

**Population Demographics, Social
Structure and Interspecific
Associations of Free-ranging Long-
finned Pilot Whales (*Globicephala
melas*) in New Zealand**

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Abstract

Despite frequently stranding on New Zealand's beaches, there remains a paucity of information about free-ranging long-finned pilot whales (*Globicephala melas edwardii*) in these waters. The purpose of this study was to assess the demographics, social structure and interspecific associations of pilot whales frequenting eastern New Zealand waters.

Photo-identification images and associated demographic data of pilot whale groups were collected opportunistically from tour operators and research vessels from the Bay of Islands to Kaikoura between January 2003 and July 2019. Group size ranged from 5 – 250 whales (median = 50, IQ = 30 – 80), with neonates and/or calves present in the majority of encounters (79%, n = 64). Pilot whales were most frequently encountered in mixed-species groups (79% n = 64), primarily accompanied by oceanic bottlenose dolphins (*Tursiops truncatus*). A total of 145 individuals were photo-identified, establishing the New Zealