supplemental table 6.11) and suggests that dolphins from this community spent a mean of 1.13 days in the area and 0.029 days outside of it. The mortality rate was estimated at 0.168/day. Both models of emigration/mortality also showed support for reimmigration ($\Delta QAIC =$ 1.11) and suggested a population size of 32 individuals, a mean residence time of 1600 days and an emigration rate of 0.000626/day. Another model showing support was emigration + reimmigration ($\Delta QAIC = 1.11$), this suggests a population size of 20 individuals, a residence time in area of 132 days and out of it of 180 days. Finally, the other model for emigration + reimmigration + mortality also showed support ($\Delta QAIC = 1.05$), suggesting a population size of 17 dolphins, a residence time of around 30 days, time out of the area was calculated in 33 days and a mortality of 0.00048/day (Table 2.8).

Table 2.8. Description of the models fitted to the lagged identification rates (LIR) for bottlenose dolphins at Great Barrier Island.

Period	Model	Model equation	Maximum-likelihood for parameters (SE)
2011-2013	Emigration + reimmigration	$g(\tau) = a2 + a3^* exp^{(-a1^*td)}$	a1 = 0.025828 (0.9455) a2 = 0.011158 (0.00052958) a3 = 0.0041362 (0.011077)
		$g(\tau) = (1/a1)*((1/a3)+(1/a2)*^{exp(-})(1/a3+1/a2)*td))/(1/a3+1/a2)$	a1 = 65.3734 (4.02) a2 = 142.8914 (24.7623) a3 = 53.007 (9.2671)
2015-2019	Emigration/mortality	$g(\tau) = a2^* exp^{(-a1^*td)}$	a1 = 0.0010514 (0.00012967) a2 = 0.012577 (0.00074755)
	Emigration/mortality	$g(\tau) = (1/a1)^* exp^{(-td/a2)}$	a1 = 79.4888 (4.7463) a2 = 950.9787 (121.0824)
2015-2019 Community B	Emigration/mortality	$g(\tau) = a2*exp^{(-a1*td)}$	a1 = 0.00047378 (0.0001245) a2 = 0.02755 (0.0015586)
	Emigration/mortality	$g(\tau) = (1/a1)^* exp^{(-td/a2)}$	a1 = 36.31 (2.0534) a2 = 2113.4338 (771.5711)
2015-2019 Community R	Emigration + reimmigration + mortality	$g(\tau) = a3*exp^{(-a1*td)}+a4*exp^{(a2*td)}$	a1 = 0.00054291 (0.34672) a2 = 1.1314 (s.e. 4.9594) a3 = 0.02925 (s.e. 0.088092) a4 = 0.16814 (s.e. 2.3993)





Figure 2.8. Lagged identification rates (LIR) for bottlenose dolphins encountered at Great Barrier Island. Standard errors (bars) were calculated using the jackknife method. Green circles (1000 bootstrap) indicate data points. Orange lines indicate the best fitting model(s) for: a) 2011-2013: Emigration + reimmigration (model E blue bars and model F orange bars); b) 2015-2019: Emigration/mortality (model C blue bars and model D orange bars); c) Emigration/mortality and d) Emigration + reimmigration + mortality.

2.5. Discussion

2.5.1. Social structure

The social structure of bottlenose dolphins was assessed at Great Barrier Island at two different time periods (2011-2013 and 2015-2019). In both time periods, bottlenose dolphins showed low indexes of association, showing a fission-fusion society characteristic of this species across most of its distribution. However, the associations were fluid among its members, the society was structured, with dolphins forming long-term bonds with some individuals and avoiding others. Using tests for modularity, I did not detect distinct communities in the population during 2011-2013 (only Great Barrier Island) but I did for the BOI-GBI and the 2015-2019 datasets. For the BOI-GBI (2011-2013) dataset, I found two distinct communities with a clear segregation. Community Y was formed by 50 dolphins, mainly from the Bay of Islands, and community P was formed by 92 dolphins, either only identified from Great Barrier Islands or sighted in both areas. Dolphins from these communities prefer to associate with dolphins from the same community, and they have long-term companions and avoidances. Similarly, during 2015-2019, two social communities were detected (named community B and R). Community B was formed by 49 dolphins, most of them found during the 2011-2013 period, and community R formed by 41 dolphins, most of them found only during the 2015-2019. The cophenetic correlation coefficient and the modularity values were high enough to support a meaningful division into communities of the population during this period. My analysis of the spatial distribution of the communities showed some segregation between communities. Although, both communities had spatial overlap of their core and home ranges, as expected, community B had double the area of the home range compared to community R, although, the core ranges were similar. Also, the social parameters analysed differed between communities. Community B showed stronger association among dolphins, above the value for the overall population, while community R showed weaker association and this value was similar to the Ais for the whole population. Furthermore, community B had higher values in all the network measures corroborating that dolphins in this community had denser and tighter relationships among dolphins than community R. Finally, I found differences in gregariousness during both periods, where some dolphins were observed in consistently smaller groups, while others were observed in consistently larger groups.

Two levels of patterns of associations were used to describe the social structure of bottlenose dolphins at Great Barrier Island. First, I used the distribution of association indexes to understand the general patterns of association at population level. Second, I used the hierarchical cluster analysis to examine patterns of association between communities of bottlenose dolphins at Great Barrier Island. Bottlenose dolphin is one of the most extensively studied cetacean species in the world, as is its social structure. Studies have shown that its social structure can be variable, with populations showing highly fluid association, typical of fission-fusion societies (Chabanne et al., 2017; Connor et al., 2000; Dinis et al., 2018; Pleslić et al., 2019) to close and stable associations between its members (Augusto et al., 2012; Louis et al., 2017; Lusseau, 2003; Vermeulen, 2018). One of the fundamental decisions for social analyses is to decide how many sightings per individual are enough to obtain relevant social information about a population; it is the right balance between including as many individuals as possible and decreasing any bias created by wrong identification of individuals (Bejder et al., 1998; Parra et al., 2011; Zanardo et al., 2018). If animals with low resignting rates are included, this might contain associations that are likely to occur by chance. On the other hand, including only animals with high resignting rates, might lead to overlooking important associations with individuals not analysed (Chilvers & Corkeron, 2002). Whitehead (2008) suggests that five is the minimum number of sightings needed to obtain reliable social information. Other authors have also recommended including only dolphins observed on more than the median number of sightings for all dolphins identified in the population, to make a more objective cut-off point (Díaz-Aguirre, 2017).

For bottlenose dolphins, different sighting thresholds have been used, from three or more sightings in São Tomé Island (Pereira et al., 2013) to 30 or more in Western Australia (Gero et al., 2005). In New Zealand, different thresholds have been used, for example, a minimum of four sightings per individual were used in the Bay of Islands (Mourão, 2006; Hamilton, 2013) and Marlborough Sounds (Merriman, 2007), and in Doubtful Sound, this includes dolphins sighted in more than 20% of the focal groups found were included (Lusseau et al., 2003). In this study, I used a minimum sighting threshold of three sightings per individual to assess the social dynamics of bottlenose dolphins at Great Barrier Island. Although it is low compared to other studies of

bottlenose dolphin, this threshold gave robust values of Pearson's correlation coefficient (*r*) and social differentiation (*S*) in both datasets and having the same number of sightings during both periods allowed a reliable comparison between them. During both periods, 2011-2013 and 2015-2019, there was a marked difference in weather conditions (due to an extreme event of La Niña during 2011-2013) and a considerable increase of new dolphins in the area during 2015-2019. Analysing both periods separately gave me more detail about the temporal dynamics of this population. Bottlenose dolphins showed low association patterns among individuals in both periods, and researchers have argued that results of association indexes can be affected by inherent biases, mostly problems of transitivity (Chilvers & Corkeron, 2002), or by issues related to the data collection. In my case, within-group sampling error probably occurred, since some identifiable dolphins within some groups were not captured in photographs during a sampling session decreasing the values of the association indexes.

Researchers have found many similarities in the social structure of odontocetes inhabiting similar habitats and this may be due to common ecological forces acting on the social behaviour of the species (Rogers et al., 2004). Populations of odontocetes living in closed areas and that have small population sizes, tend to have stronger associations among members than species living in open areas and big groups (Augusto et al., 2012; Chilvers & Corkeron, 2002; Louis et al., 2017; Lusseau et al., 2003). I found that the associations indexes (AI), in general, were low for both periods, but during 2011-2013 these associations were higher than 2015-2019. In the Bay of Islands (also part of the north-eastern North Island), Mourão (2006) and Hamilton (2013) reported low values of AI for bottlenose dolphins, these values are more similar to what I found during the 2015-2019 period. Although the associations were fluid during both periods, some dolphins associated largely with particular dolphins, reaching in some cases an AI of 1. Lusseau and collaborators (2003) reported an AI value of 0.47 for bottlenose dolphins in Doubtful Sound (Fiordland population). This unique social structure is probably driven by the isolation of this population where the rates of emigration and immigration are low, and dolphins have more opportunities to form long-term relationships with other individuals, also prey availability and topography of the area appear to be contributing factors to the high level of association among bottlenose dolphins at Doubtful Sound

(Lusseau et al., 2003). Other populations of cetaceans like sperm whales *Physeter macrocephalus* that also show a high level of geographic isolation, have been described to form stable social organisations (Gero et al., 2014). In the Marlborough Sounds, Merriman (2007) found a more stable population with AI that range from moderate to very high among dolphins, but still with certain degree of fluidity among its individuals. A fluid society was expected at Great Barrier Island, since the large area that this population occupies offers an open environment for the dolphins, with no apparent restrictions where dolphins can interact with individuals from other populations increasing the number of associates a dolphin can have.

Social communities were detected when assessing the BOI-GBI and the 2015-2019 databases. Dolphins showed homophily, with individuals associating with others that are similar to them, in this case with dolphins belonging to the same area, i.e., dolphins found at BOI associated more with other dolphins from BOI rather than dolphins from GBI. The same was true for GBI 2015-2019, where dolphins associated more with dolphins identified in 2011 than dolphins identified after 2015 (what I called "new dolphins"). In dynamic societies, the segregation into different social communities might be influenced by time and space (Beirão-Campos et al., 2016). In this case, the constant emigration of individuals might impact the change in the population composition over time possibly also influencing the change in the social structure of the population during this time. It could be suggested that constant movements of bottlenose dolphins between the Bay of Islands and Great Barrier Islands could cause the segregation between these two communities, but comparisons of the catalogues between both places have shown only few dolphins in common (Supplemental table 6.12). However, these findings may be somewhat limited by the fact that I only took into consideration dolphins sighted near either Bay of Islands or Great Barrier Islands, ignoring the few records from the inner Hauraki Gulf, hence, these results should be interpreted with caution.

One of the aims of this study was to understand the general social and spatial division of the population into communities at Great Barrier Island, without investigating the details of a fine-scale structuring and ranging patterns within them. This approach was taken as Great Barrier

Island is just a portion of the distribution of the species in the North Island of New Zealand. As mentioned before, during 2015-2019 two communities were detected with some sort of spatial segregation and different social parameters between them. A similar pattern to what I found at Great Barrier Island was also found in bottlenose dolphins present in the Indian River Lagoon, Florida, and Western Australia, where the social organisation also differed among the communities detected. Some of them having highly interconnected networks while others were formed by loose networks and short-lived associations among individuals (Chabanne et al., 2017b; Titcomb et al., 2015). Researchers have suggested that community segregation could be due to individual preferences to specific habitats (Chilvers & Corkeron, 2002; Wiszniewski et al., 2009); foraging specialisations (Chilvers & Corkeron, 2002; Rossbach & Herzing, 1999; Torres & Read, 2009); environmental differences (Rossbach and Herzing, 1999) or the social preferences of individuals (Titcomb et al., 2015). In this case, the formation of communities seems to be driven by the latest as supported by the preference for and the avoidance of dolphins.

The level of segregation between communities can vary from socially and spatially segregated (e.g., Pleslić et al., 2019; Titcomb et al., 2015; Urian et al., 2009) to communities socially segregated despite the considerable home range overlap (Chilvers & Corkeron, 2002; Genov et al., 2019; Lusseau et al., 2006), as in this study. It is worth noting that, during 2015-2019, there was a high influx of new individuals to the area, as confirmed by the high number of newly identified dolphins, and this could cause the segregation of individuals. Community B was mainly formed by dolphins identified during 2011-2013, while community R was formed mainly by individuals identified during 2015-2019. This was supported by the Mantel test that showed that dolphins have stronger association with dolphins from the same community than with dolphins from the other community. Also, it is important to note that the associations between dolphins from community B were stronger and more stable than the associations showed that dolphins from community B had both long-term and avoided companions, while community R did not have neither long-term nor avoided companions during this period. As previously mentioned, the spatial or social aspects of a population social structure can change over time (Pleslić et al., 2019).

For example, in Moreton Bay, Australia, two different communities, with overlapping home ranges, were initially socially segregated based on different foraging techniques ('trawlers' and 'non-trawlers'). After the decrease of the commercial trawling, these two communities started to blend (Ansmann et al., 2012). I hypothesised, that this can occur at Great Barrier Island as the 'new' individuals establish themselves and begin to form associations with the 'old' dolphins.

At the population level, dolphins at Great Barrier Island showed both long-term and avoided companions during both periods. Similarly, Mourão (2006) found long-term preferred associations and avoidance among dolphins in the Bay of Islands. In the same location, Hamilton (2013) found that dolphins still showed long-term preferred companions in the population. Other delphinids, also have shown similar patterns of long-term preferred associations in New Zealand, for example, dusky dolphins *Lagenorhynchus obscurus* in Admiralty Bay (Pearson, 2008) and common dolphins *Delphinus* sp. in the Hauraki Gulf (Hupman, 2016). For example, I observed three identified dolphins always together during my study period. Associations of trios of males has been described in Shark Bay, Australia where dolphins usually form a multi-layered network (Connor et al., 2017; Connor et al., 1992). Also, in Sarasota Bay (Florida), adult females associate with others of similar reproductive age as a strategy to protect their calves and learn from more experienced females (Wells, 2014). Unfortunately, sexing of the animals was not possible during this study, and it will be very interesting to understand how sex influences the social structure of this population.

Regarding to the differences in gregariousness among individuals, differences in group sizes have been reported along the north-eastern North Island bottlenose dolphin population. At the Bay of Islands, group sizes range from 3-28 dolphins during 2009-2012 (mean = 20.9; median = 25; Hamilton, 2013). Dwyer et al. (2014) found at Great Barrier Island, group sizes ranging from 1-82 dolphins (mean = 36.4; median = 35), relatively higher than at the Bay of Islands. Interestingly, during 2016-2019 I found group sizes in the same range (1-81 dolphins) but the average number of individuals per group was smaller (mean = 22.9; median = 13). Since bottlenose dolphins at Great Barrier Island clearly show dynamics of a fission-fusion society, preference for larger or smaller groups can signify an advantage for dolphins in certain situations. Larger groups can be advantageous for cooperative feeding, increased vigilance, and care of young dolphins. Smaller groups also can offer an advantage for delphinids, for example, less competition for resources, or promote affiliative tactile contact (Johnson & Norris, 1994). At Great Barrier Island, bottlenose dolphins are typically found in rather large groups (over 20 individuals) and usually are the only cetaceans species found near the coasts of this island. The preference for larger or smaller group might be associated to the social context (i.e., who is present; Connor et al., 2000) and/or the behavioural/ecological context (e.g., feeding, breeding, vigilance; O'Corry-Crowe et al., 2020).

2.5.2. Temporal patterns of associations and residency times

At Great Barrier Island, bottlenose dolphins showed a different temporal pattern of associations between both periods. During 2011-2013, the model showed a decline during the first 100 days to later stabilize for the rest of the study period. This sharp fall might indicate that dolphins are leaving the study area constantly, after this time, dolphins remain in the area for longer periods. The best model describing these patterns was rapid dissociation + preferred companions + casual acquaintance. In the short term, the decay in the association among dolphins is due to a disaffiliation among individuals, but in the long-term this change can be due to movements between groups, changes in affiliations or a demographic factor such as emigration or mortality (Whitehead, 2008a). The population showed combinations of stable associations among individuals and those individuals that associate, disassociate, and may reassociate again, with most dolphins spending the majority of their time with the same dolphins, a quarter of them stayed associated with the same individual for about two months and just a small portion of the population were only sporadically with other dolphins. This pattern in the LAR can be explained by demographic effects as observed in *LIR* (explained below). This seems consistent with what Dwyer (2014) found, that frequently sighted dolphins move away from GBI during autumn, but occasional visitors arrive to the island during this time. I also found the highest values for affinity, clustering coefficient, and strength during this time, supporting the description of a population with nonrandom associations and with a dense, well-connected network, where dolphins actively choose their companions and avoid other individuals. During 2015-2019, the model showed two peaks around 50 and 250 days, this is characteristic of a population with two levels of casual

acquaintances, where the individuals associate for short periods of times before breaking up, happening at two different times. At community level, community B presented the same patterns as the whole population during this time (i.e., two levels of casual acquaintances), as mentioned before. Community R showed a quick decline in associations with almost half of the community having a preferred companion. The change on the dynamics of this population between periods and within communities, could be created by the influx of new dolphins into the study area. Around of 47% of the dolphins sighted more than three times at Great Barrier Island were new animals. These "new" dolphins formed association mainly with other "new" dolphins, while "old" dolphins (i.e., dolphins identified during 2011-2013) associated mainly with other "old" individuals. Network measures were lower in 2015-2019 compared to the previous period, which is expected if dolphins associate non-randomly and are only forming bonds with certain individuals in the population and avoiding others, in addition, some dolphins were found in consistently smaller or larger groups than others. The temporal patterns of associations of bottlenose dolphins have shown high variability throughout its global distribution, from associations of constant companions that last years (Lusseau et al., 2003) to casual acquaintances that last less than a day (Chabanne et al., 2017b).

Two models that best explain the residence time of the dolphins in the area were identified during both periods, emigration + reimmigration and emigration/mortality. During 2011-2013, the models explaining the number of dolphins in and out of the study area seem close to what was observed in the field and the count of individuals obtained. The population showed high levels of mortality/emigration during the first three months, but later stabilises indicating high fidelity or a high rate of immigration. During 2015-2019, the model fell constantly probably due to continuous movements of dolphins in and out of the study area. Both models showing support during this time suggest a mortality rate of 0.3 per year, which is high compared to other studies (e.g., Chabanne et al., 2017) but makes sense if I consider the turnover rate in dolphins that occurred during this period. Within the communities, the patterns were similar between the two periods, with dolphins leaving the area at high rates and some staying for short periods of time.

2.6. Conclusions

At larger scales, the north-eastern population of bottlenose dolphin showed low association indexes among individuals and the presence of two communities socially and spatially segregated, where dolphins have preferences for certain individuals and avoid others. Likewise, at a smaller scale (restricted to Great Barrier Island), dolphins showed similar patterns of a fluid society but structured, with preferred/avoided companions. At different time scales, I found some differences between the two periods analysed. During 2011-2013, dolphins exhibited higher levels of association among individuals, forming a single, more clustered and connected network than in 2015-2019. During 2015-2019, dolphins were segregated in two communities, that again, differ between them. Unlike other populations of bottlenose dolphins where there is usually significant spatial segregation among social communities, this appears to be low at Great Barrier Island. Here, the segregation between communities might be attributed to social preferences instead of just geographic overlap. Community B had more dolphins, with a more clustered and connected network, and presented higher associations than community R. Also, community B presented long-term companion and avoidance unlike community R. There was some degree of spatial segregation of these communities, where community B occupied larger ranges than community R. The changes observed in association patterns, community formation, and the temporal and residence patterns in this population are probably due to the influx of new individuals to the study area. These new individuals were establishing new associations, and this could explain the weaker associations among dolphin during 2015-2019, also contributing to the formation of the social clusters detected during this time. As in other studies, dolphins in this area exhibited preferred and avoided associations probably due to differences in social behaviour, age, sex, kinship, or anthropogenic factors, although the last four variables could not be assessed in this study.

2.7. References

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SKIN LESIONS & TOOTH RAKES



3. Prevalence of skin lesions and tooth rakes in an endangered population of common bottlenose dolphins in New Zealand.

3.1. Abstract

With escalating anthropogenic pressures on marine environments around the world, there has been a renewed interest in the health of free-living dolphins. The health of both individuals and populations of these top marine predators are strong indicators of the health of the ecosystems they inhabit. It has been suggested that sociality plays an important role in susceptibility and transmission of infectious diseases in both human and animals. Skin diseases are an easily observable and trackable trait, which can be useful to correlate to the animal's health and are associated with changes in the ecology of the host and/or pathogen, often directly attributable to anthropogenic environmental modifications. Skin diseases can have severe effects on dolphin populations, therefore, the description of skin diseases in a population and quantifying the prevalence and severity are crucial for the management of vulnerable populations such as the population at the focus of my study. Most studies of skin lesions in cetaceans have included tooth rakes as a category. For my study, I analysed tooth rakes separately from skin lesions since these are produced, usually, due to interactions among conspecifics and not directly by microorganisms. Tooth rakes were defined as superficial and parallel lines, and easily distinguished from other skin markings.

My research focused on describing the most common skin lesions present in bottlenose dolphins at Great Barrier Island. In addition, I assessed the prevalence of skin lesions and tooth rakes, determined their distribution along the body of the dolphins, and developed a standardised protocol for skin lesion classification for bottlenose dolphins in New Zealand. Finally, I described the relationship between the presence of tooth rakes with the dolphins' measurement of strength in the social network and tooth rakes and presence of skin lesions. A total of 154 bottlenose dolphins were photo-identified at Great Barrier Island during 2016-2019. A protocol with 19 definitions of skin lesions was created, and eight of these were present in adult bottlenose

dolphins. Ninety percent of the dolphins showed between one and six lesions and prevalence of the major skin lesions was higher for pale lesions, followed by black lesions, white-fringed spots, dark-fringed spots, nodules, spotted lesions, white fin fringe, and tattoo-like disease. Along the body, lesions were found in all body regions, either in one body part like tattoo-like diseases that was only found in the dorsal area, or in up to four body parts (e.g., pale lesions). Similarly, to skin lesions, dolphins had a high prevalence of tooth rakes on their bodies (97%). Higher proportions of tooth rakes were found on dorsal fin, mid-flank, and anterior areas. In addition, I assessed if dolphins accumulate tooth rakes with time. Results showed that mean tooth rake coverage in dolphins did not change with time. Models that compared tooth rake coverage score with strength (to assess whether having tooth rakes was dependent on the strength of associations with other dolphins) were not significant. My research is the first to describe and quantify the skin lesions and tooth rakes in this nationally endangered population.

3.2. Introduction

With escalating anthropogenic pressures on marine environments around the world, there has been a renewed interest in the health of dolphins. The health of both individuals and populations of these top marine predators are strong indicators of the health of the ecosystems they inhabit (Bossart, 2011). Skin lesions in cetaceans haves been described since the 1950s (Daura-Jorge & Simoes-Lopes, 2011; Gonzalvo et al., 2015; Greenwood et al., 1974; Powell et al., 2018; Simpson et al., 1958; Taylor et al., 2021; Van Bressem et al., 2014; Van Bressem & Van Waerebeek, 1996; Wilson et al., 1999), and are defined as an abnormality in the gross appearance of the body tissue (Lane et al., 2008). These lesions can be widely spread in some populations, and they can last for decades, mainly in estuarine and inshore populations, however, their impact on the health of these populations is relatively unknown (Chan & Karczmarski, 2019). Skin lesions are an observable and trackable trait, which can be useful to correlate to the animal's health and are associated with changes in the ecology of the host and/or pathogen, often directly attributable to anthropogenic environmental modifications (Hart et al., 2012; Van Bressem et al., 2009a). Skin diseases can have severe effects on dolphin populations increasing stranding events, reducing population viability, and even transmitting diseases to humans (Cowan, 1993; Daura-Jorge & Simoes-Lopes, 2011; Ramos et al., 2018; Van Bressem et al., 2009a).

Skin lesions can have different origins such as virus, fungus, or bacteria, each with different consequences for cetaceans. Common viruses include herpesvirus, calicivirus (e.g., genus *Vesivirus*), papillomavirus and poxvirus (Bossart et al., 2005; Smith et al., 1983; Van Bressem & Van Waerebeek, 1996). Poxviruses, for example, are responsible for the occurrence of tattoo skin disease (Smith et al., 1983; Van Bressem et al., 2003), and have been found in 12 species of odontocetes including bottlenose dolphin *Tursiops truncatus* and, in at least one species of baleen whale (Fury & Reif, 2012; Powell et al., 2018; Van Bressem et al., 2003; Van Bressem et al., 2015b; Van Bressem et al., 2009b). Fungi known to cause skin lesions in cetaceans include *Candidiasis*, *Fusarium, Trichophyton* and *Lacazia loboi*. The latter can appear in cetaceans associated with injuries and in immuno-compromised animals (Dunn et al., 1982; Hart et al., 2010; Mouton & Both, 2012; Van Bressem et al., 2008; Van Bressem et al., 2015c). Bacteria identified on cetacean's skin

lesions includes *Brucella ceti, Dermatophilus, Erysipelothrix rhusiopathiae, Pseudomonas* and *Mycobacterium*. For example, *Mycobacterium* causes non-healing, chronic cutaneous or subcutaneous lesions in cetaceans (Lane et al., 2014; Mouton & Both, 2012; Van Bressem et al., 2008; Van Bressem et al., 2009a).

Due to the lack of hair, cetacean skin is more prone to external injuries such as cuts and abrasions compared to other marine and terrestrial mammals. Scarring in cetaceans come from different sources including parasites, predators, accidents, and intraspecific interaction, and tend to acquire a different colouration, usually white or unpigmented (MacLeod, 1998). Intra-specific interactions among bottlenose dolphins involve intra- and inter-sexual aggressive behaviours. Aggression can be directed between males to gain access to females, or from males to females because of sexual cohesion (MacLeod, 1998; Marley et al., 2013; Scott et al., 2005). As a result of these interactions, adult bottlenose dolphins tend to accumulate scars, usually in form of tooth rakes. Tooth rakes are superficial wounds characterised by parallel lines of depigmentation or broken skin (Lee et al., 2019). Tooth rakes are a useful tool to assess conspecific aggression in highly social species such a as bottlenose dolphins (Scott et al., 2005). These behaviours can promote the transmission and spread of diseases (Félix et al., 2019; Van Bressem et al., 2009a), since tooth rakes have been identified as a way of entry of pathogens into the dolphin body and might help the proliferation of certain skin lesions (Mouton & Botha, 2012). Therefore, models of disease prediction can be used for effective management of vulnerable populations.

The bottlenose dolphin is a socially complex species that live in fission-fusion societies in which individuals associate in groups that often change in size and composition (Connor et al., 2000; Würsig & Würsig, 1977). Gregariousness is a key factor for transmission of diseases, as animals with high contact rates increase the chance for this, augmenting vulnerability among their populations (Sah et al., 2018). Bottlenose dolphins' societies are characterised by complex and diverse relationships among its individuals. Understanding the relationships among members of a population can shed light on how diseases can be transmitted. For example, in a social network animals occupying a more central position will have more chances of transmitting information

(Evans et al., 2020) or diseases in the population (Godfrey et al., 2009; 2010). Likewise, animals in this position have more connections with other members of the population, consequently, they will have more opportunities for intra-specific interactions with other animals increasing their chances of contracting diseases.

Photo-identification (hereafter photo-id) is a non-invasive technique that has been widely used in cetaceans to recognise individuals based on natural markings such as nicks, notches, and scars (Würsig & Jefferson, 1990). This technique has also been implemented to assess the prevalence and incidence of skin lesions and tooth rakes in several populations of free-ranging cetaceans (e.g., Bearzi et al., 2009; Félix et al., 2019; Harzen & Brunnick, 1997; Kiszka et al., 2009; Leone et al., 2019; Marley et al., 2013; Ramos et al., 2018; Scott et al., 2005; Thompson & Hammond, 1992; Wilson et al., 2000; Wilson et al., 1997). Through photo-id techniques, it is possible to calculate minimum values of skin disease prevalence and tooth rake coverage since photographs usually focus on the upper body parts of the dolphins (Burdett Hart et al., 2012). Although, the aetiology of the skin lesions cannot be confirmed using photographs, the morphological descriptions of the lesions can help to identify potential pathogens present in the studied area. Since some species might already be under threat, the use of non-invasive techniques is a useful tool for monitoring populations without posing additional risks or stress.

The North Island population of bottlenose dolphin in New Zealand faces numerous anthropogenic pressures including commercial tourism (Constantine et al., 2004), boat strikes (Dwyer et al., 2014), poor water quality, and collapsed fisheries (Hauraki Gulf Forum, 2020). In addition, bottlenose dolphins exhibit a high frequency of tooth rakes due to intra-specific interactions (perhaps due to increased competition for resources), which can lead to the development of skin lesions. Considering the sub-optimal and deteriorating environmental conditions of this region, it is important to describe the current prevalence of skin lesions and tooth rakes in this population. Monitoring of wildlife health is important in conservation management because the appearance of any disease can be an indicator of anthropogenic disturbance (Deem et al., 2001). In addition, comparisons between populations are important to understand how anthropogenic impacts

affect different ecosystems (Rowe et al., 2010). Until now, no systematic health assessments have been conducted on this population of bottlenose dolphins.

The aim of this chapter is to estimate the prevalence of skin lesions and tooth rakes in bottlenose dolphins at Great Barrier Island, Hauraki Gulf, using photo-id data collected between 2016-2019. More specifically, I planned to:

- 1- Describe the most common skin lesions present in bottlenose dolphins.
- 2- Assess the prevalence of skin lesions and tooth rakes in the population.
- 3- Determine the distribution of skin lesions and tooth rakes along the body of the dolphins.
- 4- Develop a standardised protocol for skin lesion classification for bottlenose dolphins in New Zealand.
- 5- Describe the relationship between the presence of skin lesions and tooth rakes with the strength of the dolphins in the social network, and tooth rakes and presence of skin lesions.

3.3. Methods

3.3.1. Study area

The Hauraki Gulf is an area of 4000 km² located on the northeast coast of the North Island of New Zealand, bordering Auckland, the largest city in the country, the Hauraki Plains, the Coromandel Peninsula, and Great Barrier Island (Black et al., 2000; Zeldis et al., 2004). The Gulf is a relatively shallow body of water that can reach depths of up to 60 m (Chart NZ 522, Land Information New Zealand). Due to the influence of the East Auckland Current, the area is productive, with high levels of nutrients (Booth & Sondergaard, 1989; Chang et al., 2003). The Hauraki Gulf contains a variety of marine habitats from open ocean to shallow bays and inlets (Hauraki Gulf Forum, 2020). Great Barrier Island is situated in the outer Hauraki Gulf, approximately 80 km to the east of North Island, New Zealand (Figure 3.1). The island is approximately 28,500 ha (Nichol et al., 2003) and its coastline is characterised by numerous bays and a rocky shoreline, especially on the western coast where bays and inlets have received little sediment (Nichol et al., 2003).



Figure 3.1. Map of Great Barrier Island. Darker shades of blue represent deeper waters. Inset: Great Barrier Island in relation to the North Island of New Zealand.

3.3.2. Data collection

I conducted a series of photo-id surveys from December 2016 to May 2019. I took the photographs from a 90° angle or perpendicular to the body axis of the dolphins following Würsig and Jefferson (1990), from a 5.5 m Stabicraft aluminium vessel. I conducted the three to five day surveys when weather conditions were optimal (i.e., good visibility, good light conditions and sea state Beaufort \leq 3). Monthly surveys were initially planned but due to bad weather conditions, surveys during the winter months (i.e., June, July, and August) were uncommon. I conducted my surveys using the Massey University research vessel *Aronui Moana*, a 5.5 m aluminium Stabicraft vessel powered by a four-stroke 100 hp outboard engine with maximum capacity for five people (Figure 2.2). I conducted non-systematic surveys, between Miners Head and Ross Bay and between 7 am. to 6 pm. at a speed of 15 knots, along the west coast of Great Barrier Island (Figure 3.1).

A group of dolphins was defined as individuals observed in apparent association, moving in the same direction, and often, not always, focused on the same activity (Shane, 1990), and separated by no more than 5 body lengths (~10 m) between them. Each focal group was monitored until all dolphins from the initial group were lost from sight for a period of ten minutes or more, or the dolphins showed signs of avoidance. At each encounter, I approached the group parallel or from the rear at a low speed of <5 knots or at the speed of the travelling group (Tezanos-Pinto, 2009). All individuals in a group were photographed regardless of the extent of their markings to avoid bias towards highly marked animals (Würsig and Jefferson 1990). At the end of each encounter, I took a 'blank' shot to differentiate between consecutive encounters and recorded time, position, and frame number (Tezanos-Pinto, 2009).

The bottlenose dolphin population at the Hauraki Gulf has been photographed and individuals identified and photo-catalogued since 2000 (Berghan et al., 2008). The dolphin images from my photographs were matched to the Hauraki Gulf Bottlenose Dolphin catalogue (HGBDC; Berghan et al., 2008) based on nick and notches on the leading or trailing edge of the dorsal fin (Wilson et al., 1999), and in cases where new dolphins were identified, I assigned a temporary catalogue number (i.e., JP001). Photographs were also classified as poor, fair, good and of excellent quality depending on whether they met at least three of the following attributes: focus, contrast, size and/or angle (See chapter 2 for details). To avoid false positive or false negative errors, only photographs catalogued as good or excellent quality were used to identify individual dolphins (Tezanos-Pinto, 2009). Once all dolphins were identified, the photos were screened manually to detect the presence of skin lesions and tooth rakes.

3.3.3. Developing a protocol to study skin lesion in bottlenose dolphins in New Zealand

Hypopigmented lesions

Hypopigmented lesions refer to lesions that are lighter that the surrounding skin. Lesions considered as hypopigmented include depigmentation, discolouration, cream, pale, spotted, and white lesions. One of the first references to these types of lesions was Thompson and Hammond (1992) where they referred to them as depigmentation, but they did not provide further details. After this study, several other operational definitions have been proposed.

Pale lesions: Wilson et al. (1997) proposed a category called pale lesions that was subdivided into four categories: cream, white and white fin-fringe lesions, and abraded fin tips. *White lesions* were described as circular or amorphous lesions with rounded edges and a smooth surface that lays flush with the rest of the skin, sometimes with a matt, chalky appearance (Wilson et al., 1997). This definition has been used in several publications without any modification (e.g., Bearzi et al., 2009; Burdett Hart et al., 2012). *Cream lesions* were described as very similar to white lesions "but often had a diffuse border and were cream coloured". *White fin-fringe lesions* also look like white lesions, but they occur specifically along the leading and trailing edges of the dorsal fin. Dolphins with this type of lesion, often have white fin-fringe lesions are often rounded, sometimes jagged and more often distinct than diffuse. Finally, *abraded fin tips* present as "white areas of the top third of the leading edge of the dorsal fin. Their edges were jagged or diffuse or both. On close inspection, most abraded fin tips appeared to be composed of a mass of criss-crossed scratch marks and tooth rakes suggesting that they may represent scar tissue resulting from physical wounds rather than disease".

Whitish, velvety lesions: Flach et al. (2008) defined this lesion as a "greyish to whitish, verrucous lesions leading to ulcerations in some cases. When healing, the lesions lose their velvety texture and become light and/or grey in colour". These lesions are often associated with skin injuries, scars, or tooth rakes. Later, Van Bressem et al. (2015a), in what appears to be a publication based on the same data, described *pale dermatitis* as a "suspected primary infectious or super-infected skin lesion characterized by irregular, slightly raised skin sores, pale in colour, either ulcerated or

with a smooth velvety aspect". Evidently, both definitions refer to the same lesions. Van Bressem et al. (2015a) argue that pale dermatitis is consistent with the pale lesion category described by Wilson and colleagues (1997), although their description does not describe the skin as being raised or ulcerated. Based on the photographs provided in both publications, in some cases, this lesion might be associated with a physical damage rather than a pathogenic origin.

Discolouration: Maldini and colleagues (2010) defined a category as discolouration where a whitish patina makes the skin to have a lighter coloration than the surroundings. This discolouration can be found in patches or widespread over the whole body. The authors highlight this lesion as new to the literature. Furthermore, Maldini and colleagues (2010), also defined two additionally categories as *miscellaneous markings* either rounded or irregular in shape. The descriptions of these two categories are somewhat vague and include lesions "well-defined but variably shaped markings, flush with the skin and of contrasting colour". "They were present on body and/or dorsal fin, mostly isolated and, occasionally, in clusters". According to the photos in the publication, these two categories could also fit Wilson et al. (1997) *pale lesions* definition. A discoloured head/nuchal patch have been described to occur in some cetaceans (Toms et al., 2018). This lesion is clearly distinguished from others because there is a clear contrast between a dark/light head against an also dark/light nuchal area (Toms et al., 2018). Due to these very distinctive characteristics, this lesion was kept for further analysis.

Pale skin patch: Sanino et al. (2014) described this lesion as "areas of opaque to translucent skin that seemed to have completely or partially lost their normal pigmentation and had acquired a light grey or whitish coloration. The patches had variable shapes and rounded, distinctive borders". This lesion can appear flush with the skin or raised. The aetiology of this disease was not confirmed, and it can vary in size, covering small areas to over a quarter of the body of a dolphin. According to the photographs in the publication, this definition is similar to the white lesion definition proposed by Wilson and colleagues (1997). Finally, some authors opt to group skin lesion into broad categories. For example, Wilson et al. (1999) in a study including several populations of bottlenose dolphins worldwide, used the category pale lesion. Similarly, Hupman et al. (2017) used

broader categories to group the skin lesions present in common dolphins *Delphinus* sp. in New Zealand and grouped all the light-coloured lesions under a *hypo-pigmented* category without differentiating by colour, size, or shape of the lesions.

Summarising, the definition of hypopigmented skin lesion can be difficult. During the analysis, it was evident that the differentiation between white and cream, can be difficult in photos and can lead to unnecessary categories that can make the task of classification more subjective. During the selection process I followed Wilson and collaborators' (1997) definition of pale lesions for lesions that presented a white or cream colour. Since Wilson and colleagues' (1997) definition of abraded fin tips suggested that this type of lesion originates by physical trauma and not due to pathogens, I decided to exclude this type from my analyses. White fin-fringe lesions, following Wilson et al. (1997) definition, were included in the final protocol since its definition did not overlap with those of other categories.

Hyperpigmented lesions

This category groups lesions that appear on the body of the dolphins and show darker colouration than that of the surrounding area. The following lesions can be considered under this category: black lesions, dark black dot lesions, dark spots, and lunar lesions.

Black lesions: this skin lesion was initially described by Wilson et al. (1997) as "uniformly black, circular, or amorphous patches with rounded edges". They can look slightly depressed below the surrounding skin and its surface appears to be smooth. This definition does not limit the size of the lesions, hence very small or very large hyperpigmented lesions fit this definition.

Dark black dot lesions: Described by Bertulli et al. (2012) as "small black dot lesions resembling those associated with herpesvirus".

Focal skin diseases: Sanino et al. (2014) defined these skin disorders as clusters of round or oval lesions that are small and highly distinctive of unknown aetiology, presenting three different

polymorphisms. The polymorphisms can be light, dark, or ulcerative. The dark polymorphism was described as "...numerous small or medium-sized dark grey, round or oval skin lesions".

Hupman et al. (2017), defined a broad category of skin lesions called hyperpigmented with two subcategories that consider the size of the lesion. One subcategory includes dark, circular, small lesions, and the other dark, clumped lesions of variable sizes.

Dark spots: this type of lesion was defined by Toms et al. (2018) and has similarities to the description by Hupman et al. (2017) as dark, circular, small lesions. Furthermore, Toms et al. (2018) elaborated on this definition by adding "...vary from small and freckled in appearance to a single spot". In addition, these spots can be pitted or not and the "edges are not darker than the spot".

From the definitions above and the photos provided in the publications, it can be inferred that the definitions of Bertulli et al. (2012), Sanino et al. (2014), and Toms et al. (2018) referred to the same lesion, therefore two unique, no overlapping hyperpigmented lesions can be drawn from the above definitions: black and dark spots dot lesions (See Table 3.1).

Lunar lesions: Wilson et al. (1997) described lunar lesions as "...a complex mixture of black, grey, blue-grey, and white skin. The surface of these lesions, is uneven, being both raised and pitted and give the skin an appearance of corroded aluminium. Borders are either jagged or rounded but always distinct". This definition came after the splitting of a previous definition by Thompson and Hammond (1992) of dark lesions (Wilson et al., 1997). Although the definition might be complex, an important aspect of it is the description of the borders as corroded aluminium. Photos from different publications (e.g., Toms et al., 2018) showed that this lesion is distinct enough from other hyperpigmented lesions to be in a different category (Toms et al., 2018).

I found in the literature some definitions that may be synonyms of lunar lesions. For example, Flach et al. (2008) defined some *large, rounded lesions* as "irregular and circular large to very large lesions with an orange or dark outline and lighter inside", resembling a superinfected tattoo lesion. This is what Van Bressem et al. (2015a) later described as expansive annular lesion. Maldini et al.

(2010) define a type of skin lesion which they called *polygons*, described as lesions that are "…presented as shallow depressions of the skin, generally with a hexagonal or polygonal shape and ≤1 cm in diameter. They were characterised by the presence of a dark pinhole in the middle of the depression and occurred either in clusters or isolated…". Similarly, Bertulli et al. (2012) and Van Bressem et al. (2015a) described an *expansive annular lesion*. Bertulli et al. (2012) described them as ring-shaped marks with a light centre and a hyperpigmented outline. Later, Van Bressem et al. (2015a) added more detail to the definition and described them as "ring-like lesions, consisting of a sharply circumscribed light grey outer ring and a paler inner core either of which may or may not be partially obscured by an orange tinge". Based on the definitions and the photographs published, these skin lesions can be considered as a synonym of lunar lesions. Since the definition given by Wilson et al. (1997) offered more details and align well with the aims of my research, I included it as a main category in the final selection of skin lesions included in my analyses (Table 3.1). Nonetheless, I suggest a change in the name to reduce ambiguity as the current name implies a characteristic relating to the moon (e.g., colour, shape, etc.). No lunar lesions were observed in bottlenose dolphins at Great Barrier Island.

Nodules, vesicles, and cutaneous elevations

These names were found in the literature to define any prominent surface found on the skin of the dolphins. Flach and colleagues (2008), defined a *vesicular skin disease* present in some cetaceans of South America as the presence of small to medium vesicles. Van Bressem et al. (2014) defined the skin lesion *nodules* as delineated elevations of skin, with normal colouration and intact skin, that varies in sized from 2 to > 30 mm in its widest part. Later, Van Bressem et al. (2015a) came up with a new description for *cutaneous nodules* defined as "circumscribed skin nodules, grey or normally pigmented". Some publications have described vesicular lesions to be ulcerated (e.g., Hupman et al., 2017; Van Bressem et al., 2007). Hupman et al. (2017) used a category called *raised and proliferative* where they included raised lesions that are nodular/vesicular, multinodular, or plaques. The definition used here was the one given by Van Bressem and collaborators (2014) for nodules (Table 3.1).

Dark and white fringe lesions

Broad categories have been used to group these two lesions. Hupman and colleagues (2017) defined a category called targetoid described as small (< 3 cm) lesions of any shape "with dark- or light-fringed borders, either flat or slightly raised". This category has two sub-categories: lightfringed and dark-fringed. Similarly, Bearzi et al., (2009) also used only one category to group whitefringed and dark-fringed lesions. In one of the first descriptions of this skin lesion, Wilson, and colleagues (1997) defined dark-fringed spots as "pale areas of skin surrounded by a dark halo", often circular. On the other hand, they described white-fringed spots as a "cream or white halo surrounding small circles of normally coloured or black skin". Geraci et al. (1979) described ring lesions as "...each lesion is flat or slightly raised and consists of a solitary 0.5 to 3 cm round or elliptical blemish. These sometimes coalesce". The definition continues with what looks like a definition of white and dark-fringed lesions and tattoo lesions "...early lesions are light grey in colour and may have a dark grey border. In some cases, a reversal of this colour pattern is evident. Advanced stages of the lesion generally have depressed black punctiform centres which may form a stippled pattern of varying design, known as tattoos". Based on the photograph provided, this definition apparently was applied to white-fringe lesions only according to the description given by Wilson and colleagues (1997). In this research, I followed the definitions provided by Wilson et al. (1997) for white-fringed and dark-fringed spots, since they are different enough to be distinguished from other skin lesions and I opted to keep them separated.

Tattoo lesions

Tattoo diseases have been described in the literature since 1979 (Geraci et al., 1979). This lesion is caused by a poxvirus (Blacklaws et al., 2013) and its appearance in an individual may be related to the environmental conditions and the overall health of an animal (Geraci et al., 1979; Van Bressem et al., 2009; 2018). Geraci and colleagues (1979) used the term tattoo to describe an advanced stage of what they named *ring lesion* (according to their definitions this lesion could refer to dark and white fringe lesions). According to the authors, these tattoos "generally have depressed black punctiform centres which may form a stippled pattern of varying design". Later, Van Bressem et al. (2003) described a skin lesion called *tattoo skin disease* "characterized by

irregular, slightly in relief grey, black, or yellowish, stippled skin lesions", using the same "stippled" term used by Geraci and colleagues (1979). Maldini and colleagues (2010) defined a category called 'Pox-like' lesions where they grouped ring and tattoo lesions following the descriptions of Geraci et al. (1979) and Van Bressem (1999). In their definition, they described the variability in size and coloration of these lesions and how the lesions vary in appearance from completely raised to flush with the skin. The authors highlight that although they used the word pox-like, they did not suggest that this is the cause of these lesions and used it descriptively due to its resemblance to other diseases produced by poxvirus. To avoid this issue, some authors have used the term tattoo-like disease to describe skin lesions with similar symptomatology and physical description as tattoo skin disease when there is no confirmation of the pathogen (Powell et al., 2018). Since no skin samples were taken in this research, I followed the category used by Powell and colleagues (2018) and used the definition suggested by Van Bressem et al. (2003). Caution should be exercised when identifying these lesions using the definitions found in the literature, as lesions can change in appearance as they progress. Blacklaws and colleagues (2013) found three different morphologies of tattoo lesions identified initially visually and later confirmed by PCR and transmission electron microscopy. In the acute phase of infection, the lesions are dark, irregular, or rounded with a stippled pattern. This 'stippled pattern' is the key feature to differentiate tattoo lesions from others. In the next stage, healed tattoos present a "coalesced, circular, light grey blemishes with a darker outline". Finally, in the last stage of the infection, the tattoos look like "grey rounded marks surrounded by a darker ring". This last definition overlaps with the definition used for dark fringed lesions. In addition, the authors highlight that the experience of the researchers assessing the photos visually is crucial to achieve accurate identification. To minimise these issues, the definition I used fits the description for tattoo lesions in the acute phase.

Lobomycosis

Lobomycosis (also known as Lobo's disease, Jorge Lobo's disease, keloidal blastomycosis [only in humans], or Lacaziosis) is a chronic granulomatous cutaneous mycotic disease caused by the yeast-like organism *Lacazia loboi* described initially in humans in 1931 in Recife, Brazil (de Carvalho et al., 2015). In humans, this disease is commonly found in populations in tropical regions such as

the north of South America and some areas of Central America and Mexico (Cowan, 1993). This disease only occurs naturally in cetaceans and humans (Murdoch et al., 2008; Reif et al., 2006). Cowan (1993) offered a record of a male bottlenose dolphin found in Texas exhibiting Lobomycosis. It was initially suspected to be this disease based on its appearance and then confirmed with microscopic analysis, although no description of the disease was offered in the publication. According to Reif and colleagues (2006), this disease is characterised by the appearance of cutaneous nodules that "may be smooth, ulcerated, verrucous, or plaque-like and develop on exposed areas of the body" and that in dolphins "may be more extensive, covering large areas of the body". The occurrence of this lesion is associated with places of apparent previous trauma (Reif et al., 2006). Lobomycosis defined as "characterised by greyish, whitish to slightly pink, verrucous lesions, often in pronounced relief, that may ulcerate and form plaques exceeding 30 cm in their broadest part" (Caldwell et al., 1975; Reif et al., 2006; Van Bressem et al., 2015a) was used in this study. Similar to tattoo-like disease, I opted to follow a conservative approach with this disease and use "-like disease" when there is no certainty about the agent causing the lesion following similar studies (e.g., Murdoch et al. 2008; Van Bressem et al. 2007, 2015c; Ramos et al., 2018; Félix et al., 2019).

Orange lesions

Wilson and colleagues (1997) described two different orange colourations that appear on dolphins. First, they described an *orange hue*, where the entire skin of some animals appears orange. The other type is *orange patches*, where the lesion acquires a similar orange or a rusty colour to orange hues, but occurs only in distinct patches, with the edges jagged, rounded or both. Maldini et al. (2010) combined both definitions in a category called *orange film*. This category grouped "orange or rusty-coloured films over the skin either uniformly covering the body or found in dense but small patches on dorsal fin and/or body". Bearzi et al. (2009) also combined both definitions in one category called *orange*. Van Bressem et al. (2015a) defined orange patches as "generally non-raised, orange or rusty-coloured dots, some of which coalesce to form larger blotches". Hupman et al. (2017) described a category for common dolphins called yellow/orange discolouration as an "abnormal yellow/orange discolouration of the epidermis where the skin

remains intact". In my study, I followed Maldini and colleagues' (2010) definition with a minor modification adding the description of the edges given by Wilson et al. (1997).

Spotted and mottle lesions

Spotted and mottle lesions were first described by Burdett Hart and colleagues (2012). Spotted lesion was defined as "localised or widespread in distribution, paler dot in colour than the surrounding skin, circular in shape, and did not have a dark border". In contrast, mottle lesions were described as "scattered flecks of white, pale grey, or dark grey pigmentation, irregularly shaped, and were usually located laterally". Since both definitions did not overlap with others used in this research, I included them in my protocol without any modification.

A summary of the skin lesions and their descriptions is found in table 3.1.

Skin lesion	Description	Reference	Source
Black lesions (B)	Uniformly black, circular, or amorphous patches with rounded edges. They can look slightly depressed below the surrounding skin. The lesion surface itself appears to be smooth.	Wilson et al., 1997	a)
Cloudy white spots (CS)	Blue, grey to white, and cloudy in appearance. Circular in shape with either distinct or diffuse edges, and flush with the skin but could appear as a slight depression.	Toms et al., 2018	b)
Cream lesions* (C)	Similar to white lesions but often have a diffuse border and are cream coloured.	Wilson et al., 1997	a)
Dark black dot lesions (DBL)	Small black dot lesions resembling those associated with herpesvirus.	Bertulli et al., 2012	0
Dark-fringed spots (DFS)	Pale areas of skin surrounded by a dark halo, often circular.	Wilson et al., 1997	a)

Table 3.1. Description of the skin lesions assessed in bottlenose dolphin at the Hauraki Gulf, New Zealand.

Discoloured head/nuchal (DH)	'Hyper- or hypopigmentation on melon and/or associated with the post nuchal depression'. It can occur alone or together 'with hyperpigmentation anterior of nuchal patch & hypopigmentation associated with the nuchal patch.'	Toms et al., 2018	b)
Large, rounded lesions (LRL)	Irregular and circular large to very large lesions with an orange or dark outline and lighter inside.	Flach et al., 2008	d)
Lobomycosis- like disease (LLD)	Characterised by greyish, whitish to slightly pink, verrucous lesions, often in pronounced relief, that may ulcerate and form plaques exceeding 30 cm in their broadest part. Used when virological confirmation is not possible.	Caldwell et al., 1975, Reif et al. 2006, Van Bressem et al. 2007	e)
Lunar lesions (LUN)	A complex mixture of black, grey, blue-grey, and white skin. The surface of these lesions, is uneven, being both raised and pitted and give the skin an appearance of corroded aluminum. Borders are either jagged or rounded but always distinct.	Wilson et al., 1997	() () () () () () () () () () () () () (
Mottled lesion (ML)	Scattered flecks of white, pale grey, or dark grey pigmentation, irregularly shaped, and are usually located laterally.	Burdett Hart et al., 2012	g)
Nodules (N)	Delineated elevations of skin, with normal colouration and intact skin, that varies in size from 2 to > 30 mm in its widest part.	Van Bressem et al., 2014	a)
Orange lesions (O)	Orange or rusty-coloured lesions over the skin either uniformly covering the body or found in dense but small patches with the edges jagged, rounded or both.	Wilson et al., 1997 Maldini et al., 2010	h)
Spotted lesion (SL)	Localised or widespread in distribution, paler dot in colour than the surrounding skin, circular in shape, and do not have a dark border.	Burdett Hart et al., 2012	g)
Tattoo-like disease (TLD)	Characterised by irregular, slightly in relief grey, black, or yellowish, stippled lesions; used when virological confirmation is not possible.	Van Bressem et al., 2003; 2004 Powell et al., 2018	a)

Velvety lesions (VL)	Greyish to whitish, verrucous lesions leading to ulcerations in some cases. When healing, the lesions lose their velvety texture and become light and/or grey in colour. Often associated with skin injuries, scars, or tooth rakes.	Flach et al., 2008	d)
Warts (W)	Cutaneous infection produced by Papillomaviruses. Warts are growths similar in colour to the rest of the skin, usually found in the genital area of cetaceans, although they also can be found on other parts of the body.	Van Bressem et al., 1999 a)
White fin-fringe lesions (WFF)	They look like white lesions, but they occur specifically along the leading and trailing edges of the dorsal fin. Animals with white dorsal fin-fringes often also have white fringes on the leading edges of their pectoral fins and tail flukes. The inner margins of white fin-fringe lesions are often rounded, sometimes jagged and more often distinct than diffuse.	Wilson et al., 1997	a)
White-fringed spots (WFS)	Cream or white halos surrounding small circles of normally coloured or black skin.	Wilson et al., 1997	a)
White lesions* (W)	Circular or amorphous lesions with rounded edges. Their surface is smooth and lay flush with the rest of the skin. Sometimes have a matt, chalky appearance.	Wilson et al., 1997	a)

3.3.4. Skin lesions classification

To develop a protocol for the analysis of skin lesion in bottlenose dolphins in New Zealand, I collated the definitions of the different skin diseases/lesions reported in the literature. Here, I only include cutaneous conditions that macroscopically resembled a known disease (Bertulli et al., 2012), hence, tooth rakes were analysed separately. From the literature, I found 19 skin lesions and their descriptions are summarised in table 3.1. After this information was compiled, photographs of individually identified dolphins were manually reviewed in search of skin lesions on any part of the body of the dolphin. Photos were graded by quality as follows: 1) good – the presence/absence of skin lesions in an individual is clearly identifiable; 2) average –the presence/absence of skin lesions for an individual is uncertain (Burdett Hart et al., 2012). Each photo was assessed by at least two researchers and in cases of disagreement, the photograph was

discarded. Only photos graded as *good*, and *average* were included in the analysis. Once the photos were graded for quality, each lesion present on each dolphin was recorded (e.g., Burdett Hart et al., 2012; Wilson et al., 1997). To associate a mark with a particular location on the dolphin, the body of the dolphin was divided into five parts: head, ventral side, dorsal side, dorsal fin, and fluke (Sanino & Van Bressem, 2014; Figure 3.2). The overall prevalence of skin lesions was calculated as the proportion of the population with at least one skin lesion type following the equation shown below:

$$P_{overall} = \frac{\text{number of distinct individuals with at least one skin lesion}}{\text{all distinct individuals sighted during the study period}} x 100 \text{ (Eq. 3.1)}$$

Similarly, I also calculated the proportion of the prevalence of each skin lesion identified as:

$$P_{lesion type} = \frac{\text{number of distinct individuals with a particular skin lesion}}{\text{all distinct individuals sighted during the study period}} x 100 \text{ (Eq. 3.2)}$$

Dolphins included in the denominator of both equations were counted only once, even if a dolphin was sighted with multiple skin lesions during several sightings (Taylor et al., 2020). In addition, if a dolphin was recorded with several skin lesions, this was included in each calculation of the prevalence of the different types of skin lesions (Eq. 3.2; Taylor et al., 2020). Finally, I scored all the good photos available for an individual.



Figure 3.2. Body sections used for analysis of skin lesion in bottlenose dolphin at Great Barrier Island, New Zealand.

3.3.5. Tooth rakes

Tooth rakes were analysed separated from skin lesions since these are produced usually due to interactions among conspecifics and not by microorganisms. Following the same criteria above, I only used *good* and *average* photos of identifiable dolphins (based on unique dorsal fin profiles) for this analysis. A tooth rake was considered as such if the rake was superficial and parallel, and easily distinguished from other marks made for predators such as sharks (Figure 3.4; Scott et al., 2005). I divided the body of the dolphin in 12 parts to assess where the tooth rakes were more predominant (Figure 3.3). Following Scott and colleagues' (2005) methodology, I assessed the absence or presence of tooth rakes on each part of the body. Each body section was then scored based on the presence (1) or absence (0) of tooth rake marks. The sum of these, gave me a value for **presence** of tooth rakes for each dolphin. For example, a score of 12 was given to an animal with tooth rakes present in every body part. Likewise, I scored each photograph for the presence or absence of tooth rakes in each visible part of the body as follow. Depending on the visibility of a body part, I gave a 1 if more than 75% of the body region was visible, or a 0.5 if less than 75% of the body region was visible. The sum of these gave me a value for **visibility** for each dolphin. I used these values to calculate a *Coverage Score (CS)* for each dolphin as follows:

$$CS = \frac{\sum \text{ presence of tooth rakes}}{\sum \text{ visibility of body parts}} \text{ (Eq. 3.3)}$$

During my surveys, I often had multiple good photographs of individual dolphins that varied in how much of the dolphin was visible above the water. Hence, to determine a single coverage score for an individual dolphin I combined the values for all body sections observed in the photo series. If the same body part was observed in multiple photographs, only the most obvious tooth rake was coded (Scott et al. 2005). Finally, I assessed the overall prevalence (Eq. 3.4) and the prevalence on each body part (Eq. 3.5) of tooth rakes in the dolphins as a proportion using the following equations:

$$P_{Overall} = \frac{\text{number of distinct individuals with tooth rakes}}{\text{all distinct individuals sighted during the study period}} x 100 (Eq. 3.4)$$





Figure 3.3. Body sections used for analysis of tooth rakes in bottlenose dolphin at Great Barrier Island, New Zealand. Modified from Scott et al. (2005).



Figure 3.4. Example of tooth rakes on the dorsal fin (left) and body (right) of bottlenose dolphin.

3.3.6. Temporal changes in coverage score

I also tested if dolphins exhibited "more" tooth rakes as they aged, this can be due to dolphins receiving more aggressions as adults, or when tooth rakes simply do not disappear with time (Scott et al. 2005). To test this, I used photographs of dolphins that were sighted at least 20 months apart since it has been estimated that tooth rakes take between 5-20 months to heal (Lockyer & Morris, 1990). I performed a Wilcoxon Matched-Pairs Signed-Ranks test to assess if the mean coverage scores of the first sighting of the dolphins differ from the coverage scores after 20 months. This test was run using RStudio statistical software (v1.4.1717, R core Team, 2017).

3.3.7. Tooth rakes and network strength

In a social network, strength represents how well an individual is connected to other individuals, i.e., it is the individual's gregariousness (Sosa et al., 2020; Whitehead, 2008). I assessed a possible relationship between strength and tooth rakes present in bottlenose dolphins. I wanted to know if the presence or absence of tooth rakes was defined by the strength in their social network and if dolphins with a higher coverage score of tooth rakes had a higher strength in their social network. To verify this, I first did a generalised linear mixed model with a binomial distribution where presence and absence of tooth rakes was the response variable. The strength of each individual in the network was obtained using the uncompiled version of SOCPROG 2.9. I included dolphins sighted four or more times during the study period, resulting in 50 dolphins being assessed. I used strength as the fixed factor and individual identity and body parts as the random factor. Then, I developed a generalised linear mixed model with a log-gaussian distribution with tooth rake score as the response variable, strength as the fixed factor and individual identity and body part as the random factors. If dolphins with more connections have more opportunities to interact with more individuals, these should have more agonistic interactions with more dolphins in their network, therefore, I predicted that they had a higher coverage score. I calculated the strength of dolphins sighted four or more times at Great Barrier Island during 2016-2019, using the uncompiled version of SOCPROG 2.9 (Whitehead, 2009). I chose this threshold to minimise the influence on the network of transient animals in the population. After refining my database, I

included 50 dolphins in the final analysis. The generalised linear mixed models were done in R statistical software version 4.1.0. (R core Team, 2017).

3.3.8. Skin lesions and sociality

As in the previous section, here I wanted to know if two social measures (mean half-weight index [HWI] and strength) affect the presence or absence of the four most common skin lesions present in this population of dolphins (black and pale lesions, and dark-fringe and white-fringe spots). The mean HWI is used as a proxy for general sociability based on the strength of a dolphin's social ties. Strength was defined previously (see section 3.3.6), and high strength indicates that an individual has strong associations with other individuals (Whitehead, 2009). I calculated the mean HWI and strength using the uncompiled version of SOCPROG 2.9 (Whitehead, 2009). I used a logistic regression to determine if there was a significant association with lesion presence or absence and each measure of sociality. The models were run using R statistical software version 4.1.0. (R core Team, 2017).

3.3.9. Tooth rakes and skin lesions

Finally, I wanted to know if tooth rake scores were different based on the presence and absence of skin lesions. To test this, I performed a Wilcoxon rank sum test in R statistical software version 4.1.0. (R core Team, 2017).

3.4. Results

3.4.1. Skin lesions

3.4.1.1. Skin lesions prevalence in bottlenose dolphins at Great Barrier Island

Previously, only one study in Fiordland has assessed the presence of skin lesions in bottlenose dolphins in New Zealand (Rowe et al., 2010; Rowe & Dawson, 2009). For the North Island population, no previous assessment of the skin conditions has been attempted. For this reason, I compiled all the skin lesions that have been described in the literature until now aiming to propose

a standardised protocol to study skin lesions in New Zealand (e.g., Wilson et al., 1997; Van Bressem et al., 2007, 2009a, 2014; Maldini et al., 2010; Bertulli et al., 2012 and Burdett Hart et al., 2012). As a result of compiling photos and descriptions of skin lesions from the literature, I found 19 different definitions. I used 17 of these 19 definitions to assess my population. These included: black lesions, dark black dot lesions, pale lesions, abraded fin tip, white fin-fringe lesions, darkfringed spots, white-fringed spots, tattoo-like disease, nodules, spotted lesion, lobomycosis-like diseases, lunar, mottle, orange, cloudy white spots, discoloured head/nuchal patch, and warts. During the process of skin lesion categorisation, the definitions were refined since certain characteristics of the lesions, such as colour, can be difficult to differentiate in a photograph and, since I could not be sure of the aetiology of the lesions because biopsies were out of scope of my study, it was more logical to group lesions that were similar in their description (e.g., white, and cream lesions).

A total of 154 bottlenose dolphins were photo-identified at Great Barrier Island during 2016-2019. To assess the prevalence of skin lesion of bottlenose dolphins in this area, I used 5392 good and excellent quality photos. Of the 17 skin lesions selected for assessing prevalence in the bottlenose dolphin population of Great Barrier Island, eight were present in the population: black lesions, dark-fringed spots, nodules, pale lesions (white and cream lesions), tattoo-like disease, spotted lesion, white fin-fringe lesions, and white-fringed spots. The other lesions, lobomycosis-like diseases, warts, discoloured head/nuchal patch, dark black dot, lunar, mottle, orange, velvety, large rounded, and cloudy white spots were not found. Skin lesion prevalence was highest for pale lesions (PL; 84.4%, n = 130), followed by black lesions (BL; 33.1%, n = 51), white-fringed spots (WFS; 17.5%. n = 27), and dark-fringed spots (SL; 10.4%, n = 16), white fin fringe (WFF; 5.84%; n = 9), and tattoo-like disease (TLD; 4.54%, n = 7; Figure 3.5).



Figure 3.5. Prevalence of skin lesion in bottlenose dolphins observed between December 2016 and May 2019 at Great Barrier Island, New Zealand. Pale lesions (PL); Black lesions (B); White-fringed spots (WFS); Dark-fringed spots (DFS); Nodules (N); Spotted lesions (SL); White fin fringe (WFF); and Tattoo-like disease (TLD).

The number of skin lesions per individual varied from one to six (mean = 2.63, SD = 1.27) with an overall prevalence of skin lesions in the population of 90% (n = 138). From the 154 dolphins assessed, 10.4% (n = 16) did not present any skin lesion, 12.3% (n = 19) presented one, 33.1% (n = 51) presented two types of skin lesions, while only 3.90% (n = 6) presented six different lesions in their skins (Figure 3.6).



Figure 3.6. Proportion of bottlenose dolphins presenting different skin lesion types observed between December 2016 and May 2019 at Great Barrier Island, New Zealand.

3.4.1.2. Distribution of skin lesions along the dolphins' body

For this analysis, I discarded white fin-fringe since this lesion only occur on the dorsal fin. From the remaining skin lesions, tattoo-like disease was observed on the dorsal area of all dolphins with this lesion. Black, pale lesions, white fringe spots and nodules were found in four out of five body sections. Most of the dolphins presented black lesions and white fringe spots predominantly on the dorsal area (60%, 85.7% and 81.5%, respectively), followed by the dorsal fin (44%, 33.3% and 14.8%), head (26%, 21.4% and 11.1%) and ventral area (16%, 5.95% and 11.1%). About 91.8% of dolphins with pale lesions presented this more commonly on the dorsal fin and 74.6% of them on the dorsal area, followed by head (21.3%) and ventral section (0.82%). For nodules, 56.6% of the dolphins presented this on the flukes and 44.4% on the dorsal section. Only 5.55% of dolphins were observed with nodules on the head and 3.39% on the dorsal fin. Dark-fringed spots were found on three body sections, 66.7% of the dolphins were observed with the lesion on the dorsal area, 33.3% on the dorsal fin and 12.5% on the head. Spotted lesions were found in two body

sections, 87.5% of the dolphins presented this lesion on the dorsal fin and 50% on the dorsal area (Figure 3.7).



Figure 3.7. Percentage of bottlenose dolphins with different skin lesion in five body sections observed between December 2016 and May 2019 at Great Barrier Island, New Zealand. Pale lesions (PL); Black lesions (B); White-fringed spots (WFS); Nodules (N); Dark- fringed spots (DFS); Spotted lesions (SL); Tattoo-like disease (TLD).

3.4.2. Tooth rakes analysis

A total of 8739 photographs of dolphins with tooth rakes were used to assess their prevalence in this population. From all photographs, the majority were found on the dorsal fin, followed by the other dorsal sections of the dolphins. The body parts that are usually underwater were photographed less frequently (Figure 3.8). The number of body sections with tooth rakes varied from 1-12, with an average of five (mean = 4.73; SD = 2.27) body sections with tooth rakes per individual. The coverage score ranged from 0.4 to 1.6 in the population, with a mean = 1.02 (SD = 0.23).



Figure 3.8. Number of photos per body section used to assess the presence of skin lesions in bottlenose dolphin.

3.4.2.1. Prevalence and distribution of tooth rakes along the dolphins' body

The overall prevalence of tooth rakes was 97.4% (n = 150) of photo-identified bottlenose dolphins. All dolphins showed tooth rakes on the dorsal fin, followed by mid-flank (90.2%, n = 139), anterior section (88.3%, n = 136), anterior peduncle (87.0%, n = 134), head (57.8%, n = 89) and posterior peduncle (49.3%, n = 76). Tooth rakes were less prevalent on the belly (16.9%, n = 26), jaw (16.2%, n = 25), ventral peduncle (10.4%, n = 16) fluke (8.44%, n = 13), chest and throat (4.54%, n = 7; Figure 3.9).



Figure 3.9. Prevalence of tooth rakes observed in bottlenose dolphins between December 2016 and May 2019 at Great Barrier Island, New Zealand.

3.4.2.2. Changes in tooth rake coverage

There was no significant change in the mean tooth rake coverage in dolphins sighted at least 20 months apart (Matched-Pairs Signed-Ranks test, z = -1.422, p = 0.155, N = 36). The coverage score increased in 19 dolphins, decrease in 12 and in five of them remained the same for over two years.

3.4.2.3. Tooth rakes and network strength

For this analysis, I included dolphins sighted four or more times totalling 50 identifiable bottlenose dolphins. The social network illustrating the relationship between these dolphins is shown below (Figure 3.10). The first model, where I compared tooth rake coverage score with strength, was not significant (supplemental table 6.13), meaning that the strength of the individual in the social network does not affect the presence of tooth rakes in an individual. In the second model, I looked at whether having tooth rakes is dependent on strength. This model was also not significant (Figure 3.11; supplemental table 6.14).


Figure 3.10. Social network diagram of bottlenose dolphin four or more times at Great Barrier during 2015-2019. Nodes (circles) represent individual dolphins with their corresponding catalogue number.



Tooth rakes (present or absent)

Figure 3.11. Differences in strength between presence and absence of tooth rakes in dolphins at Great Barrier Island.

3.4.2.4. Skin lesions and sociality

The logistic regression models showed that HWI and strength did not affect the presence or absence of the four skin lesions assessed (Supplemental table 6.15).

3.4.2.5. Tooth rakes and skin lesions

This model showed that there was no significant difference in coverage score between presence and absence of skin lesions (for all types, Wilcoxon rank sum test, p > 0.05; Figure 3.12; Supplemental table 6.16).



Figure 3.12. Graphical representation of the variation of the tooth rake score among dolphins with or without different skin lesions. Black lesions (B); dark fringed spots (DFS); pale lesions (PL); spotted lesions (SL); tattoo-like disease (TLD); Nodules (N); white fin-fringed lesions (WFF); and white-fringed spots (WFS).

3.5. Discussion

3.5.1. A standardised protocol to study skin lesions in cetaceans in New Zealand

I proposed a standardised protocol to monitor the health status of dolphins in New Zealand, where I included 19 skin lesions categories, of which 8 were found in the population of bottlenose dolphins at Great Barrier Island. When developing an efficient protocol, it is important to have categories that minimize overlapping definitions and are not overly complex; too many categories can reduce agreement among assessors and make the assessment process time consuming (Toms et al., 2018). In addition, too many categories decrease the frequency of certain skin lesion in the data set limiting the analytical power (Toms et al., 2018).

In this protocol, I included the minimum number of skin lesion categories that I could retrieve from the literature trying to avoid 'synonyms' (i.e., same skin lesion different name). Some lesion characteristics, such a colour, can be difficult to interpret using photographs. For example, Wilson and collaborators' (1997) definitions of white and cream lesions have the same description, with the only difference being colour. These subtle differences cannot always be captured by a photograph or require substantial experience by the research team to differentiate between these two lesions. In this research, I opted to combine both categories into one, "pale lesions", making the classification system both less complex and more accurate. In addition, I removed redundant definitions found in the literature, replacing these with the most efficient single definition. For example, according to the descriptions and photographs provided by the authors, cloudy (Wilson et al., 1997) and velvety lesions (Flach et al., 2008) appear to correspond to the same lesion. Velvety lesion was kept in the protocol and cloudy lesions were replaced for cloudy white spots, a new category which definition does not overlap with others. A similar situation was found for annular and large rounded skin lesions that appear to be the description of the same lesion type. Even, the photo presented by Bertulli et al. (2012) describing annular lesions resembles the definition of lunar lesion I used in this research. Vesicles and nodules appeared to be used to describe the same lesion. In this last case nodules, as described by Van Bressem and collaborators (2014), had a more detailed description, and this was the definition I used for my research. Finally, in the case of tattoo skin and Lobomycosis disease, I decided to keep the existing definitions of tattoo-like disease and Lobomycosis-like disease, as this is a more conservative approach since no histological analyses were performed in my study.

Although an effort should be made to increase the reliability of the study and the power of the analysis, new categories continue to be defined depending on the characteristics of each population and new discoveries. For example, Toms and colleagues' (2018) defined new skin

lesions categories or refined existing ones in accordance with what they saw in their studied population. They defined cloudy white spots and white freckles, arguing that these two lesions are novel (Toms et al., 2018). Some studies expand the overall definition of a lesion to include tooth rakes as a category (e.g., Hupman et al., 2017; Luksenburg, 2014; Toms et al., 2018). The inclusion of tooth rakes as a skin lesion will ultimately depend on the question being asked (Toms et al., 2018). In my study, I did not include tooth rakes as a category of skin lesions primarily because there is no aetiological agent causing their presence. In addition, tooth rakes are usually the result of intra- and/or inter-specific interactions (MacLeod, 1998). However, tooth rakes do provide an attractive ecosystem for certain microorganisms (e.g., viruses) that facilitates invasion of the host and the formation of skin lesions (Van Bressem et al., 2015a). For this reason, I also removed another non-aetiological category of skin lesions, abraded fin tip. The description of abraded fin tip lesions results from the accumulation of tooth rakes on the dorsal fin of the dolphin and not because of a microorganism. Having a robust classification system in place can help researchers save time when designing a study and the protocol I describe here can also be modify based on the needs of a particular project (Toms et al., 2018). A key advantage of a more universal skin lesions protocol is that it opens more opportunities to compare between studies. The protocol I propose here will be useful for studies where operational definitions are needed to answer specific questions and the use of a specific protocol will vary depending on the necessities of the study.

In these types of studies, photographs are an essential, inexpensive, and non-invasive tool that provides baseline information for monitoring cetacean populations worldwide (Dungan et al., 2012; Hupman et al., 2017; Toms et al., 2018; Würsig & Jefferson, 1990). Relevant to my study, photo-identification has been widely used to study skin lesions and other visible disorders and has proven to be an effective approach (e.g., Hupman et al., 2017). Some skin lesions are easily identifiable from their gross morphology (e.g., Lobomycosis), but others present different aspects during disease progression and can be more difficult to identify based on photos alone (Toms et al., 2018). Furthermore, studies of skin lesions in free ranging marine mammals tend to be opportunistic in nature, mainly, taking advantage of the large number of photographs that are collected during photo-identification-based surveys. For a range of reasons, including restricted

permitting, most published studies do not have biopsy samples to corroborate the aetiology of the pathologies observed in these marine mammal photographs. Therefore, it is important to create standardised protocols for the study diseases such as skin lesions; protocols that can be used by a diversity of conservationists and scientists anywhere in the world.

3.5.2. Prevalence of skin lesions and tooth rakes in bottlenose at Great Barrier Island

I assessed 154 photo-identified bottlenose dolphins, of which 90% showed at least one type of skin lesion. Dolphins at Great Barrier were found to exhibit one to six lesions simultaneously. However, lobomycosis-like diseases, warts, discoloured head/nuchal patch, dark black dot, lunar, mottle, orange, velvety, large rounded, and cloudy white spots were not found in this population. A prevalence of 97.4% of tooth rakes were found in 150 bottlenose dolphins included in this analysis. Most of the tooth rakes were found on the dorsal fin and the dorsal sections of the dolphins, with an average of five body sections exhibiting tooth rakes in a single individual. Only one other study similar to this has been carried out in the Hauraki Gulf (Hupman et al., 2017). Bottlenose dolphins in the Hauraki Gulf are exposed to heavy metals, copper, and zinc, and, to a lesser extent, lead and mercury coming mainly from urbanisation, historical mine activity, and agriculture (State of the Gulf, 2020). It has been suggested that exposure to heavy metals persistent organic pollutants (POPs) can weakened dolphins' immune system making them more susceptible to viral infections (Maldini et al., 2010). According to the State of the Environment Report 2020 (Hauraki Gulf Forum, 2020), land development is one of the main contributing factors to poor water quality and collapse of fisheries and marine ecosystems in the Hauraki Gulf. Hupman and collaborators (2013) found a prevalence of skin lesions in common dolphins Delphinus sp. In the inner Hauraki Gulf that varied from 0.3% to 43% (Hupman et al., 2013). It is important to note that in this study, the researchers included in their analysis of lesions, categories such as tooth rakes, scars, indentations, and impressions, categories that I did not consider as skin lesions.

In Fiordland, Rowe, and colleagues (2010) assessed the presence and extent of epidermal conditions of two populations of bottlenose dolphins. The authors found a prevalence > 96% of skin lesions in both populations, and the extent of the lesions were higher for dolphins from

Doubtful Sound, and higher for females compared to males inhabiting the same location (Rowe et al., 2010). Unlike my study, the authors did not describe specific categories of skin lesions, consequently it is not possible to compare whether the lesions affecting dolphins at Great Barrier Island are the same as those found in Fiordland. What is clear is that the extent of the lesions present in Fiordland's dolphins are likely to be much greater than those observed in this study. In a publication for the Department of Conservation (New Zealand), Rowe and colleagues (2009) presented a photo of a female heavily affected by a skin lesion. From the photograph, the lesion appears to be a lunar lesion. In comparison to GBI, none of the dolphins observed were as heavily affected by a skin lesion as this individual from Fiordland, although I did not quantitatively assess the extension of the skin lesions of my population. When comparing the populations of bottlenose dolphins in New Zealand, the Doubtful Sound populations is more exposed to high levels of tourism (Guerra et al., 2014; Lusseau et al., 2003) and habitat modification due to the large volumes of freshwater discharge from an hydroelectric that affects the salinity and temperature regime of the Sound (Rowe et al., 2010) than dolphins at Great Barrier Island, which could be influencing that the presence of skin lesions be minimal.

Prevalence of skin lesions in bottlenose dolphins world-wide have been reported between 30-100%, when multiple skin lesions are assessed (Burdett Hart et al., 2012; Daura-Jorge & Simoes-Lopes, 2011; Gonzalvo et al., 2015; Harzen & Brunnick, 1997; Leone et al., 2019; Maldini et al., 2010; Murdoch et al., 2008; Rowe et al., 2010; Van Bressem et al., 2003; Wilson et al., 2000). At Great Barrier Island, a high percentage of bottlenose dolphins presented at least one type of skin lesion. Here, bottlenose dolphins have a higher prevalence of pale lesions, followed by black lesions, white-fringed spots, and dark-fringed spots. The prevalence estimated here should be considered as a minimum, since most of the photograph only included the dorsal side of the animals. Wilson et al. (1997) reported a general prevalence of 95% of skin lesion in dolphins in Moray Firth, Scotland. The prevalence of specific skin lesion in this Scottish population varied from 5.6% for white-fringed spots to 54.2% for cloudy white spots. Similarly, Bearzi et al. (2009) found a general prevalence of skin lesions of 79% among bottlenose dolphins in Santa Monica Bay and adjacent areas in California, USA. Prevalence for specific skin lesions range from 0.8% for cream lesions (a subtype of pale lesions) to 51.3% for black lesions. In a study of three adjacent populations in the USA, Burdett Hart et al. (2012) found varying levels of prevalence in skin lesions between 38% and 58.7%. Likewise, the prevalence of specific skin lesions varied among the populations. In Sarasota, tattoo-like disease had the highest prevalence (42.6%) and in Charleston and Georgia dark-fringe lesions showed the highest prevalence (55% and 57.7%, respectively; Burdett Hart et al., 2012). The authors suggested that this might be consequences of variances in environmental factors such as temperature and salinity, or differences in susceptibility dolphins as a result of exposure to anthropogenic contaminants (Burdett Hart et al., 2012). Wilson and collaborators (1999) compared the prevalence and severity of skin lesions in 10 populations of bottlenose dolphin worldwide. They found that the populations living in the extremes of the species' distribution, i.e., Scotland and New Zealand, presented the most extended skin lesions. Commonly, the appearance of skin lesions has been attributed to environmental variables such as low water temperature and low salinity (Wilson et al., 1999, Reif et al., 2006, Murdoch et al., 2008), chemical pollution (Wilson et al., 1997, Van Bressem et al., 2008, Bearzi et al., 2009), immune system disorders (Powell et al., 2018; Yang et al., 2013), physiological stress due to habitat degradation (Rowe et al., 2010), and factors specific to the area inhabited (Rowe et al., 2010).

In the literature, pale lesions have been associated with ectoparasite attachment sites, prior viral infection, inflammation, healing processes due to traumas and herpesvirus (Burdett Hart et al., 2012). Hupman et al. (2017) reported the presence of orange/yellow discolouration and concentric ring in a population of common dolphins present at the Hauraki Gulf. They found a prevalence of 13.2% for this lesion type, which is high compared to reports of bottlenose dolphins world-wide. For example, in Moray Firth, Scotland, orange hue and orange patches had a prevalence of 1.3% and 3.8%, respectively (Wilson et al., 2007). In the USA, Burdett Hart et al., (2012) found a prevalence of orange patches of 6.9% in two adjacent populations of bottlenose dolphins. The definition of concentric ring in Hupman and colleagues' (2017) work, matches the definition I used for lunar lesion, but neither of these two lesions were identified in my bottlenose dolphin population. This could be related to a sampling issue (e.g., photographs with these skin lesions may not have passed the quality check) or bottlenose dolphins in this area are not affected

or affected at a low prevalence by these diseases. However, some other skin lesions were found in both species. For example, pale lesions (84.4%) had the highest prevalence in bottlenose dolphins followed by black lesions (33.1%). In common dolphins, the prevalence was higher for hyper-pigmented (43.1%; this category is equivalent to dark lesions in my research) compared to hypo-pigmented lesion (37.4%; category equivalent to pale lesions). It is important to note that Hupman and collaborator's (2017) definition is broader than the one used in my work, i.e., their hyper-pigmented definition can fit the definitions I used for black and dark black dot lesions, therefore, the comparison of skin lesions prevalence should be viewed with caution. Bottlenose dolphin had similar prevalence of white-fringed spots (17.5%) and dark-fringed spots (15.6%). Similarly, common dolphins exhibit higher prevalence of white-fringed (19.8%) than black-fringed (8.20%). Tattoo-like disease prevalence (4.54%) in bottlenose dolphins was higher than in common dolphins in the same area (1.9%). The appearance of tattoo lesions has been related to the presence of poxvirus mainly in captive animals (Blacklaws et al., 2013; Bossart et al., 2015; Bracht, 2005; Geraci et al., 1979). Although, lesions that have been described initially as tattoo-like disease have been tested negative for poxvirus in laboratory analysis (Burdett Hart et al., 2012). The prevalence of nodules (11.7%) in bottlenose dolphins was higher than in common dolphins (category named raised/proliferative: 0.3% in Hupman et al., 2017).

In my study, I did not record any bottlenose dolphins with signs of lobomycosis-like disease, but this skin lesion has been observed in common dolphins in the Bay of Plenty (Meissner pers. comm.), as this disease can be disseminated by contact among individuals (Felix et al., 2019), future studies should continue to pay attention for its presence since the disease could be spread to other species such as bottlenose dolphins. Although dolphins can live long periods of time with the disease (Kiszka et al., 2009; Murdoch et al., 2008; Reif et al., 2009; Van Bressem et al., 2009; 2015), with advanced lobomycosis and lobomycosis-like disease dolphins often die or vanish (Van Bressem et al., 2009a; Van Bressem et al., 2015b). Information about the health status of free-living marine mammals is crucial for conservation management since this can give us an idea of the quality and physical conditions of the habitat they occupy. Although, knowing the aetiological agent causing a disease is significant, to get this type of detailed information from cetaceans'

studies is usually challenging. Cetaceans live in areas of remote or difficult access, and/or are endangered, which limits the opportunities for taking skin samples to directly identify these agents. This is indeed the situation for obtaining skin samples from bottlenose dolphins in New Zealand.

Most of the studies that have assessed skin lesions, have included tooth rakes as one of their categories (Harzen & Brunnick, 1997; Bearzi et al., 2009; Rowe et al., 2010; Maldini et al., 2010; Toms et al., 2018). In this study, I decided to assess tooth rakes separately from the skin lesions as they are not the direct result of an infection by a microorganism (Van Bressem et al., 2008). But it is important to consider that tooth rakes can offer a route of entry through the skin to these disease-causing microorganisms. All bottlenose dolphins assessed in the Hauraki Gulf showed evidence of tooth rakes in at least one body part. These tooth rake marks were assumed to be mainly from aggressive interactions with conspecifics. Similar rates of tooth rakes have been found in the populations of bottlenose dolphins in Shark Bay, Australia, and Scotland (Scott et al., 2005; Marley et al., 2013; Leone et al., 2019). Tooth rakes were more prevalent in the dorsal fin, the mid-flank, anterior section, anterior peduncle, head, and posterior peduncle. The ventral parts of the body had less prevalence of tooth rakes probably because these areas are less likely to be photographed in photo-identification surveys. Studies of intra-specific tooth rakes rates in populations with different social structures would shed light on how this relates to the levels of aggressive behaviour among conspecifics (Scott et al., 2005). Few studies have attempted to study the role of social behaviour on the presence of tooth rakes in dolphins.

3.5.3. Tooth rake and sociality

In my study, I wanted to know if dolphins with higher coverage scores (i.e., more tooth rakes in the body) exhibit higher gregariousness (measured using strength in social network models) but I did not find a relation between these two variables. It has been suggested that the position of an individual in its social network can influence this, where more gregarious dolphins inflict more tooth rakes than they received. This is similar to disease transmission, where individuals with the most social connections, are not usually at the greatest risk of infection (Drewe, 2010). Wound

healing also could explain the results found here. It has been suggested that wound healing in primates is influenced by age, sex, nutritional states, among others (Archie et al., 2014). For example, alpha male baboons heal faster than lower-ranking males (Archie et al., 2012). A disparity in tooth rakes healing among individuals due to access to resources can bias this type of study (Hamilton et al., 2019). In some species of dolphins, it has been observed that males usually accumulate more scars than females (Rowe & Dawson, 2009). It has also been observed that more reproductively successful male bottlenose dolphins engage in more agonistic interactions (Hamilton et al., 2019). These two factors could lead to males accumulating more tooth rakes due to a sexual behaviour rather than their specific position in the network. Similarly, cycling female received higher rates of aggression than non-cycling females (Scott et al., 2005). In addition, high rate of scar re-pigmentation has been reported in bottlenose dolphin, and if this occurs in my study population, then the coverage scores of animals will be underestimated and any relationship between this and the strength of the dolphins in the social network would not be detected. Further investigation on this topic is necessary to fully understand the relationship between tooth rakes and sociality.

Although I did not find a relation between the coverage score and gregariousness in dolphins, it is important to understand how the sociality of this species is likely to influence the transmission of diseases in a population and assess conservation implications. Félix and colleagues (2019) investigated whether the social behaviour of a population of bottlenose dolphins in Ecuador could influence the epidemiology of lobomycosis-like disease (LLD). The study showed that the prevalence of LLD among social communities varied from low-moderate to high, depending on the rank of the males in each community. In communities with low rank males, the prevalence of LLD was low to moderate, conversely, communities with high rank males have higher prevalence of the disease. They also suggest a horizontal transmission of LLD since they observed male pairs where both dolphins were infected, implying that this is an important risk factor for infections. I assessed whether the tooth rake marks increased with age, comparing photographs of dolphins sighted more than 20 months apart. I found that adults neither accumulate tooth rakes nor have more tooth rakes over time. Similar results were found by Scott et al. (2005) in Shark Bay, Australia,

where they found that differences in tooth rakes prevalence across age groups cannot be solely attributed to the accumulation of scars with age.

3.6. Conclusions

In this study, I developed a robust protocol to study skin lesions in dolphins since the literature on this topic has numerous ambiguities and redundancies due to the same skin lesion type having different names. My protocol offers a foundation for researchers undertaking field-based assessments of dolphin skin diseases. It is true that this will not suit all potential research questions, but this protocol will help to reduce the time associated with establishing baseline datasets. From the 19 categories of skin lesion define in my study, eight were found in my study population. The skin lesions found in this population were: pale lesion, black lesions, white-fringed spots, dark-fringed spots, nodules, spotted lesions, white fin fringe, and tattoo-like disease. Unlike some published skin lesions studies, I did not analyse tooth rakes as a type of skin lesion since these are not triggered by a microorganism. However, I acknowledge that they can be an access route for the microorganisms such as Vibrio spp. that can go on to produce skin lesions. The prevalence of both skin lesions and tooth rakes in my population were high, comparable with bottlenose dolphin populations in Moray Firth, Scotland (Wilson et al., 2000), Monterey Bay, USA (Maldini et al., 2010) and Doubtful and Dusky sound, NZ (Rowe et al., 2010). Most of the dolphins presented at least two skin lesions simultaneously. The areas of the body most affected by skin lesions and tooth rakes were the dorsal area and the dorsal fin. This may be caused by these areas being more vulnerable to damage by conspecifics or the environment (e.g., damage caused by solar radiation), or because these areas are more heavily photographed compared to other areas of the body. Dolphin populations are usually monitored using photo-id that aim to photograph the dorsal fin of the dolphins creating a sampling bias for this region.

The possible relationship between coverage score (a measurement of tooth rake coverage) and the strength of the dolphins in their social network was explored. Surprisingly, no relationship was found between these two variables. As mentioned before, this might be related to hierarchical status where alpha animals tend to heal faster (Archie et al., 2012), biases in a sex receiving more

aggression due to sexual behaviours (e.g., male bottlenose dolphins; Scott et al., 2005) or during oestrus (e.g., female bottlenose dolphins; Scott et al., 2005), or fast healing rates of tooth rakes (Hamilton et al., 2019). These possible causes should be assessed in future studies. The monitoring of tooth rakes can help us to understand the dynamics of aggression in a population (Scott et al., 2005) and contribute to the general knowledge of how conflict operates in this species. Although only eight skin lesions categories were detected in this population, it is important to consider that some rarer categories could have been missed if the photos did not comply with the quality requirements (this could be the case with orange lesions where some photos were discarded due to disagreement between the reviewers). Also, skin lesion prevalence could be higher than detected here due to the areas of the body where they occurred. For example, Papillomaviruses appears as a series of warts in the genital area of affected dolphins. This area is difficult to photograph and therefore, if the disease is present in the population, its prevalence is likely to be underestimated. In the Bay of Plenty, an area that is part of the distribution of this species in the North Island, there have been reports of common dolphin with lobomycosis (Meissner pers. comm.) and should be monitored due to the risk of spreading to other species of cetaceans such as bottlenose dolphin. This highlights the importance of assessing the general health status of cetaceans in the North Island and the need of more accurate and systematic assessments of the skin lesions of this population and other cetaceans in the area. To fully understand the causes and the implications of skin lesions in dolphins, these types of studies need to be combined with more detailed information such as stress, hormonal levels, and body condition parameters (Barlow et al., 2019). More systematic and collaborative assessments would prompt better management of this important population to ensure its long-term viability.

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4. Geographic variation of whistles in New Zealand's bottlenose dolphins

4.1. Abstract

Dolphins are highly social and vocal animals that depend on sound to communicate, navigate, and find food. Dolphins can produce sounds that can be classified into three structural categories: clicks, burst-pulsed sounds, and whistles. Whistles are narrowband frequency modulated sounds with a harmonic structure and are used for various social purposes such as group cohesion, group coordination, individual identification, and to maintain distance between individuals. Dolphins can vary their whistle characteristics in response to vessel presence, social factors such as group size and presence of immatures, and behaviour. Geographic variations in whistle acoustic parameters have been reported worldwide. In this chapter, I focused on four aspects of dolphin acoustics: 1) I applied quantitative classifications to whistles of bottlenose dolphins using seven time-frequency parameters; 2) I described and compared the characteristics of whistles of two isolated bottlenose dolphin populations at Great Barrier Island and Doubtful Sound; 3) I assessed the influence of geographical and social variables in whistle characteristics, and 4) I compared the whistle characteristics of bottlenose dolphin populations from around the world with New Zealand populations. Four of the parameters measured (minimum frequency, end frequency, duration, and inflection points) differed between Great Barrier Island and Doubtful Sound. At Great Barrier Island, the most common type (defined by frequency contour shape) of whistle was upsweep followed by sine. At Doubtful Sound, convex and sine whistles were the most common whistle types. Random Forest models were used to discriminate between whistles from my two study populations. The accuracy of the model was estimated at 90% and the most important variables for classification were whistle type contour, duration, and end frequency. Linear Mixed Models were used to assess if whistle acoustic parameters are influenced by location, group size, and presence of immatures using the two principal components obtained from the NIPALS PCA analysis. PC1 did not differ between areas or with the presence of immature animals. However, minimum frequency and duration differed between the two populations. Whistle parameters of my two populations were compared with 20 populations of *Tursiops* sp. from around the world. The whistle parameters of my two populations were comparable to those of other populations, although, curiously, these parameters where more similar to populations from the northern hemisphere than from the southern hemisphere. My research addressed fundamental gaps in current knowledge of dolphin vocal behaviour, almost non-existent in New Zealand, and how it is shaped by geographical and social variables.

4.2. Introduction

Most social vertebrate species use acoustic signals to convey and gather information about identity, location, and state of the signaller (sender) to a receiver (Wilkins et al., 2013). Many species also use acoustic signals to navigate and find food (King & Janik, 2015; Vasconcelos et al., 2012). In marine environments, acoustic forms of communication can provide advantages over other transmission modes. For example, the long distances that acoustic signals can travel in aquatic environments mean that individuals can communicate at a distance effectively and reduce some of the costs associated with close encounters with conspecifics (Wilkins et al., 2013). Dolphins, in particular, are highly vocal animals and depend on sound to communicate, navigate, and find food (Clark & Clark, 1980). Toothed whales can produce sounds that can be classified into three structural categories: clicks or pulsed signals, burst-pulsed sounds, and whistles or tonal signals (Au & Hastings, 2008; Janik, 2009). Clicks are broadband, short sounds with frequencies between 10 and 200 kHz (ultrasonic range) and are used commonly for echolocation but also are used in conspecific communication (Au & Hastings, 2008; Janik, 2009). Burst-pulsed sounds are broadband pulses consisting mainly of clicks with most of their energy focused on the low frequency trains (Au & Hastings, 2008; Janik, 2009). It is understood that burst-pulsed sounds are also used for communication. Whistles are narrowband frequency modulated sounds with a harmonic structure. Whistles can have frequencies between 3 and > 30 kHz (Gridley et al., 2012; Hiley et al., 2017), and a duration between 100 ms and 4 s (Buckstaff, 2004). Whistles are intense signals and, in free-ranging bottlenose dolphins, have been recorded reaching up to ~169 dB re. 1µPa (Janik, 2000). With few exceptions, all odontocetes can produce whistles (e.g., genus Cephalorhynchus, Kogia, Neophocena, Phocoena, Phocoenoides and Physeter; Au & Hastings, 2008).

Whistles are used in social communication, and cetacean species that have them in their repertoires tend to occur in large groups and are more social, unlike species that lack whistles that tend to be more solitary or form small groups of few individuals (Richardson et al., 1995). Two exceptions to this are orcas *Orcinus orca* and sperm whales *Physeter macrocephalus*, highly social animals that use burst pulses and clicks sounds, respectively (Richardson et al., 1995). Dolphins

produce two types of whistles; signature whistles that are highly stereotyped frequency modulated whistles and non-signature or variant whistles (Caldwell & Caldwell, 1979; Janik et al., 2006; Sayigh et al., 2007). Signature whistles have been extensively studied and were first described in bottlenose dolphins *Tursiops* sp. (Erbe et al., 2020; Fearey et al., 2019; Janik et al., 2006; Jones et al., 2020; King et al., 2013; Kriesell et al., 2014; Quick & Janik, 2012). Currently, signature whistles have been described in many species of dolphins such as common dolphins *Delphinus delphis* (Fearey et al., 2019), Guiana dolphins *Sotalia guianensis* (Duarte de Figueiredo & Simão, 2009; A. Lima & Le Pendu, 2014), Pacific white-sided dolphins *Lagernorhynchus obliquidens* (Caldwell & Caldwell, 1970), Pacific humpback dolphin *Sousa chinensis* (Cheng et al., 2017; van Parijs & Corkeron, 2001), and Risso's dolphin *Grampus griseus* (Favaro et al., 2011). Whistles are used for various social purposes such as group cohesion (Janik & Slater, 1998), group coordination (Acevedo-Gutiérrez & Stienessen, 2004), individual identification (Janik et al., 2006; Janik & Slater, 1998), and to maintain distance between dolphins (May-Collado & Wartzok, 2007).

Whistles have been the focus of extensive communication research in odontocetes since their fundamental components are within the human hearing range and can be easily recorded and analysed (Au & Hastings, 2008). Numerous descriptions of whistle characteristics of bottlenose dolphins have been done around the world (Díaz López, 2011; Gridley et al., 2012; Hawkins & Gartside, 2010; Hernandez et al., 2010; Hiley et al., 2017; Ward et al., 2016) and comparison among populations, although these studies are less common, have demonstrated the vocal plasticity of this species (Bazúa-Durán, 2004; Hawkins, 2010; La Manna et al., 2017; Lima et al., 2020; Luís et al., 2021; May-Collado & Wartzok, 2008; Morisaka et al., 2005; Papale et al., 2014). The characteristics of the acoustic signals used to communicate can vary due to a range of factors. Variation in acoustic signals has been attributed to genetic differences, stochastic processes (Campbell et al., 2010; Trefry & Hik, 2010), cultural drift, ecological and/or sexual selection (Wilkins et al., 2013), and variation in body size (May-Collado et al., 2007a). In cetaceans, vocal variations, at large scale, have been documented in the low frequency calls of both humpback whale *Megaptera novaeangliae* and blue whale *Balaenoptera musculus* songs (Fristrup et al., 2003; Noad et al., 2000; Stafford et al., 2001). At smaller scales, geographic differences have been

reported in several species of odontocetes such as beluga whales Delphinapterus leucas (Panova et al., 2019), spinner dolphins Stenella longirostris (Bazúa-Durán & Au, 2004), striped dolphin S. coeruleoalba (Azzolin et al., 2013), Indo-Pacific Humpback dolphin Sousa chinesis (Dong et al., 2021), bottlenose dolphins Tursiops truncatus (La Manna et al., 2019; Luís et al., 2021) and Indo-Pacific bottlenose dolphins T. aduncus (Hawkins, 2010; Morisaka et al., 2005b). Variations in acoustic signals can have a substantial impact on an individual's ability to recognize a conspecific, hence having consequences for mating, reproductive isolation, and speciation (Slabbekoorn & Smith, 2002; Wilkins et al., 2013). Nevertheless, acoustic variation may also encode specific identity information facilitating individual recognition (Bee & Gerhardt, 2002). In addition, groups can develop shared call repertoires or use vocalisations with similar acoustic properties that enhance group distinctiveness (Crockford et al., 2004; Rendell & Whitehead, 2003). It has been widely documented that dolphins can vary their whistle characteristics in response to vessel presence (Guerra et al., 2014; Ortega-Pérez et al., 2021), social factors such as group size and presence of immatures, and behaviour (Gospić & Picciulin, 2016; Gridley et al., 2016; La Manna et al., 2013; La Manna et al., 2020; Quick & Janik, 2008; Romeu et al., 2017). For example, Pacific humpback dolphins in Moreton Bay Australia, increase their rate of whistle production when boats move into the area (van Parijs & Corkeron, 2001). In Lampedusa, Italy, bottlenose dolphins change their acoustic behaviour in the presence of trawlers to avoid masking of their signals by boat noise (La Manna et al., 2013).

Social factors can also promote variation in whistles. La Manna and collaborators (2019) found that group size and presence of calves influence the whistle parameters of bottlenose dolphins in the Mediterranean Sea. When comparing between sites, the authors found that minimum, maximum, start, and end frequencies tend to increase in the presence of calves in one site, while decrease in the other (La Manna et al., 2019). Behaviour can also promote changes in whistles characteristics. Romeu and collaborators (2017) assessed the difference in whistle parameters of two social communities ("non-cooperative" and "cooperative") of bottlenose dolphin in Brazil in two foraging contexts: interactions with fisherman and other foraging types. Cooperative dolphins tended to emit shorter and higher frequency whistles mostly when not interacting with fishermen,

in addition, these whistles also had more inflections than those emitted by non-cooperative dolphins (Romeu et al., 2017). Moreover, the type of whistle (ascending, descending, concave, convex, multiple, constant) also varied between the social communities, for example, ascending whistles were more common when foraging without fishermen (Romeu et al., 2017).

Bottlenose dolphins are one of the most well-studied marine mammal species (Chilvers & Corkeron, 2002) and are widely distributed around the world. This species can be found in almost all warm temperate and tropical seas, both inshore and offshore (Rice, 1998; Wells et al., 2019; Wells & Scott, 2009). Bottlenose dolphins tend to be primarily coastal, but they can also be found in pelagic waters. Two ecotypes have been described; an inshore form that can be found in estuaries, bays, lagoons and other shallow coastal regions and an offshore form that is apparently less restricted in range and movement (Wells et al., 2019). Individuals in fission-fusion societies, such as bottlenose dolphins, associate in groups that change in size and composition frequently (Connor et al., 2000; Würsig & Würsig, 1977). Bottlenose dolphin populations exhibit various patterns of association that vary in age and gender (Connor et al., 2000) as well as in response to environmental influences (Chilvers & Corkeron, 2001). Female dolphins in Sarasota Bay, for example, like to connect with other females of comparable reproductive stage and age, whereas juvenile dolphins prefer to engage with other juveniles rather than adults. Males also tend to create strong bonds with other males (Wells, 1991) in what are denominated as male dolphin alliances (Connor et al., 2000), however, this is not true in all populations (e.g., at Moray Firth, Scotland; Wilson, 1995).

Geographic variation in acoustic parameters of bottlenose dolphins have been found in sympatric and neighbouring populations worldwide (e.g., Lima et al., 2020; Luís et al., 2021). Lima and colleagues (2020) analysed whistle characteristics of three neighbouring populations of bottlenose dolphin *Tursiops truncatus gephyreus* in southern Brazil and Uruguay. They compared five frequency parameters, duration, and inflexion points among the populations and found variations only in the frequency parameters analysed (Lima et al., 2020). Hawkins (2010) assessed the whistle parameters between bottlenose dolphins from the east and the west coasts of Australia. The

results indicated that whistle acoustic parameters vary between groups based on their tonal class and the acoustic parameter being assessed, and that these differences were most likely motivated by specific environmental factors, such as ambient noise from shipping and boating activities, in addition to varying behavioural circumstances and group sizes (Hawkins, 2010). In a recent study of the vocal repertoire of nine bottlenose dolphin populations in the Atlantic Ocean and the Mediterranean Sea, researchers found that among the acoustic signals assessed (including whistles, burst pulsed sounds, brays, and bangs), only social signals showed acoustic divergence, and the authors suggested that this might imply that cultural transmission is important in driving geographic variation. In addition, the repertoire dissimilarity values among populations were low and did not reflect population distances (Luís et al., 2021).

In New Zealand waters, there are four discrete populations of coastal bottlenose dolphins found in the north-east coast of the North Island, Marlborough Sounds, Fiordland, and Stewart Island (Baker et al., 2019; Bräger & Schneider, 1998; Brough et al., 2015; Constantine, 2002; Tezanos-Pinto, 2009). Genetic analyses show low gene flow among at least three of the populations (excluding the Stewart Island population not included in this analysis; Tezanos-Pinto, 2009). In recent years, new hotspots for the species have been identified around New Zealand at Great Barrier Island (Dwyer et al., 2014), Stewart Island (Brough et al., 2015), and the Kermadec Islands (Baker et al., 2010, 2019). Bottlenose dolphins are classified as Nationally Endangered in New Zealand waters due to the decline in the abundance of the populations in the Bay of Islands and in Doubtful Sound, areas where dolphins have been monitored long-term (Constantine, 2002; Currey et al., 2007; Hamilton, 2013; Hartel et al., 2015; Tezanos-Pinto et al., 2013). Currently, there is an estimate of 1000 bottlenose dolphins in New Zealand (Baker et al., 2019). In this study, I focus on the populations present at Great Barrier Island (part of the north-eastern population) and Doubtful Sound (Fiordland). These two populations differ in factors such as habitat type, social organisation, population size, and anthropogenic pressures. Great Barrier Island is characterised by moderately exposed to sheltered bays, inlets, and a rocky shoreline (Nichol et al., 2003). The social organisation of bottlenose dolphins there appears to be a fluid society but structured, with preferred/avoided companions (Chapter 2). The only estimation of abundance in this area was

done by Dwyer (2014) where she calculated an abundance of 60-131 dolphins depending on the season (Dwyer 2014). Compared to Bay of Islands, Great Barrier Island is a relative quiet place with no commercial marine mammal tourism operations occurring in the area (Dwyer, 2014). On the other hand, Doubtful Sound is characterised by shores formed by almost vertical rock walls that can reach about 100 m depth (Elliott et al., 2011). This population is formed by around 60 bottlenose dolphins (Guerra, 2013) that form large, mixed-sex groups where all members are closely associated. In general, the community structure is temporally stable and constant companionship are prevalent in the temporal association pattern (Johnston et al., 2017; Lusseau et al., 2003).

There have been five studies assessing different aspects of the acoustic behaviour of bottlenose dolphins In New Zealand (Boisseau, 2005; Guerra et al., 2014; Outhwaite, 2018; Peters, 2018; Snell, 2000). Boisseau (2005; 2004) assessed the vocal repertoire of bottlenose dolphins in Fiordland, describing 12 acoustic signals including four broad structural classes: "tonal," "single bursts," "click bursts," and "repeat bursts". In addition, Boisseau (2004) compared the call repertoire of the populations present at Doubtful and Dusky Sound finding significant variation between the fiords, suggesting the presence of dialects between these two neighbouring populations (Boisseau, 2004). Also in Fiordland, Guerra et al., (2014) quantified the effects of tour boats and the research boat on the group structure and vocal behaviour of bottlenose dolphins. Results showed that groups with mother-calf pairs vocalised more when the boats were nearby and while heading away. Moreover, when fast tour boats approach pods, the pods with calves tend to increase their whistle rate while groups without calves are quieter (Guerra et al., 2014). In the North Island, Snell (2000) described the bottlenose dolphins' whistle repertoire in the Bay of Islands and more recently, Peters (2018) compared call rates of two bottlenose dolphin ecotypes and the influence of vessels in the same area. Her results suggest a call divergence based on the consistent differences in the social vocalisations of the ecotypes. Furthermore, the vocal repertoire of oceanic bottlenose dolphins is more complex than that of coastal bottlenose dolphins (Peters, 2018).

In this chapter, I contribute with new information about dolphin whistle characteristics and, for the first time, quantitatively compare these characteristics between geographically and genetically isolated populations of bottlenose in New Zealand. I aimed to do this by:

- 1- Applying quantitative classifications to whistles of bottlenose dolphins using some commonly measured time-frequency parameters.
- 2- Describing and comparing the characteristics of whistle vocalisations of two isolated bottlenose dolphin populations: Great Barrier Island and Doubtful Sound.
- 3- Assessing the influence of geographical (study area) and social variables (group size and presence of juveniles and calves) in whistle characteristics.
- 4- Comparing the whistle characteristics of bottlenose dolphin populations from around the world with New Zealand populations.

This research addresses fundamental gaps in current knowledge of dolphin vocal behaviour, almost non-existent in New Zealand, and how vocalisations are shaped by geographical (i.e., study area) and social variables (e.g., group size and presence of juveniles and calves). It was expected that the two populations presented different vocal characteristics due to habitat, group size, and composition. In addition, research on the geographic variation of acoustic signals can provide insights into the factors that influence the divergence and evolution of these signals (Endler, 1983). Moreover, comparative analysis between populations is essential to test different hypotheses about the drivers behind the evolution of acoustic signals (Carroll & Corneli, 1999).

4.3. Materials and methods

4.3.1. Study site

The bottlenose dolphin populations at Great Barrier Island and Doubtful Sound are approximately 1,200 km apart and genetic analysis of these populations have demonstrated little, if any, gene flow between them (Tezanos-Pinto et al., 2009). For these reasons they are considered isolated populations. Great Barrier Island (36°12′S 175°25′E; Figure 4.1) is situated in the outer Hauraki Gulf, approximately 80 km to the east of North Island, New Zealand. This island is approximately

28,500 ha (Nichol et al., 2003), and covers 36 km from north to south and is 20 km wide (Morley & Hayward, 2009). The acoustic data were collected on the western side of the island where numerous bays and inlets occurred along a rocky shoreline, ranging from moderately exposed to sheltered (Nichol et al., 2003). Water depth in the area can reach up to 60 m (Chart NZ 522, Land Information New Zealand), considerable deeper than more inshore areas of the Hauraki Gulf. Sea water temperatures around Great Barrier Island are warmest in February when they peak at 22°C and lowest in August when they drop to 15°C. Although, Great Barrier Island is the largest island in the Hauraki Gulf, the human population density is low, and significant parts of its western coast remain uninhabited (Dwyer et al., 2014). Currently, there are no commercial marine mammal tourism operations in the area (Dwyer et al., 2014) and, in general, boat traffic is low most of the year except for the summer months (Dwyer, 2014; Outhwaite, 2018). Doubtful Sound (45°30S, 167°00E, Figure 4.1) is in Fiordland National Park on the west coast of the South Island of New Zealand. The National Park is formed by 14 fiords, being Doubtful Sound the second longest at 40.3 km. Doubtful Sound has two main openings to the Tasman Sea; the Main Fiord and Thompson Sound and is characterised by shores formed by almost vertical rock walls that can reach about 100 m depth (Elliott et al., 2011). During winter and spring, the average sea water temperature reaches 13°C while during summer and autumn the average is 15°C.



Figure 4.1. Map of New Zealand showing the locations where acoustic data was collected. Inset: Doubtful Sound in the left and Great Barrier Island top-right.

4.3.2. Acoustic data collection

Acoustic recordings at Great Barrier Island were collected during boat-based surveys between November 2017 and May 2019, when weather conditions were optimal (i.e., good visibility, good light conditions and sea state Beaufort \leq 3). When a group of dolphins was sighted, boat speed

was decreased and a slow approach to the group was made. The following information was recorded in every encounter: date, time of day, composition of the group (adult, juveniles, calf, and neonate), size of the group and position of the group. Standardised photo-identification methods were followed during each encounter (see Würsig & Jefferson, 1990; and chapter 2 for more details) using a camera Cannon EOS 7D Mark II fitted with 100-400mm lens. After completing the photo-identification, the acoustic recordings were made with the boat engine off if the dolphins stayed in a bay or if they stayed within range. Acoustic recordings at Great Barrier Island were made using two different hydrophones. A C55 hydrophone (Cetacean Research Technology, Seattle, USA) was used in November 2017 and a SoundTrap 300 HF (Ocean Instrument, Auckland, New Zealand) for the rest of the study. The C55 hydrophone had an effective sensitivity of -165 dB re $1V/\mu$ Pa and sounds were recorded using a TASCAM DR-44WL 4track Portable Digital Recorder with a frequency response up to 96 kHz/24-bit resolution Broadcast WAV Format File for 4 channels. The SoundTrap 300 HF is a self-contained hydrophone set to record continuously at a high gain (+12 dB) with a sample rate of 576kHz and with 16-bit resolution. Settings also include a high pass filter (400 Hz), effective sensitivity of -171 dB re 1 V/ μ Pa, and a flat frequency response of 400 Hz – 150 kHz ± 3 dB. One or two hydrophones were deployed during the observations and were recording continuously while dolphins were within 100 m from the research vessel. Acoustic recordings from Doubtful Sound were collected by Dr. Marta Guerra (University of Otago) and were provided for comparison. These recordings were obtained between December 2011 to November 2012 and were made using a custom-built stereo-hydrophone array consisting of two hydrophone elements separated by 5 m. Each hydrophone node contained a 40 dB pre-amplifier with a 3 dB/octave high-pass filter (corner frequency: 3.39 kHz). Sounds were recorded using an Edirol R44 digital recorder with a frequency response up to 48 kHz/16-bit (More details on data collection and equipment used in Guerra et al., 2014).

4.3.3. Acoustic analysis

Recordings made with the Soundtrap 300 HF hydrophone were downsampled using Audacity[®] software, version 3.0.5, to the same sampling rate used by the C55 hydrophone (48 kHz).

Recordings were then inspected visually and aurally using Raven Pro 1.6 (Cornell Lab of Ornithology, Ithaca, USA). Spectrograms were created to visualise the whistles using a Hann window (Bopardikar et al., 2018; Kaplan & Reiss, 2017; Dong et al., 2021; Luís et al., 2021) with Fast Fourier Transformations (FFT) of 1024 and 50% overlap (Luís et al., 2021). Whistles were selected and measured from the spectrograms. Most of the measurements were calculated automatically by Raven Pro 1.6 after drawing a box on the whistles selected and others, such as start and end frequency, inflection points, type of whistles and quality, were manually entered (Figure 4.2).



Figure 4.2. Raven Pro 1.6 spectrogram window produce by FFT of 1024 and 50% overlap using a Hann window. Blue boxes are the selections from where the measurements are calculated.

Whistles were defined as narrow-band tonal signals longer than 0.1 s in duration, often with harmonics (Gridley et al., 2015; Janik & Sayigh, 2013; Neves, 2013) and where at least part of the fundamental frequency starts above 3 kHz (Gridley et al., 2012). Whistles were assigned to one of three categories based on their signal-to-noise ratio (SNR) as follow: (1) signal is faint but visible on the spectrogram; (2) signal is clear and unambiguous; (3) signal is prominent and dominates (Gridley et al., 2015). Only sounds graded 2 and 3 were retained for further analysis. Whistles were also discarded if they overlapped with other whistles, the contours were unclear (especially at their start and end points; Figure 4.3), or the upper frequency limit was clipped (Bazúa-Durán &

Au, 2002). When whistles were separated by less than 1 s, they were considered different whistles if the gap between both whistles are more than 200 ms, or if smaller, larger than the duration of the whistle. Also, the difference between the ending and the beginning of each whistle must be greater than 3 kHz, lastly, the second whistle is twice as intense as the first one (Bazúa-Durán & Au, 2002).



Figure 4.3. Example of whistles discarded from analysis due to overlapping. Spectrogram made in Raven Pro 1.6, produced by FFT of 1024 and 50% overlap using a Hann window.

Seven parameters were measured for every whistle selected for analysis: Minimum frequency (MinF), maximum frequency (MaxF), frequency range (FR), start frequency (SF), end frequency (EF), number of inflection points (IF), and duration (D) (Figure 4.4; Table 4.1). Whistles were assigned to one of six whistle types (Bazúa-Durán & Au, 2002; Dong et al., 2021) based on their fundamental time-frequency contour as follow: constant frequency whistle where the frequency changed by about 25% or less over the total duration of the signal. In upsweep whistles the frequency is modulated with the instantaneous frequency increasing over time and do not have any large inflection points. Similar to upsweep whistles, downsweep whistles are frequency

modulated but with the instantaneous frequency decreasing. Convex and concave whistles are frequency modulated whistles with one inflection point. In the convex whistle, the frequency initially decreasing with time, followed by an ending portion in which the frequency increases with time, opposite to concave whistles frequency initially increasing with time, followed by an ending portion with the instantaneous frequency decreasing with time. Sine whistles are frequency modulated with more than one repetition of a hill or a valley and the contour appearing somewhat like a sinusoidal signal with at least two inflection points (Table 4.2).



Figure 4.4. Illustration of a whistle contour showing the parameters measured.

Table 4.1. Definitions of the seven acoustic parameters measured in each whistle Units: Hertz (Hz), n = number, and s = seconds.

Acoustic parameter	Unit	Definition
Minimum frequency (MinF)	Hz	Frequency at the lowest point in whistle contour
Maximum frequency (MaxF)	Hz	Frequency at the highest point in whistle contour
Frequency range (FR)	Hz	MaxF minus MinF
Start frequency (SF)	Hz	Frequency at the start of the whistle contour
End frequency (EF)	Hz	frequency at the end of whistle contour
Number of inflection points (IF)	n	Number of points where contour changes between
		positive and negative slope or vice versa
Duration (D)	S	End time minus start time
Table 4.2. Definitions and examples of the six contour types of common bottlenose dolphins at Great Barrier Island, New Zealand.

Contour	Definition	Example
Constant frequency	Frequency changed by about 25% or less over the total duration of the signal.	
Upsweep	Whistles that are frequency modulated with the instantaneous frequency increasing over time and do not have any large inflection points.	
Downsweep	Whistles that are frequency modulated with the instantaneous frequency decreasing over time and do not contain any large inflection points.	
Convex	Whistles that are frequency modulated with the instantaneous frequency initially decreasing with time, followed by an ending portion in which the frequency increases with time.	A
Concave	Whistles that are frequency modulated with the instantaneous frequency initially increasing with time, followed by an ending portion with the instantaneous frequency decreasing with time.	
Sine	Whistles that are frequency modulated with more than one repetition of a hill or a valley and the contour appearing somewhat like a sinusoidal signal with at least two inflection points.	AV/

Ansmann (2005) proposed a sub-categorisation of the six main types of whistles described in Table 4.2. The sub-categorisation was made based on the degree of modulation of these general types, as followed: A number one was given when the main whistle type did not present further modulation (e.g., A1, B1, C1, D1, E1, and F1), 2 when there is a modulation at the start of the general type (e.g., A2, B2, C2, D2, E2, and F2) and 3 when the modulation is at the end (e.g., A3, B3, C3, D3, E3, and F3). A number 4 means a further modulation at both sides of the main whistles type. A 5 was added, following this logic, to upsweeps and downsweeps whistles indicating a step within the general whistle type (e.g., B5 and C5), Finally, the sine whistle type was described in a different way. Every number indicates the degree of sinusoidal modulation, i.e., the number of inflections, as well as whether the sine contour starts with a rising or a falling frequency section. For example, F1 starts with a rising section and has two inflection points. In contrast, F8 starts with a falling section and has five or more inflection points. In my thesis, this information was considered for the variable "whistle complexity" that was used in different analysis explained in the next section.



Figure 4.5. Idealised contours of the different whistle subtypes. Taken from Ansmann (2005).

4.3.4. Statistical analysis

All analyses were carried out using R statistical software version 4.1.0. (R core Team, 2017). Minimum values, maximum values, standard deviations (SD), and coefficient of variations (CV) for each whistle parameter were calculated for each population to describe inter- and intrapopulation variability. A Kruskal-Wallis test was used to assess the difference between acoustic parameters in each whistle type. To compare different whistles parameters among the different populations, a two tailed t-test (t) for equal variances and a Cochran-Cox t-test (t') for unequal variances were employed using the mean value, standard deviation (SD) and sample size (n) of each population to calculate the p value. To classify whistles to a specific population, I used Random Forest (RF) analysis (Oswald et al., 2021; Rankin et al., 2017; Webster et al., 2016) using the 'randomForest()' function in the RF package (Liaw & Wiener, 2002). Random Forest is a machine-learning method that creates a series of decision trees that work collectively and is widely used in acoustic studies (de Melo et al., 2021; Garland et al., 2015; Henderson et al., 2012; Papale et al., 2021; Rankin et al., 2013; Serra et al., 2020; Webster et al., 2016; Yang et al., 2020). Each individual decision tree produces a class prediction and the class prediction with most 'votes' becomes the model's prediction (Breiman, 2001). The advantage of RF analysis is in its capacity to model complex interactions among variables and provide high classification accuracy (Webster et al., 2016). In this study, 66.6% of the data were used to train the supervised RF model and the remaining data were used to validate the model. Study area was used as the response variable; hence, each tree was grown using a classification method (the response variable is categorical), and each of the acoustic parameters described in table 4.1, in addition to type of whistle contour (Table 4.2) were used as predictor variables. The number of predictor variables to be searched at each node (mtry) was 3 and the number of bootstrap replicates or trees to grow (ntree) was set to 500. Out-of-bag (OOB) estimates were used to monitor error from the bootstrap training set. Bagging is useful since this enhances accuracy when random features are used. Also, bagging may be used to provide continuous estimates of the generalisation error of the combined ensemble of trees, as well as estimates of strength and correlation (Breiman, 2001). I used the Gini Variable Importance Index to understand the contribution of each variable to the model prediction (Breiman, 2001; Oswald et al., 2021) and mean decrease in accuracy to understand what variables provide more accuracy to the models.

Since acoustic variables are highly correlated, I used a principal component analysis (PCA) to reduce the number of variables into two independent variables (La Manna et al., 2019). I used a Non-linear Iterative Partial Least Squares (NIPALS) algorithm to generate the principal components as this algorithm allows for incomplete data to remain in the analysis (Stacklies et al., 2007). I used the package 'ade4' (Dray & Siberchicot, 2020) for these analyses. Two components of the PCA (PC1 and PC2) were retained for further analysis and together these explained 99.99% of the total variance. I used linear mixed effects models to test the association between PC1 and PC2 and geographical (study area) and social variables (group size and presence of juveniles and calves) with a Gaussian distribution (La Manna et al., 2019). Group size was used as the random variable in the models. I used the package 'Ime4' (Bates et al., 2007) to develop the models.

To test for differences in the level of variation in acoustic parameters of New Zealand bottlenose dolphins with other populations from around the world, I compared the coefficients of variation from diverse populations. The acoustic parameters for other populations of bottlenose dolphins were obtained from published and unpublished literature (Table 4.8). For these global comparisons, I used summary statistics (mean, SD and sample size) as raw measurement data were not available for all studies. I compared the level of variation in six whistles parameters between populations using the function *'asymptotic()'* in the package *'cvequality'* (Marwick & Krishnamoorthy, 2019). A hierarchical cluster analysis was performed to visualise differences or similarities among population using the squared Euclidean distance matrix used to compute the distance between each pair of rows, and Ward's method (Dong et al., 2021) that minimises the total within cluster variance and attempts to create equal size clusters. The mean values of six whistle acoustic parameters were used for the hierarchical cluster analysis was done using the *'hclust'* function in the *'stats'* package (v.4.1.0., R core Team, 2017).

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4.4. Results

Recordings of bottlenose dolphins were obtained from the Great Barrier Island region during nine encounters totalling 34 h and 48 min. For analysis, 577 whistles graded 2 or 3 were selected. Group size for pods, where recordings were possible, ranged from seven to 81 individuals, with a mean group size of 49 dolphins. The mean number of immatures present in the groups was 3.7 juveniles and 2.9 calves. In Doubtful Sound, data were obtained from 25 dolphin encounters totalling 60 h and 15 min of recording. A total of 509 good quality whistles were selected for further analysis. Group sizes ranged from six to 54 dolphins, with a mean group size of 24. Mean number of immatures were 2.3 juveniles and 0.48 calves per group.

4.4.1. Description of whistles parameters at Great Barrier Island and Doubtful Sound

Dolphin whistles at Great Barrier Island averaged 0.9 s in duration, ranging from 0.082 s to 3.34 s. Whistle MinF averaged 6.87 kHz reaching an average MaxF of 14.44 kHz, and 4.51% (n = 26) of the whistles had a MaxF over 20 kHz (ultrasonic range). Whistles without inflexion points accounted for 42.8% (n = 247) of the total whistles, the rest of the whistles (n = 330) had between one and 11 inflection points. In comparison, whistles from Doubtful Sound were longer, lasting between 0.029 s and 5.91 s (t-test, p < 0.05). Mean values of MaxF and MinF were similar between both populations (t-test, p > 0.36 and p > 0.029, respectively), but SF and EF were lower at Great Barrier Island (t-test, p < 0.05) while FR was higher (t-test, p < 0.05). The Doubtful Sound population presented whistles with considerably more inflexion points than Great Barrier Island (29 and 11 inflection points, respectively. Figure 4.6). Summary descriptive of the whistle parameters are shown in table 4.8.



Figure 4.6. Graphical representation of the variation of the whistle's parameters measured at two locations in New Zealand. DS: Doubtful Sound and GBI: Great Barrier Island. MinF: Minimum frequency; MaxF: Maximum frequency; FR: Frequency range; SF: Start frequency; and EF: End frequency.

All whistle contours defined in table 4.2 were found in both populations. For Great Barrier Island, upsweep whistles were the most common type, accounting for 44.7% (n = 248) of the total whistles. This type was followed by sine whistle types that comprised 26.3% (n = 152) of all whistle types. Convex, downsweep, constant, and concave whistle contours accounted for 12.5% (n = 72), 7.80% (n = 45), 6.41% (n = 37) and 3.64% (n = 21) of all whistles, respectively (Figure 4.7). Summary of the descriptive statistics for all the acoustic parameters measured per whistle type are shown in table 4.3. All whistle parameters varied between the six whistle contours analysed (Kruskal-Wallis tests, p < .005). The higher MaxF, FR and longest D were found in whistles with a sine contour. Concave whistles showed the highest mean values for ST and EF and its MaxF was similar

to the sine whistles. Lower MinF mean values were found for convex whistles, followed by downsweep and sine type whistles. Mean values of duration where similar for constant and downsweep whistles. In Doubtful Sound, convex whistles comprised more than half of the whistle types assessed (54.5%, n = 277), followed by sine and upsweep, accounting for 19.8% (n = 101) and 15.5% (n = 79), respectively (Figure 4.7). At a lower proportion, concave and constant whistle types were found representing together 2.16% of the whistle types. All whistle parameters varied between the six whistle contours analysed (Kruskal-Wallis tests, p < 0.005). Constant frequency whistles were rarely found in this population but had higher MinF, SF and D than constant frequency whistles at Great Barrier Island that had higher FR and EF. MaxF cannot been compared since the sample size from Doubtful Sound was small (n = 2). Upsweep whistles at Great Barrier Island presented higher mean values in all the parameters measured, whereas downsweep presented higher values in all the parameters at Doubtful Sound. Convex whistles had similar values in both population in MinF, MaxF and FR, but SF and D were higher for Doubtful Sound. Mean values for concave whistles were higher for Great Barrier Island except for MinF. Lastly, for sine whistles MaxF, FR, SF and D mean values were higher for Doubtful Sound. Summary of descriptive statistics for all whistle types are presented in table 4.4.



Figure 4.7. Frequency of whistle type at DS = Doubtful Sound and GBI = Great Barrier Island.

Param	eters	Constant (n = 37)	Upsweep (n = 248)	Downsweep (n = 45)	Convex (n = 72)	Concave (n = 21)	Sine (n = 152)
	Mean ± SD	7.57 ± 2.97	7.05 ± 1.50	6.45 ± 2.78	6.03 ± 2.02	8.99 ± 4.14	6.65 ± 2.04
MinF (kHz)	Minimum	2.56	3.12	0.9	2.23	4.97	2.30
	Maximum	15.0	12.7	16.1	11.1	22.2	16.1
	Mean ± SD	10.1 ± 3.56	15.0 ± 2.86	12.6 ± 3.69	14.0 ± 2.87	14.8 ± 4.38	15.3 ± 2.90
MaxF (kHz)	Minimum	3.74	8.06	5.19	4.77	10.5	8.88
	Maximum	17.9	24.2	20.4	20.6	27.0	28.3
	Mean ± SD	2.58 ± 1.91	7.94 ± 2.80	6.13 ± 2.80	8.01 ± 3.07	5.78 ± 2.66	8.63 ± 3.08
FR (kHz)	Minimum	0.35	8.06	1.52	1.33	1.07	1.87
	Maximum	10.5	24.2	13.6	14.6	11.9	17.8
	Mean ± SD	8.40 ± 3.12	7.31 ± 1.67	11.0 ± 4.04	6.96 ± 2.22	13.5 ± 4.44	8.01 ± 2.77
SF (kHz)	Minimum	2.49	1.20	3.53	1.06	8.72	1.08
	Maximum	15.0	12.7	20.4	13.8	25.8	16.8
	Mean ± SD	10.2 ± 5.82	14.7 ± 2.99	8.11 ± 3.08	7.50 ± 3.22	13.5 ± 4.67	13.1 ± 4.21
EF (kHz)	Minimum	2.49	2.15	3.27	1.06	9.58	3.18
	Maximum	15.5	24.2	16.2	7.50	26.9	28.2
D (s)	Mean ± SD	0.77 ± 0.53	0.66 ± 0.29	0.77 ± 0.39	0.94 ± 0.44	0.75 ± 0.43	1.35 ± 0.57
	Minimum	0.12	0.082	0.11	0.16	0.14	0.26
	Maximum	2.05	1.51	1.89	2.18	1.85	3.34

Table 4.3. Summary of descriptive statistics of the acoustic parameters measured on the six whistle contours found in bottlenose dolphins at Great Barrier Island. SD = standard deviation, N = 575.

Note: two whistles were not assigned to any of these contour categories.

Param	neters	Constant (n = 2)	Constant (n = 2) Upsweep (n = 79)		Convex (n = 277)	Concave (n = 9)	Sine (n = 101)
	Mean ± SD	9.06 ± 0.78	6.83 ± 1.54	8.87 ± 1.90	6.13 ± 1.46	9.25 ± 1.82	7.38 ± 1.87
MinF (kHz)	Minimum	8.28	4.15	3.98	3.12	5.30	4.19
	Maximum	9.85	14.3	13.6	11.9	10.8	11.4
	Mean ± SD	10.4 ± 0.016	13.1 ± 3.19	16.0 ± 3.95	14.6 ± 3.39	13.2 ± 4.13	16.9 ± 3.02
MaxF (kHz)	Minimum	10.3	7.52	9.03	9.25	6.65	11.3
	Maximum	10.4	22.3	24.0	24.0	18.8	24.00
	Mean ± SD	1.29 ± 0.80	6.24 ± 2.82	7.09 ± 3.40	8.46 ± 3.19	3.97 ± 3.00	9.53 ± 3.20
FR (kHz)	Minimum	0.49	1.83	1.47	2.94	0.865	4.05
	Maximum	2.09	12.7	14.7	17.6	8.62	16.6
	Mean ± SD	9.94 ± 0.39	6.89 ± 1.71	14.9 ± 3.91	7.67 ± 2.31	12.00 ± 3.55	9.92 ± 3.14
SF (kHz)	Minimum	9.55	4.15	6.20	4.81	5.78	4.26
	Maximum	10.3	14.3	23.1	17.9	16.5	20.8
	Mean ± SD	9.06 ± 0.78	12.5 ± 2.84	9.75 ± 3.27	6.74 ± 2.54	12.9 ± 3.76	11.4 ± 4.61
EF (kHz)	Minimum	8.28	7.52	3.13	1.66	6.65	1.11
	Maximum	9.85	22.3	18.1	18.8	18.4	23.7
D (s)	Mean ± SD	1.54 ± 1.27	0.40 ± 0.41	0.86 ± 0.38	1.09 ± 0.26	0.58 ± 0.34	1.49 ± 0.82
	Minimum	0.27	0.029	0.30	0.49	0.14	0.47
	Maximum	2.81	1.32	2.04	2.59	1.28	5.90

Table 4.4. Summary of descriptive statistics of the acoustic parameters measured on the six whistle contours found in bottlenose dolphins at Doubtful Sound. SD = standard deviation, N = 508.

Note: one whistle was not assigned to any of these contour categories.

4.4.2. Whistle classification in two populations of bottlenose dolphins in New Zealand

Random forest (RF) models were used to assess if dolphins could be assigned correctly to one of the study areas based on whistle acoustic parameters and whistle type. The RF models had a classification accuracy of 90% (Table 4.5; Supplemental figure 6.1) for testing data. According to the Gini index, the most important variables for classification were whistle type contour, duration, and end frequency (Figure 4.8). The mean decrease accuracy, which explains how much accuracy the model losses by removing each variable, shows that duration, whistle complexity, and start frequency are important for the accuracy of the model (Supplemental table 6.17).

Table 4.5. Cross-validate classification of whistles to the study areas based on six time-frequency parameters, inflexion points, whistle type, and whistle complexity.

	Predicted					
	Doubtful Sound	Great Barrier Island				
Doubtful Sound	130	38				
Great Barrier Island	26	163				



Figure 4.8. Random Forest variable importance plot. On the left, mean decrease accuracy where the points represent the loss of accuracy in the model if a variable is removed. On the right, mean decrease Gini value indicates the importance of each variable in the model.

I obtained two principal components from the NIPALS PCA analysis (Figure 4.9). The first principal component (PC1) explained 55.6% of the variance and is mainly influenced by MaxF. The second component (PC2) explained 44.4% of the variance and is influenced by MinF and duration (Table 4.6). I built models using LMMs on PC1 and PC2 to assess the effect on area, group size, and presence of immatures (i.e., juveniles and calves). I developed two models using PC1 and PC2 as response variables with area and presence of immatures as fixed effects and group size as the random effect. PC1 was not different between areas or with the presence of immatures (Supplemental table 6.18). However, MinF and duration differed between the two populations (Table 4.7).



Figure 4.9. Distribution of the mean whistle parameters along size principal component 1 and size principal component 2. DS = Doubtful Sound, GBI = Great Barrier Island.

Table 4.6. Loading scores, total variance explained and eigen values from a NIPALS PCA of acoustics parameters. Loading scores > 0.4 were assumed to contribute to the PCA.

Measurement	PC1	PC2
Minimum frequency	0.55	0.70
Maximum frequency	0.92	-0.11
Frequency range	0.63	-0.54
Start frequency	0.63	0.44
End frequency	0.56	0.37
Inflexion points	0.34	-0.58
Duration	0.32	-0.72
Eigen value	2.48	1.97
Total variance explained	55.6%	44.4%

Table 4.7. Results of generalised linear model comparing PC2 and area. GBI: Great Barrier Island. Significant effects are in bold.

	Estimate	SE	df	t-value	p-value
(Intercept)	-0.20	0.13	23.7	-1.44	0.16
Area GBI	0.52	0.22	21.1	2.40	0.02

4.4.3. Comparison with other population of bottlenose dolphins

Duration and five frequency parameters (MinF, MaxF, FR, SF, and EF) were compared among 21 populations of bottlenose dolphins worldwide (Table 4.8). A hierarchical cluster analysis was used to visualise similarities in bottlenose whistle parameters. A dendrogram of the populations shows a split into two main clusters (Figure 4.10). One cluster contains all the populations in the southern hemisphere and the population of Bocas del Toro, Panama. All the populations (except for Bocas del Toro) had a higher level of intraspecific variation in FR than Great Barrier Island (1) (p < 0.03; supplemental table 6.19). Patos Lagoon estuary, Brazil, showed a higher level of intraspecific variation in SF (p < 0.05; supplemental table 6.19) than other populations in that cluster. The other cluster contains populations from the northern hemisphere in addition to all the New Zealand populations and the populations in MinF, MaxF, FR, and duration compared to Great Barrier Island (1) (supplemental table 6.19). Among the bottlenose dolphin populations in New Zealand there were high levels of intraspecific variation in MinF and EF in all populations except Great Barrier

Island (2) (p < 0.05; supplemental table 6.19). The variation of whistle duration was high only in Doubtful Sound (3) population (p < 0.05; supplemental table 6.19), although duration in the Bay of Island could not be compared due to lack of appropriate data for the analysis. FR was highly variable in all the populations regardless of cluster (Asymptotic test, p < 0.02).



Figure 4.10. Hierarchical cluster visualisation of population similarity based on the mean values of six time-frequency parameters for 21 populations of bottlenose. Coloured rectangles show two main clusters. The Byron Bay population corresponds to *Tursiops aduncus* and it was used as external group for the analyses.

Table 4.8. Comparison of whistle parameters among 21 population of bottlenose dolphins worldwide. Mean ± SD are shown for each parameter unless something different is specified.

Location	n	MinF (kHz)	MaxF (kHz)	FR (kHz)	SF (kHz)	EF (kHz)	D (s)	Reference
Great Barrier Island, NZ (1)	577	6.87 ± 2 17	14.44 ± 3 34	12.5 ± 4 45	7.57 ±	8.06 ±	0.90 ± 0.52	This study
Doubtful Sound, NZ (1)	509	6.76 ± 1.82	14.9 ± 3.59	8.20 ± 3.4	8.61 ± 3.34	8.91 ± 4.05	1.04 ± 0.57	This study
Great Barrier Island, NZ (2)	7606	7.86 ± 2.36	14.21 ± 3.32	6.35 ± 3.17	9.63 ± 3.02	11.66 ± 4.22	0.84 ± 0.52	Outhwaite, 2018
Doubtful Sound, NZ (3)	560	7.16 ± 1.75	15.2 ± 3.98	8.07 ± 3.80	9.64 ± 3.80	10.4 ± 4.22	0.86 ± 0.61	Boisseau, 2005
Milford Sound, NZ	305	7.14 ± 1.72	15.9 ± 4.00	8.78 ± 3.89	9.58 ± 3.62	10.68 ± 4.41	1.00 ± 0.62	Boisseau, 2005
Bay of Islands, NZ	12643	6.49 ± 3.44	15.71 ± 4.59	9.42 ± 3.11	10.27 ± 3.87	12.84 ± 5.30	0.75ª	Peters, 2018
Sardinia, Italy	600	7.86 ± 3.65	13.1 ± 5.44	5.31 ^b	9.07 ± 4.24	11.4 ± 6.64	0.62 ± 0.76	Díaz López, 2011°
Walvis Bay, Namibia	693	5.72 ± 1.99	12.88 ± 2.87	7.16 ± 3.24	8.64 ± 3.56	7.21 ± 3.10	1.11 ± 0.65	Gridley et al., 2015
Lampedusa Island, Italy	166	7.45 ± 2.36	13.51 ± 3.75	6.06 ± 3.39	9.06 ± 3.19	11.1 ± 4.27	0.67 ± 0.36	La Manna et al., 2017
West Sardinia, Italy	183	7.30 ± 2.52	13.78 ± 3.38	9.51 ± 3.50	10.04 ± 3.21	8.95 ± 3.63	0.71 ± 0.45	La Manna et al., 2017
Rio de Janeiro, Brazil	91	9.90 ± 2.90	17.3 ± 4.30	7.40 ± 4.20	12.3 ± 3.50	13.2 ± 4.50	0.80 ± 0.64	Lima et al., 2016
Uruguay	42	4.90 ± 1.6	10.6 ± 3.5	5.70 ± 3.80	7.00 ± 3.10	6.70 ± 2.30	0.70 ± 0.50	Lima et al., 2019
Tramadaí, Brazil	100	5.30 ± 1.6	11.4 ± 2.3	6.10 ± 2.60	6.50 ± 2.50	8.90 ± 3.30	0.60 ± 0.50	Lima et al., 2019
Patos Lagoon estuary, Brazil	788	5.96 ± 2.15	12.2 ± 3.20	6.25 ± 3.34	8.28 ± 3.11	8.37 ± 3.70	0.55 ± 0.39	Azevedo et al., 2007

Gandoca-Manzanillo,	77	5.68 ±	17.61 ±	11.94 ±	8.43 ±	13.15 ±	0.89 ±	May-Collado and Wartzok
Costa Rica	//	2.24	4.93	4.32	3.66	5.57	0.69	2008
	74	5.34 ±	5.34 ±	10.18 ±	9.10 ±	9.19 ±	1.10 ±	May-Collado and Wartzok
Bocas del 1010, Pallallia	74	1.90	1.90	3.50	3.70	4.27	0.74	2008
Maditarrangan Saa	207	6.13 ±	14.19 ±	8.052 ±	8.31 ±	9.34 ±	1.03 ±	Papala at al 2014
Mediterranean Sea	207	2.08	3.67	3.43	3.58	4.51	0.58	Papale et al., 2014
Canary archipelago, Spain	94	7.20 ±	16.27 ±	9.07 ±	11.1 ±	11.9 ±	0.77 ±	Papale et al., 2014
		1.82	5.00	5.10	4.41	4.62	0.52	
Azores archipelago,	252	6.36 ±	15.3 ±	8.90 ±	10.1 ±	8.66 ±	0.97 ±	Papala at al 2014
Portugal	552	2.00	3.90	3.49	4.08	4.09	0.49	Papale et al., 2014
Bay of Biscay	94	7.19 ±	16.9 ±	9.77 ±	9.40 ±	11.3 ±	$1.10 \pm$	Papala at al 2014
		1.61	2.42	2.54	3.59	4.56	0.43	Papale et al., 2014
Sado Estuary, Portugal	735	5.4 ±	15 ± 2.7 9.6^{d} 5.8 ± 2.3	o cd	F 0 + 1 0	12.1 ±	0.86 ±	dos Santos et al. 2005
		1.2		5.0 ± 1.8	4.4	0.4	uos santos et al., 2005	

^Median reported; ^b SD not reported; ^c SD taken from Gridley et al., 2012; ^d calculate in this study from the reported values FR = MaxF - MinF.

4.5. Discussion

4.5.1. Description of whistles parameters at Great Barrier Island and Doubtful Sound

The acoustic parameters measured in both populations of bottlenose dolphins in New Zealand were between the ranges of what has been described for the species at other locations around the world. At a local scale, both populations of bottlenose dolphins exhibited differences in several acoustic parameters of whistles. Whistles from Doubtful Sound were longer in duration and had more inflection points than whistles from Great Barrier Island. Using a quantitative method (Random Forests analysis) to assign whistles to respective populations based on seven acoustic parameters, I was able to achieve 90% assignment accuracy. This clearly indicates that the populations are acoustically distinct. Furthermore, at a global scale, the acoustic parameters of the whistles from the two New Zealand populations were more similar to populations found in the Northern hemisphere than to those in the Southern hemisphere. Given that dolphins learn vocalisations from conspecifics, my results lead me to speculate that whistles are highly plastic in their form and are likely to culturally evolve in isolated populations.

Bottlenose dolphin whistles recorded at Great Barrier Island showed a frequency between 0.90 kHz and 28.3 kHz, with most of the whistles occurring between 5 and 18 kHz. Although, whistles have usually been described as occurring between 2 and 20 kHz, it is known that dolphins can hear whistles as low as 100 Hz and produce whistles up to 200 Hz (Herzing, 1996; Johnson, 1968; Turl, 1993). Whistles above 20 kHz (ultrasonic whistles) have been reported in other population of bottlenose dolphins (Hiley et al., 2017). Whistle duration ranged between 0.082 and 3.34 s, with a mean of 0.89 s. The number of inflection points ranged from 1 to 11. The whistles of bottlenose dolphins at Great Barrier Island are structurally simple whistles, as almost half of all whistles assessed do not have inflection points. Within whistle sub-types, the simplest type of the upsweep category, B1, was the most common. Common dolphins in the Celtic Sea also showed a high proportion of simple whistle and the upsweep type was the most common for this population (Ansmann et al., 2007). Guiana dolphin, along the eastern coast of Central and South America, also showed predominance of upsweep calls in their whistle repertoires (Azevedo & Van Sluys, 2005; de Andrade et al., 2015; May-Collado & Wartzok, 2009). Behaviourally, upsweep whistles have

been reported more frequently during socialising and directional swimming in beluga whales *Delphinapterus leucas* (Sjare & Smith, 1986). Functionally, in bottlenose dolphins, it has been suggested that this type of whistle plays an important part in communication and function as contact call in the species (Díaz López, 2011; Janik et al., 1994).

My study population at Great Barrier Island exhibited different whistle characteristics compared to other north-eastern bottlenose dolphin populations. For example, in the Bay of Islands, coastal bottlenose dolphins exhibit whistles with higher mean frequency values in maximum frequency, start frequency, and end frequency, compared to Great Barrier Island (Peters, 2018). Median values in whistle durations were similar between populations as were minimum frequencies. A previous smaller study carried out at Great Barrier Island also analysed the whistle characteristics of bottlenose dolphins. Overall, time and frequency parameters of the whistles sampled were different between 2015-2016 and 2017-2019 (Outhwaite, 2018 and present study, respectively). When comparing types of whistles, Outhwaite (2018) found that sine and upsweep were the most common types in the population, this was comparable to what I found in my study. Although, Outhwaite (2018) used finer scale definitions for whistle types, for example, he used sinusoidal, multi-looped, and 3-loops, these all fell within the definition of a sine whistle type used in this study, hence general comparisons are reasonable. Likewise, Outhwaite (2018) found that downsweep and concave whistle types were the less frequent in the population, as I found in my study.

Differences in whistle parameters between bottlenose dolphins at two locations around the North Island of New Zealand are potentially driven by differences in local habitat characteristics and anthropogenic pressures. Bay of Islands is characterised by sheltered bays and reefs (Peters, 2008), while Great Barrier Island is located within open sea and the western coast, where this study was carried out, is characterised by a range of moderately exposed to sheltered bays, inlets, and a rocky shoreline. It is known that in terrestrial environments, sound transmission is affected by local environmental factors such temperature, humidity, vegetation type and environmental noise (Slabbekoorn & Smith, 2002). Sound transmission in the ocean can vary because of changes

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in temperature, salinity, pressure, and bottom topography (Ranz, 2007). Azzolin and collaborators (2013) found that with increasing wind intensity, frequency and duration parameters decreased in striped dolphins *Stenella coeruleoalba*. Furthermore, Bonato et al. (2015) found a correlation between spinner dolphin *Stenella longirostris* habitat-dependent variables and frequency parameters in the Comoros archipelago. Further understanding of the role of this behavioural plasticity is needed through more field-based studies focused on sound transmission and the processes that influence variation. Anthropogenic noise is another contributing factor in variation in whistles parameters. Researchers have found that in some cases, dolphins lower their whistle frequencies to increase efficiency in transmission and detectability (Gospić & Picciulin, 2016). In Panama, May-Collado and Quiñones-Lebrón (2014) found that bottlenose dolphins emitted lower frequency, longer, and more modulated whistles in presence of boats, and suggested that this allows dolphins to communicate during noisy environment. Moreover, these changes happened when dolphins were foraging but not during socialising or travelling, likely because dolphins are more engaged in the last activities and are not easily distracted from them, unlike with foraging (May-Collado & Quiñones-Lebrón, 2014).

Differences in the whistle parameters at Great Barrier Island between two time periods (2015-2016 and 2017-2019) may be attributed to behavioural state, differences in data collection methods, and annual variation. As discussed above, dolphins can emit different types of whistles depending on the behaviour in which they are engaged (Díaz López, 2011). Hence, differences between both time periods may be due to variations in behaviour that was occurring during recordings. For example, resting was the behaviour most frequently recorded during my study followed by socialising and then foraging (pers. obs.). Outhwaite (2018) earlier study at Great Barrier Island also found resting to be a common behaviour, but dolphins were rarely sighted engaged in socialising and foraging behaviours. Although the relationship between behaviour and whistle parameters was beyond the scope of my study, these relationships are an exciting prospect for future studies. Variation between studies might be also related to differences in sampling effort, and sample sizes. Outhwaite's (2018) sampling effort was smaller than my study and sample size was a large factor likely contributing to the differences I found. Another possible explanation

for the differences in whistle parameters was the high percentage of new dolphins sighted in this area between 2016-2019 (chapter 2). Wang and collaborators (1995) suggested that yearly changes in whistle parameters can occur due to the influx of new individuals, and vocal learning is the most likely process contributing to these changes in time within each population.

Bottlenose dolphin whistles recorded at Doubtful Sound use frequencies between 3.12 kHz and 24 kHz. However, the acoustic sampling rates varied between the two locations; whistles were recorded at Doubtful Sound at an upper frequency limit of 24 kHz, which limited the maximum frequency estimate of whistle recordings. Some whistles with maximum frequencies that would have exceeded 24 kHz were observed but discarded from analysis because they did not meet the quality requirements (e.g., whistle contours were not fully visible). Whistle duration varied between short whistles of about 0.029 s to long whistles of 5.91 s, with a mean duration for all whistles of 1.04 s. These parameter measures were similar to populations found in the Mediterranean Sea, West Sardinia and the Azores archipelago in Portugal (La Manna et al., 2017; Papale et al., 2014). The maximum number of inflection points found in the Doubtful Sound population was 29, considerably higher than the maximum of 11-15 inflection point found at Great Barrier Islands (this study and Outhwaite 2018, respectively). Like other studies, most of the variation in whistles parameter measurements within my two study populations were found in inflexion points and duration. Number of inflection points in whistles has been associated to the amount of information contained in them, i.e., the simpler (no inflection points) the whistle the less information it will contain (Boisseau, 2005; May-Collado & Wartzok, 2008; Wang et al., 1995). Also, together with duration, the number of inflections it has been attributed to the emotional state of the individuals, information about individual identity, prey presence, or danger from anthropogenic activities (Boisseau, 2005, Morisaka et al., 2005; Azevedo & Van Sluys, 2005, May-Collado & Wartzok, 2008; Wang et al., 1995). The whistles of bottlenose dolphins at Doubtful Sound were structurally more complex, i.e., a greater proportion of whistles with inflection points, than at Great Barrier Island, with 76% of the whistles having at least one inflection point. When comparing the whistle parameters of this population to previous reported values at Milford Sound and Doubtful Sound, frequency parameters where lower but duration was similar (Boisseau, 2005).

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4.5.2. Geographic variation in whistles parameters in New Zealand

Geographic variations have been explained by the acoustic adaptation hypothesis, where animal acoustic signals are adapted to their environment to minimise degradation and maximise signal transmission and long-range communication (Morton, 1975). This hypothesis could explain the differences found between Great Barrier Island and Doubtful Sound populations where habitat characteristics, such as depth, differ between study sites. Bonato et al. (2015) found correlations between whistle parameters and depth in a population of spinner dolphins. They found a positive correlation of depth with beginning, end and number of minima, and a negative correlation for the number of steps, maxima, and interruptions (Bonato et al., 2015). Since frequency parameters are species-specific characteristics of signals and habitat-dependent variables should play a role to maximise transmission (Bonato et al., 2015). Water temperature and salinity are also different between Great Barrier Island and Doubtful Sound and, considering that the speed of sound increases with increasing temperature or salinity, further studies should focus on assess if these variables have any influence on whistles' frequency parameters. In addition, dolphins at Doubtful Sound are subject of higher levels of boat activity compared to Great Barrier Island which has been demonstrated to oblige dolphins to modify their whistles parameters to enable effective communication between conspecifics. Guerra et al. (2014) found that major changes in the duration, lower, and upper frequencies of whistles of bottlenose dolphins at Doubtful Sound occurred in the presence of boats. Pérez-Ortega and collaborators (2021) assessed the variation in whistles of bottlenose dolphins at two sites with contrasting boat activity at Bocas del Toro, Panama. Results showed that variation was explained by frequency modulation parameters (Pérez-Ortega et al., 2021), and modulation has been proposed as an indicator of the emotional state of the individual, and these emotional states can include danger, alertness, and stress (Pérez-Ortega et al., 2021). Currently, there are not studies of the influence of boats on whistle parameters at Great Barrier Island and efforts should be made to fill this gap.

Social factors such as presence of immature animals and the social characteristics of a population can influence acoustic signals (Gridley et al., 2016; La Manna et al., 2020; Quick & Janik, 2008; Romeu et al., 2017). Guerra and collaborators (2014) found that at Doubtful Sound groups of

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dolphins exposed to high noise levels from the boats behave differently if there were calves or not. Groups without calves, shifted their whistles to lower frequency bands. In contrast, in dolphin groups with calf, dolphins shifted to higher frequency bands. Shift in these parameters might have implications in mother-calf pairs keeping contact when situations are adverse for acoustic communication. Duration of whistles was also affected by the presence of calves (Guerra et al., 2014). Whistles were longer when groups contained calves compared to groups without them. It has been hypothesised that longer whistles might help group cohesion in social groups (May-Collado et al., 2007a). All the groups sampled at Great Barrier Island always contained at least one immature, hence, I was not able to compare whistles characteristics of groups with and without calves. However, I did use a linear mixed effects model to test the association between the two PC's variables and geographical and social variables (group size and presence of juveniles and calves). Based on my results only PC2 showed differences in minimum frequency and duration between study sites. Whistles at Great Barrier Island have a higher minimum frequency and lower duration than those from Doubtful Sound. In La Manna and collaborator's 2019 study, they did not find that the presence of calves influenced whistle parameters. Like my results, Moron et al. (2019) did not find association between group size and variation of whistle parameter measurements of several populations of Guiana dolphins at multiple locations in Latin-America.

The social complexity hypothesis predicts that with increasingly complex social structure it is necessary to increase communication complexity (Freeberg et al., 2012). This has been seen in group living species such as marmots where it has shown that social complexity is responsible for the evolution of complex alarm communication (Blumstein, 2003). The social structure of my two study populations is different. The Doubtful Sound population exhibits one of the highest levels of association among its member for a bottlenose dolphin population worldwide (Lusseau et al., 2003). In contrast, bottlenose dolphins at Great Barrier Island exhibit a more fluid, yet still structured population (chapter 2). As expected, the Doubtful Sound population was found to have more complex whistle structures with whistles with one or more inflection points making up to 76% of their repertoire. Group size also appears to influence whistle variability in a population. May-Collado et al. (2007) suggested that whistle duration increases, and frequency decreases in

scenarios where long-range communication is necessary, for example, with small and variable social group structure. Whereas, in larger or more stable social groups, the calls should be shorter and of higher frequencies. The results from my study did not support these predictions. The population at Great Barrier Island exhibited variable social groups that changed constantly in composition and structure, and they had lower frequency measures and duration than the more stable population at Doubtful Sound. Although, this differed from what has been predicted by May-Collado et al. (2007), my results may be due to the need for bottlenose dolphins at Doubtful Sound to compensate for other interfering factors such as boat noise.

Cultural transmission occurs when a behaviour is learned from conspecifics (Enggist-Dueblin & Pfister, 2002) and has been suggested as a mechanism of variability in acoustic parameters. Cultural transmission is responsible for geographic variation in acoustic signals and has been reported in several mammal groups such as whales (Deecke et al., 2000; Noad et al., 2000; Rendell & Whitehead, 2001), grey seals *Halichoerus grypus* (Stansbury & Janik, 2021), chimpanzees *Pan troglodytes* (Mitani et al., 1992), bats (Esser & Schubert, 1998; Yoshino et al., 2008), and naked mole-rats (Barker et al., 2021). Bottlenose dolphins are well known for their ability to learn new vocalisations (Tyack, 1998). Whistle types can be shared within or between social groups (McCowan & Reiss, 1997) and this may reflect different pathways of cultural transmission. Studies of bottlenose dolphins have also found indications of sex-specific ways of cultural transmission. For example, male bottlenose dolphins are more likely to produce signature whistles that are similar to those of their mothers than are female offspring (Sayigh et al., 1995). Cultural transmission is likely to occur within my study population and further study is necessary to understand this mechanism and how it drives differences within New Zealand's bottlenose dolphin populations.

Random Forest analyses have been previously used in call classifications studies for marine mammals such as southern right whales *Eubalaena australis* (Webster et al., 2016), Cape fur seals *Arctocephalus pusillus* (Martin et al., 2021), beluga whales *Delphinapterus leucas* (Garland et al., 2015), botos *Inia geofrensis*, (de Melo et al., 2021), Indian Ocean humpback dolphins *Sousa*

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plumbea and Indo-Pacific bottlenose (Yang et al., 2020), common dolphins Delphinus delphis and D. bairdii; (Oswald et al., 2021). Using Random Forest analyses, I was able to classify whistles to accurately determine population identity based on nine acoustic variables. I obtained a classification accuracy of 90% and this is comparable to similar studies using RF models (Webster et al., 2016). Indeed, the overall misclassification error for my analyses was low compared to 17% for beluga whales (Garland et al., 2015) and 28% - 30% for detections of tropical dolphins (Rankin et al., 2013). Of the nine variables included in the analyses, the most important variables in the model were whistle type contour and duration. Previous studies on delphinid vocal characterisation found that duration and inflection points are important measures to identify variation in whistles (Wang et al., 1995). Although, I found that inflection points were the less important variable for classification in my study, whistle complexity, a variable related to the number of inflection points, was important. This provides further evidence that whistle type contour and duration (both indicators of complexity) are indeed important for whistle classification. Bopardikar et al. (2018) obtained similar results to mine using CART, in their model, slope measurements and duration were the most distinguishing features of the whistle contours. Due to the nature of data collection in acoustic assessment of cetaceans, where individual animal that is vocalising is unknown, and the unit of analysis is the group, pseudo-replication is a factor that will always be present, and it needs to be addressed.

4.6. Conclusions

In conclusion, the whistles characteristics of bottlenose dolphin varied between Great Barrier Island and Doubtful Sound. Whistles at Doubtful Sound were longer and presented more inflection points than at Great Barrier Island. Some frequency parameters varied between populations such as SF and EF that were lower at Great Barrier Island while FR was higher. MaxF and MinF were similar between both populations. Convex whistles were more frequent at Doubtful Sound and constant whistles less frequent. At Great Barrier Island upsweep whistle was the most common type of whistle. Conversely, concave was less common. Random Forest models had an accuracy of 90% assigning whistles to the correct population based on their parameters. The most important variables for this classification were whistle type contour, duration, and end frequency. The

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whistle characteristics between my two populations were different enough to be classified accurately to the correct population. Random forest analysis is a powerful quantitative method for classifying animal acoustic signals, and in the case of cetaceans, it can overcome the inherent problem of pseudo-replication associated with group-based data collection that is associated with cetacean acoustic studies. Given the spatial heterogeneity of coastal environments where acoustic studies of bottlenose dolphins have been carried out, it was expected that specific signal parameters may vary in specific environments. The whistle characteristics of the populations assessed in my study are comparable to populations studied elsewhere, with the unusual finding that their characteristics are more similar to populations in the northern than in the southern hemisphere. My research describes and compares whistle parameters for two populations of bottlenose dolphins in New Zealand for the first time and will benefit future research that aims to understand the relevance of geographic variation of whistles.

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CONCLUSIONS
5. Concluding remarks

5.1. Social behaviour of bottlenose dolphins in New Zealand.

Sociality, or social behaviour, is made up of interactions that occur between two or more individuals from the same or different species that usually provide benefits for all participating individuals (Jasso del Toro & Nekaris, 2019). The social environment of an individual comprises non-random and diverse social interactions (Croft et al., 2008; Krause & Ruxton, 2002), and in vertebrate taxa, is extremely diverse, ranging from dominance hierarchies (e.g., green anole lizards Anolis carolinensis; Bush et al., 2016) to patriarchal (e.g., chimpanzees Pan troglodytes) and matriarchal societies (e.g., bonobos Pan paniscus; Sommer et al., 2011), and complex multi-level alliances in male bottlenose dolphins Tursiops sp. (Connor et al., 2000). Sociality has both costs and benefits for the individual. The cost of sociality includes increased competition for mates and resources or higher chances of disease transmission (Silk, 2007). On the other hand, the benefits of group living include enhanced opportunities to access food, mating and defence from predators (Majolo & Huang, 2018). Diverse aspects of sociality, such as social organisation, disease transmission, and communication can have effects on the individual and on the group. The social organisation of a population can be studied through its social structure defined by the nature, quality, and patterns of relationships between individuals (Whitehead, 2008). Understanding how relationships and social structure are formed will help researchers to understand the causes and consequences of sociality (Hinde 1976; Krause & Ruxton 2002; Whitehead, 2008).

Social network approaches focus on the structure of relationships and the interaction between the individual and the group (Wey et al., 2008). Social network analysis has been widely applied to the study of the social organisation of toothed whales, most of which exhibit fission-fusion societies (Croft et al., 2004). In true dolphins, social structure is highly variable within and between species. For example, world-wide groups of orcas *Orcinus orca* are characterised by strong social matrilineal bonds and long-lasting associations (Baird & Whitehead, 2000). A recent study in Galápagos found that orcas in this area have a loose social organisation similar to fission-fusion societies (Denkinger et al., 2020). On the other hand, bottlenose dolphins typically have been characterised by presenting fission-fusion societies, with groups that change in size and composition constantly and where the associations among their members are fluid (e.g., chapter 2; Baker et al., 2018; Chabanne et al., 2017; Louis et al., 2015; Pleslić et al., 2019). But for some isolated populations of bottlenose dolphins this is not the case. These isolated populations exhibit high levels of associations among individuals and the populations are relatively stable (Augusto et al., 2012; Lusseau et al., 2003). As predicted, I found that the bottlenose dolphins at Great Barrier Island exhibited fluid patterns of association, typical of fission-fusion societies that characterises the species, but also it is well structured, showing preferences for associations with specific dolphins and avoidance of others. The social structures I quantified for the two time periods contrast; dolphins showed higher levels of linkage among individuals between 2011-2013, establishing a single, more concentrated, and connected network than between 2015-2019. My results also showed the presence of two spatially separated social communities during 2015-2019. It has been demonstrated that the social networks of gregarious animals are the most fragmented (but not disconnected), compared to solitary or hierarchical species, into cohesive social groupings. One of the reasons for the presence of these two social communities at Great Barrier Island could be the behavioural inclination to switch affiliative partners within social networks of gregarious species; as a result, individuals build stable social ties with just a small fraction of individuals (Sah et al., 2018).

Associations of bottlenose dolphins at Great Barrier Island are non-random and the population, during 2011-2013 was characterised by a rapid dissociation of few associations, in addition to long-term companions and short-term acquaintances. On the other hand, during 2015-2019, the population showed an overall pattern of two levels of short-term acquaintances. This same pattern has been observed in the Bay of Islands since 2006 (Hamilton, 2013; Mourão, 2006). When compared to other populations in New Zealand, this pattern was similar to the Marlborough Sounds population where dolphins formed non-random, two levels of associations (constant companions and casual acquaintances). These results contrast with what has been described in the population at Doubtful Sound, Fiordland, where dolphins form strong and stable associations among its individuals. Unlike Great Barrier Island and Marlborough Sounds, dolphins at Doubtful Sound have very limited exchange with individuals from surrounding areas and the small size of

the population limits the number of associates an individual can have, influencing the patterns and social structure of these populations. The patterns of residence also differed between both time periods at Great Barrier Island. During 2011-2013, higher rates of emigration were detected at the beginning then stabilised as dolphins stayed longer in the area. However, the rates of emigration/mortality of dolphins increased during 2015-2019. Several other factors can influence the quality and quantity of interaction among individuals such as habitat characteristics, movement ranges, and the high influx of new individuals during 2015-2019 that could lead to the differences found in the association patterns and the detection of social communities. Many gregarious species also form groups based on age, sex, or kinship (Weiss et al., 2021). Although, I was not able to test the influence of these factors in the social structure of my study population, they should be taken into consideration in future studies.

Sociality has also shown to be crucial in the epidemiology of infectious diseases (Kappeler et al., 2015, Sah et al., 2018). In this context, costs and benefits of group living have been identified. Among the costs, it is well known that group living can enhance the opportunities for transmission of pathogens between individuals of the same or different species (Kappeler et al., 2015). Moreover, when social clusters of related individuals are present within groups, these individuals face an increased risk of associated susceptibility to pathogenic infection due to their immunogenetic similarities that increases as the degree of genetic homogeneity increases as well (Hughes & Boomsma, 2004). Sociality can promote competition leading to social stress, a factor known to cause serious health issues by increasing vulnerability to infectious and non-infectious diseases (Barik et al., 2013; McEwen, 2012). The increase in stress hormones, such as glucocorticoids, has negative consequences like reduced immunocompetence, negative effects on memory and vigilance, and delayed sexual development in juveniles (Koolhaas et al., 2011; McEwen, 2012). However, group living also has advantages that can help individuals to mitigate the negative impact of certain infectious diseases. The risks of pathogen transmission can be compensated by increasing personal immune response. Individuals can enhance their individual immunity in different ways such as density-dependent prophylaxis (Kong et al., 2013), and passive and active social immunization (Hamilton et al., 2011; Ugelvig & Cremer, 2007). In addition,

behaviour also can be an important factor when it comes to reducing individual risk of pathogen acquisition. For example, during grooming, individuals remove potentially harmful ectoparasites from the body of another member of their group (Mooring et al., 2004). Also, individuals in a group can avoid contact with obviously ill individuals stopping the propagation of diseases (Cremer et al., 2007), and social interactions between parent and offspring facilitating the vertical transmission of microbiota (Koch & Schmid-Hempel, 2011).

My research provides the first assessment of the prevalence of skin lesions and tooth rakes in the north-eastern bottlenose dolphin population in New Zealand. I aimed to describe the relationship between the presence of tooth rakes (in this case we can treat tooth rakes as a transmissible disease) with the strength of the dolphins in the social network. I hypothesised that more connected dolphins would have more tooth rakes, but this was not the case. My findings suggest that higher connectivity may not be a sufficient metric to assess this, and similar results have been obtained in other studies trying to link network metrics and presence of a disease/tooth rakes in a population (e.g., Powell et al., 2021). Previous studies assessing the sociality and disease transmission, found that contact can be an important factor for dissemination of diseases in a population. For example, Powell and collaborators (2021), found that the most important social aspect in the transmission of tattoo skin disease (TSD) was prior contact with positive Indo-Pacific bottlenose dolphins Tursiops aduncus, hence associations with infected dolphins is predictive of an individual's risk for TSD. Similarly, Félix and collaborators (2019) found evidence of horizontal transmission of Lobomycosis-like disease (LLD) due to contact in bottlenose dolphins in Ecuador. Moreover, they found that hierarchical status of male dolphins played an important role in the dissemination of LLD, with low-rank males having larger home ranges than high-ranked males, being the former ones responsible of the spread of the disease in the population. Although, the prevalence of skin lesions in my population was high, visually, the extent of the skin lesions was not as extensive as what has been observed in bottlenose dolphins in Fiordland, and this could be related to the social networks of each population. Theoretical models have shown that gregarious species' social networks are more effective than socially hierarchical species at preventing epidemics of moderately contagious diseases. In addition, animals with larger social network, as

in the case of bottlenose dolphins at Great Barrier Island, or those that socialise more, might be able to offset the risk of spreading an infection disease (social buffering effect) if well-connected individuals tend to have higher fitness, hence are able to resist infection better (Frère et al., 2010; Powell et al., 2021). It is important to highlight that bottlenose dolphins at Great Barrier Island occupy a wider area with more exchange of individuals compared to the Doubtful Sound population.

In several species, acoustic signals mediate significant social aspects such as reproduction, territorial defence, mate attraction, alarm calls, among others (Bradbury & Vehrencamp, 1998; Luo et al., 2017). It has been suggested that social pressures can lead to acoustic divergence within a species (Luo et al., 2017). Highly social organisms have developed an intricate repertoire size and syntax that allow them to communicate without ambiguity (Pollard & Blumstein, 2012). Individual distinctiveness in social calls is also increased in several birds and mammals' species living in large social groups, demonstrating that sociality can be a cause of vocal individuality (Pollard & Blumstein, 2012; Wilkinson, 2003). In addition, large groups have a greater selective pressure on individual recognition, necessitating the development of broadband calls that can convey a greater amount of social data (Gillam & Chaverri, 2012). In my research, I found differences in the acoustic parameters of the two geographically and genetically isolated populations of bottlenose dolphins in New Zealand. The whistle characteristics (start, end, minimum, maximum frequency and frequency range, duration, and inflection points) were compared using Random Forest analysis and were diverse enough for whistles to be correctly assigned to the population of origin with a 90% of accuracy. The whistle characteristics of both populations were compared to published research from other populations worldwide. Surprisingly, I found that the New Zealand whistles were more similar to populations in the northern hemisphere than in the southern. However, it is worth noting that most of the studies of acoustics of bottlenose dolphins have been done in the northern hemisphere, highlighting the importance of the contribution of my research. Researchers have attributed geographic variation in whistles parameters to adaptations to the specific habitats in which the dolphins occupy, changes in social and genetic structure, and population isolation. I investigated the possibility that these differences in whistle characteristics were due to social

factors such as the presence of juveniles and calves, and group size. I found that none of these variables were significative in the difference of whistle parameters between populations. This lack of significance could be, in part, due to low sample sizes and needs further study. The interplay between the marked difference in habitat, social structure, and anthropogenic pressure between both populations are likely to contribute to the differences found in whistles characteristics and my findings will aid future research aimed at understanding the significance of whistle regional variation and its relevance in various social contexts.

5.2. Study limitations

Due to permitting restrictions, it was not possible to collect biopsy samples of this population. Genetic information would complement direct observations of animal associations and movement at Great Barrier Island. Such studies will provide quantitative insights into occurrence of mixedsex groups and relationships among individuals. For example, kin selection has been reported as a significant aspect of sociality in other bottlenose dolphins' populations. Through genetic studies, the sex of the dolphins can be verified. In this study the sex of most of the dolphins, a key social factor, was unknown. Including sex in the analyses would have likely improved my ability to understand drivers of association: the sex of the individuals has been found to determine assortative patterns in other population of this species. In my case, I had information of the sex of only eight individuals, and most of the sexing of the individuals were through long-term photographs of female dolphins continuously seen associating with calves. In future studies, it will be interesting to know if this pattern of constant association also occurs at Great Barrier Island. Sex is also an important variable to consider when studying the prevalence of skin lesions and tooth rakes. For example, studies of scarring patterns have shown that males tend to have more tooth rakes than females, and females in oestrus also tend to have higher rates of tooth rakes than other females. Other limitations of my study include the quantity of data obtained due to weather conditions that made collection of data during the winter months unsafe. Although the data comprises three years of data collection, the uneven sampling intervals may be problematic, for example, in the case of skin lesions, the appearance of some skin lesion can flourish due to changes in environmental conditions such as a low water temperature. In addition, the prevalence of skin

lesions and tooth rakes in the population was likely underestimated as I was constrained to only include dolphins that were individually recognisable based on their unique dorsal fin markings.

The study of vocalisation of marine animals living in groups have some inherent limitations. For example, from the recordings, it is not possible to know what specific dolphin produced a particular sound, and results are based on group results. This limitation hinders understanding the individual contribution of dolphins to the patterns observed. Furthermore, due to the limitations in the recording equipment used at Doubtful Sound, the upper frequency of the whistles was often clipped making them unusable for some of the analyses. Only selected social factors (i.e., group size and presence of immatures) were taken into consideration to explain the geographic variation in both populations. Factors such as behaviour, presence of boats, water temperature and depth, among others have been suggested as sources of variability but they were not considered, and future research should assess their influence. Finally, as mentioned throughout of this thesis, Great Barrier Island, the focus of most of my data collection, is just one of the areas where bottlenose dolphins are found in the North Island, therefore, this study only included a portion of dolphins making up the North Island population and efforts should be made to integrate all the information available and identify the gaps with the aim of improving the management of this species in this area.

5.3. Recommendations for future research

- Further advances on my study should include data about demographics since sociality can be driven by sex (Connor et al. 2000) and by age. Groups formed only by juveniles and individuals mainly interacting with other individuals of the same age have been found in some dolphin populations (Lusseau & Newman, 2004; Wells, 2014). This information will help us to gain a thorough understanding of a population's social dynamics at Great Barrier Island.
- 2. Sex and age are important information that must be incorporated into future analyses of skin lesions and tooth rakes as well. Previous studies have found that in some populations

males have a greater prevalence of tooth rakes than females (Rowe et al., 2010), and there is evidence supporting sexual coercion in other populations of bottlenose dolphins (Scott et al., 2005). Also, the overall prevalence of certain skin lesions such as tattoo-like disease has been reported to be higher in young dolphins than adults (Powell et al., 2018).

- 3. In my study, I excluded the winter months from the analysis since these months were rarely able to be surveyed during 2016-2019 due to adverse weather conditions. Although logistically challenging, data from these months will help to understand the sociality of this species in the area within a much larger temporal framework.
- 4. Including habitat use in the study of social structure would be an important next step. If social structure and habitat use is shown to be linked, then this will have significant implications for population management (Cantor et al., 2012; Lusseau et al., 2006; Titcomb et al., 2015; Wiszniewski et al., 2009).
- 5. The social network research undertaken as part of my study should be expanded to other areas in the north Island where bottlenose dolphins have been reported. Coupled with movement and genetic data, this holistic approach would provide an accurate picture of the social structure of bottlenose dolphin in this region.
- 6. To have a more accurate approach to the assessment of the aetiology of the skin lesions, it would have been ideal to include tissue samples. Since the study of skin lesions in cetaceans can be used as health indicator, the isolation of the pathogens from the lesions can give insights to the potential risks to these populations. The isolation of viruses has been possible for some previous studies. For example, Burdett Hart and colleagues (2012) were able to isolate poxviruses and herpesviruses from dark and white fringe spots, respectively (Burdett Hart et al., 2012). These skin lesions have been observed in the Hauraki Gulf in common and bottlenose dolphins (*Tursiops truncatus* and *Delphinus* spp., respectively). Future studies of skin lesion should also quantify the extent of different skin lesions in the population to understand the dynamics of lesions in the population.

- 7. To further understand the changes between populations it would be ideal to study the full acoustic repertoire of bottlenose dolphins and to include the population located within the Marlborough Sounds; a population yet to be studied. In addition, acoustic data could be combined with studies of the distribution of the species to better understand the causes of signal variation in this population. Peters (2018) studied the distribution and acoustic behaviour of bottlenose dolphins in the most northern part of New Zealand, but, again, this is only a small part of the distribution of the species in New Zealand. Expanding the geographic coverage of acoustic sampling is challenging, and one approach is to standardise recording methodology and develop a combined database of acoustic information through the New Zealand bottlenose dolphin's range.
- 8. Authors have suggested that genetically distinct populations exhibit acoustic variability (La Manna et al., 2019). However, the genetic diversity of bottlenose dolphins in New Zealand is poorly understood. Genetic studies need to be carried out in the North Island, and together with acoustic data, they will tell us more about the dynamics of the population. Nonetheless, many questions have arisen regarding distribution, movements, social and genetic structure, and acoustic differentiation between the north-eastern bottlenose dolphin population. This information will help to determine the population status and will have implications on the management strategies of this endangered species. It is important to continue studying the variation of acoustic signals of cetaceans and future studies should include those factors suggested earlier that were not included in this study.

5.4. Final remark

The findings of my study add to our knowledge of bottlenose dolphin association patterns, prevalence of skin lesions and tooth rakes, and vocal variation in New Zealand. This new information will help lay the groundwork for future research and monitoring to aid conservation efforts of this species in this country. The results presented here contribute with more evidence of bottlenose dolphins' behavioural and vocal plasticity. In this research, I used non-invasive techniques that proved to be useful to increase our knowledge about the ecology of this

endangered species without adding sources of stress to the population. Further understanding of bottlenose dolphins' association patterns, skin lesions and tooth rakes prevalence, and vocal variation in New Zealand, will be achieved by adding studies about genetic and movement patterns in the North Island.

5.5. References

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Hasta que nos volvamos a encontrar

6. Appendices

6.1. Appendix A: Supplements for chapter 2

Supplemental table 6.1. Dates of the surveys included in the social network analysis. Winter months and dates of surveys where dolphins were not sighted were not included.

Date 26/01/2011 8:38 27/01/2011 17:10 28/01/2011 8:04 21/04/2011 11:38 21/04/2011 13:13 22/04/2011 9:15 22/04/2011 13:58 23/04/2011 14:16 23/04/2011 11:26 24/08/2011 9:07 25/08/2011 8:58 26/08/2011 16:21 24/10/2011 9:34 24/10/2011 13:43 25/10/2011 12:20 27/11/2011 14:13 20/12/2011 12:50 18/01/2012 15:03 20/01/2012 10:28 17/02/2012 14:43 18/02/2012 9:49 18/02/2012 16:34 27/03/2012 14:41 21/04/2012 8:05 24/05/2012 8:43

25/05/2012 8:04
17/02/2012 14:43
13/09/2012 14:26
14/09/2012 9:27
19/09/2012 15:36
20/09/2012 12:41
11/10/2012 14:06
25/10/2012 14:09
28/12/2012 11:21
1/01/2013 11:38
2/01/2013 16:14
29/09/2015 9:07
30/09/2015 14:55
1/10/2015 8:41
20/01/2016 13:56
21/01/2016 11:13
21/01/2016 14:20
22/01/2016 7:41
22/01/2016 15:05
23/01/2016 17:36
24/01/2016 12:38
14/03/2016 11:55
16/03/2016 11:51
20/12/2016 14:32
20/12/2016 17:50
21/12/2016 9:00

6/02/2017 18:26
7/02/2017 13:55
13/11/2017 12:22
13/11/2017 15:10
15/11/2017 10:17
24/11/2017 9:27
24/11/2017 13:14
25/11/2017 8:23
26/11/2017 8:12
26/11/2017 10:39
11/01/2018 12:06
11/01/2018 16:13
12/01/2018 9:34
12/01/2018 11:38
2/04/2018 15:20
3/04/2018 11:35
1/09/2018 9:05
15/09/2018 11:25
21/10/2018 8:28
12/12/2018 15:52
13/12/2018 8:00
14/12/2018 10:25
15/12/2018 13:48
16/12/2018 12:36
24/03/2019 10:38
4/05/2019 15:21

Vocal behaviour and social networks in bottlenose dolphins at GBI



Supplemental figure 6.1. Data sheet used to collect information associated to group sightings of bottlenose dolphins at Great Barrier Island during 2016-2019.

Vocal behaviour and social networks in bottlenose dolphins at GBI



Environmentals

Supplemental figure 6.2. Data sheet used to collect environmental information associated to group sightings of bottlenose dolphins at Great Barrier Island during 2016-2019.

Supplemental table 6.2. Stronger dyads than expected by chance found in two periods at Great Barrier Island. Dyads listed had HWIs > 0.76 during 2011-2013 and HWIs > 0.46 during 2015-2016.

Period	Individual's ID	HWI
	HG234-HG083	0.76
	HG283-HG204	0.86
	HG248-HG205	0.86
2011 2012	HG292-HG205	1.00
2011-2013	HG241-HG240	0.84
	HG290-HG248	0.86
	HG285-HG282	1.00
	HG292-HG290	1.00
	JP001-HG258	0.50
	JP005-HG258	0.50
	JP006-HG258	0.57
	JP036 -HG287	0.50
	JP026 -HG288	0.89
	JP036 -HG288	0.85
	JP005-JP001	0.60
	JP036-JP026	0.80
	JP090-JP030	0.60
	JP091-JP030	0.50
	JP123-JP030	0.57
	JP125-JP030	0.57
	JP126-JP030	0.50
	JP084-JP068	0.53
2015-2019	JP091-JP068	0.62
	JP090-JP084	0.50
	JP091-JP084	0.60
	JP123-JP084	0.67
	JP125-JP084	0.67
	JP126-JP084	0.80
	JP091-JP090	0.60
	JP103-JP091	0.57
	JP123-JP091	0.57
		0.50
		0.67
		0.57
		0.67
		0.80
	JLT50-JLT52	U.8b

	Clustering	Affinity	Strength
Mann-Whitney U	2080	487	1652
Wilcoxon W	6175	4582	5747
Z	-5.892	-10.323	-7.071
Asymp. Sig. (2-tailed)	.000	.000	.000

Supplemental table 6.3. Mann-Whitney test for the network metrics analysed.

Grouping variable: Group

Supplemental table 6.4. Lagged association rate of bottlenose dolphins at Great Barrier Island during 2011-2013. dis. = dissociation; pref. = preferred; comps = companion; acqs = acquaintance. In bold, the best fitted model.

Model	Explanation	QAICc	ΔQAICc
al	Rapid dis. + pref. comps	8270	141
a2*exp(-a1*td)	Rapid dis. + casual acqs	8223	94
a2+a3*exp(-a1*td)	Rapid dis. + pref. comps + casual acqs	8129	0
a2+(1-a2)*exp(-a1*td)	Pref. comps + casual acqs	8234	105
a3*exp(-a1*td)+a4*exp(-a2*td)	Rapid dis. + two levels of casual acqs	8212	83
a3*exp(-a1*td)+(1-a3)*exp(- a2*td)	Two levels of casual acqs	8223	94

Supplemental table 6.5. Lagged association rate of bottlenose dolphins at Great Barrier Island during 2015-2019. dis. = dissociation; pref. = preferred; comps = companion; acqs = acquaintance. In bold, the best fitted model. In italics, models that also show some support.

Model	Explanation	QAICc	ΔQAICc
al	Rapid dis. + pref. comps	1785	167
exp(-a1*td)	Casual acqs	1952	334
a2*exp(-a1*td)	Rapid dis. + casual acqs	1678	60
a2+a3*exp(-a1*td)	Rapid dis. + pref. comps + casual acqs	1628	10
a2+(1-a2)*exp(-a1*td)	Pref. comps + casual acqs	1631	13
a3*exp(-a1*td)+a4*exp(-a2*td)	Rapid dis. + two levels of casual acqs	1621	3
a3*exp(-a1*td)+(1-a3)*exp(- a2*td)	Two levels of casual acqs	1618	0

Supplemental table 6.6. Lagged association rate for community B at Great Barrier Island during 2015-2019. dis. = dissociation; pref. = preferred; comps = companion; acqs = acquaintance. In bold, the best fitted model.

Model	Explanation	QAICc	ΔQAICc
al	Rapid dis. + pref. comps	1263	129
exp(-a1*td)	Casual acqs	1337	203
a2*exp(-a1*td)	Rapid dis. + casual acqs	1178	44
a2+a3*exp(-a1*td)	Rapid dis. + pref. comps + casual acqs	1143	9
a2+(1-a2)*exp(-a1*td)	Pref. comps + casual acqs	1143	9
a3*exp(-a1*td)+a4*exp(-a2*td)	Rapid dis. + two levels of casual acqs	1352	218
a3*exp(-a1*td)+(1-a3)*exp(- a2*td)	Two levels of casual acqs	1134	0

Supplemental table 6.7. Lagged association rate for community R at Great Barrier Island during 2015-2019. dis. = dissociation; pref. = preferred; comps = companion; acqs = acquaintance. In bold, the best fitted model. In italics, models that also show some support.

Model	Explanation	QAICc	ΔQAICc
al	Rapid dis. + pref. comps	267	0
exp(-a1*td)	Casual acqs	435	168
a2+(1-a2)*exp(-a1*td)	Pref. comps + casual acqs	269	2

Supplemental table 6.8. Lagged identification rates of bottlenose dolphins at Great Barrier Island during 2011-2013. In bold, the best fitted model.

Equation	Model description	QAICc	ΔQAICc
al	Closed 1/a1 = N	21189	9
1/a1	Closed a1 = N	21189	9
a2*exp(-a1*td)	Emigration/mortality a1 = emigration rate; 1/a2 = N	21188	7.64
(1/a1)*exp(-td/a2)	Emigration/mortality a1 = N; a2 = Mean residence time	21188	8
a2+a3*exp(-a1*td)	Emigration + reimmigration a1 = Emigration rate; a2/(a2+a3) = Proportion of population in study area at any time	21180	0
(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	21180	0
a3*exp(-a1*td)+a4*exp(-a2*td)	Emigration + reimmigration + mortality a1 = N; a2 = Mean time in study area; a3 = Mean time out of study area; a4 = Mortality rate	21192	12
(exp(-a4*td)/a1)*((1/a3)+(1/a2)* exp(-(1/a3+1/a2)*td))/(1/a3+1/a2)	Emigration + reimmigration + mortality a1 = N; a2 = Mean time in study area; a3 = Mean time out of study area; a4 = Mortality rate	21190	10

Supplemental table 6.9. Lagged identification rates of bottlenose dolphins at Great Barrier Island during 2015-2019. In bold, the best fitted model. In italics, models that also show some support.

Equation	Model description	QAICc	ΔQAICc
al	Closed 1/a1 = N	3797	39
1/a1	Closed a1 = N	3797	39
a2*exp(-a1*td)	Emigration/mortality a1 = emigration rate; 1/a2 = N	3758	0
(1/a1)*exp(-td/a2)	Emigration/mortality a1 = N; a2 = Mean residence time	3758	0
a2+a3*exp(-a1*td)	Emigration + reimmigration a1 = Emigration rate; a2/(a2+a3) = Proportion of population in study area at any time	3786	28
(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	3760	2
a3*exp(-a1*td)+a4*exp(-a2*td)	Emigration + reimmigration + mortality a1 = N; a2 = Mean time in study area; a3 = Mean time out of study area; a4 = Mortality rate	3760	2
(exp(-a4*td)/a1)*((1/a3)+(1/a2)* exp(1/a3+1/a2)*td))/(1/a3+1/a2)	Emigration + reimmigration + mortality a1 = N; a2 = Mean time in study area; a3 = Mean time out of study area; a4 = Mortality rate	3759	1

Supplemental table 6.10. Lagged identification rates of bottlenose dolphins' community B at Great Barrier Island during 2015-2019. In bold, the best fitted model. In italics, models that also show some support.

Equation	Model description	QAICc	ΔQAICc
al	Closed 1/a1 = N	13681	27
1/a1	Closed a1 = N	13681	27
a2*exp(-a1*td)	Emigration/mortality a1 = emigration rate; 1/a2 = N	13654	0
(1/a1)*exp(-td/a2)	Emigration/mortality a1 = N; a2 = Mean residence time	13654	0
a2+a3*exp(-a1*td)	Emigration + reimmigration a1 = Emigration rate; a2/(a2+a3) = Proportion of population in study area at any time	13680	26
(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	13656	2
a3*exp(-a1*td)+a4*exp(-a2*td)	Emigration + reimmigration + mortality a1 = N; a2 = Mean time in study area; a3 = Mean time out of study area; a4 = Mortality rate	13658	4
(exp(-a4*td)/a1)*((1/a3)+(1/a2)* exp(1/a3+1/a2)*td))/(1/a3+1/a2)	Emigration + reimmigration + mortality a1 = N; a2 = Mean time in study area; a3 = Mean time out of study area; a4 = Mortality rate	13658	4

Supplemental table 6.11. Lagged identification rates of bottlenose dolphins' community R at Great Barrier Island during 2015-2019. In bold, the best fitted model. In italics, models that also show some support.

Equation	Model description	QAICc	ΔQAICc
al	Closed 1/a1 = N	2241	11
1/a1	Closed a1 = N	2241	11
a2*exp(-a1*td)	Emigration/mortality a1 = emigration rate; 1/a2 = N	2232	2
(1/a1)*exp(-td/a2)	Emigration/mortality a1 = N; a2 = Mean residence time	2231	1
a2+a3*exp(-a1*td)	Emigration + reimmigration a1 = Emigration rate; a2/(a2+a3) = Proportion of population in study area at any time	2236	6
(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	2231	1
a3*exp(-a1*td)+a4*exp(-a2*td)	Emigration + reimmigration + mortality a1 = N; a2 = Mean time in study area; a3 = Mean time out of study area; a4 = Mortality rate	2230	0
(exp(-a4*td)/a1)*((1/a3)+(1/a2)* exp(1/a3+1/a2)*td))/(1/a3+1/a2)	Emigration + reimmigration + mortality a1 = N; a2 = Mean time in study area; a3 = Mean time out of study area; a4 = Mortality rate	2231	1

Supplemental table 6.12. Dolphins matched between Bay of Island and Great Barrier Island. Sightings at Great Barrier Island happened between 2016-2019.

Great Barrier ID	BOI ID	Last observed in BOI	Time range of BOI dataset
JP076	NEC043	31-Mar-15	
JP079	NEC075	24-Feb-15	December 2012 - December 2019
JP138	NEC136	31-Oct-14	Data 2012-2016 – C Peters (Massey
JP141	NEC035	31-Mar-15	Data 2016 2010 TriOcoans
JP153	NEC073	26-Nov-14	Data 2010-2019 - MOCEalls

6.2. Appendix B: Supplements for chapter 3

Supplemental table 6.13. Results of the generalized linear mixed model comparing tooth rake coverage score with the strength of the dolphins in the social network.

	Estimate	Std. Error	t-value	p-value
Intercept	-0.03855	0.01290	-2.987	0.00281
scale(strength)	-0.01318	0.01232	-1.070	0.28447

Supplemental table 6.14. Results of the generalized linear mixed model comparing presence/absence of tooth rakes with the strength of the dolphins in the social network.

	Estimate	Std. Error	t-value	p-value
Intercept	9.9844	1.0076	9.909	< 0.05
scale(strength)	-0.3950	0.7111	-0.555	0.579

Supplemental table 6.15 Logistic regression results for skin lesion presence or absence and sociality measures (mean half-weight index [HWI] and degree centrality).

	Estimate	SE	z-value	p-value						
Black lesions										
Intercept	1.49641	0.81327	1.84	0.0658						
Strength	-0.0983	1.65576	-0.059	0.9527						
Mean_HWI	1.51322	80.4877	0.019	0.985						
	Ра	le lesions								
Intercept	0.7757	2.2128	0.351	0.726						
Strength	6.0173	12.2148	0.493	0.622						
Mean_HWI	-280.86	591.791	-0.475	0.635						
	Dark-f	ringed spo	ots							
Intercept	1.7121	0.9366	-1.828	0.0675						
Strength	-0.987	1.9907	-0.496	0.62						
Mean_HWI	49.6528	96.7989	0.513	0.608						
White-fringe spot										
Intercept	-0.4143	0.8166	-0.507	0.612						
Strength	0.9014	2.2283	0.405	0.686						
Mean_HWI	-47.706	108.588	-0.439	0.66						

Supplemental table 6.16. Wilcoxon-test results for the difference in coverage score between presence and absence of skin lesions.

Skin lesion type	Wilcoxon-test statistic	p-value
Black (B)	2239.5	0.927413
Dark fringe spots (DFS)	1060.5	0.082322
Pales lesions (PL)	482.5	0.734141
Spotted lesions (SL)	1028.5	0.727542
Tattoo-like disease (TLD)	510	0.618106
Nodules (N)	1198	0.454231
White fin fringe (WFF)	671	0.434288
White fringe spots (WFS)	1184	0.089537

6.3. Appendix C. Supplemental for chapter 4

Supplemental table 6.17. Variables use to classify bottlenose dolphin's whistles in New Zealand. The variables are presented from descending importance by the mean decrease Gini (in bold).

Parameters	Mean decrease accuracy	Mean decrease Gini
Whistle complexity	40.7	84.4
D	54.7	55.8
EF	31.8	42.1
SF	39.5	37.4
MinF	33.7	35.3
MaxF	35.7	31.8
FR	29.6	28.2
TW	16.1	24.4
IP	17.9	16.7

Supplemental table 6.18. Results of generalised linear model comparing PC1 and area. GBI: Great Barrier Island.

	Estimate	SE	df	t-value	p-value
(Intercept)	-0.06	0.17	23.9	-0.37	0.71
Area GBI	0.22	0.27	23.7	0.83	0.41



Supplemental figure 6.3. The ROC curve of the random forest classification models of six whistle acoustic parameters and whistle type for bottlenose dolphins at two different locations in New Zealand. Doubtful Sound = Green line; Great Barrier Island = Red line.

Supplemental table 6.19. Summary of the results of the asymptotic test. Test statistics (MinF, MaxF, FR, SF, EF, and D) and *p*-values for 20 populations of bottlenose dolphins. Bold values denote parameter differences regarding to the bottlenose dolphin's population assessed in study (Great Barrier Island (1)). NA denotes absence of data.

Location	MinF	p- value	MaxF	p- value	FR	p- value	SF	p- value	EF	p- value	D	p- value
Great Barrier Island, NZ (2)	2.43	0.12	0.10	0.76	62.09	0.00	109.74	0.00	0.11	0.74	2.73	0.10
Doubtful Sound, NZ (1)	11.58	0.00	0.81	0.37	9.75	0.00	3.64	0.06	19.13	0.00	0.92	0.34
Doubtful Sound, NZ (3)	31.77	0.00	7.78	0.01	32.82	0.00	2.66	0.10	4.65	0.03	13.02	0.00
Milford Sound, NZ	22.77	0.00	2.59	0.11	15.59	0.00	4.23	0.04	4.64	0.03	1.19	0.28
Bay of Islands, NZ	120.86	0.00	41.71	0.00	5.50	0.02	14.81	0.00	10.68	0.00	NA	NA
Sardinia, Italy	64.65	0.00	155.25	0.00	NA	NA	3.48	0.06	83.41	0.00	112.87	0.00
Lampedusa Island, Italy	0.0018	0.97	8.42	0.00	49.85	0.00	6.35	0.01	0.51	0.47	0.79	0.37
Gandoca-Manzanillo, Costa Rica	6.47	0.01	5.09	0.02	0.03	0.87	0.03	0.86	2.51	0.11	8.43	0.00
Mediterranean Sea	1.33	0.25	3.58	0.06	8.28	0.00	0.02	0.89	20.02	0.00	0.12	0.73
Canary archipelago, Spain	5.69	0.02	14.16	0.00	35.54	0.00	0.57	0.45	0.46	0.50	2.56	0.11
Azores archipelago, Portugal	0.0071	0.93	3.77	0.05	3.27	0.07	0.95	0.33	22.45	0.00	4.73	0.03
Bay of Biscay	12.45	0.00	23.64	0.00	10.18	0.00	1.34	0.25	1.28	0.26	11.41	0.00
Sado Estuary, Portugal	71.64	0.00	38.26	0.00	NA	NA	53.00	0.00	0.02	0.88	20.22	0.00
West Sardinia, Italy	1.89	0.17	0.88	0.35	0.25	0.62	14.89	0.00	2.40	0.12	1.46	0.23
Rio de Janeiro, Brazil	0.70	0.40	0.77	0.38	36.36	0.00	14.22	0.00	0.59	0.44	11.97	0.00
Bocas del Toro, Panama	1.67	0.20	29.79	0.00	0.12	0.73	0.21	0.64	6.90	0.01	1.99	0.16
Uruguay	0.07	0.79	11.88	0.00	40.57	0.00	0.08	0.78	0.24	0.63	2.45	0.12
Tramadaí, Brazil	0.28	0.60	2.60	0.11	4.90	0.03	1.25	0.26	0.02	0.88	16.59	0.00
Patos Lagoon estuary, Brazil	9.29	0.00	9.15	0.00	70.69	0.00	8.36	0.00	17.14	0.00	14.48	0.00
Walvis Bay, Namibia	4.75	0.03	0.8	0.37	26.28	0.00	0.57	0.45	12.11	0.00	0.07	0.80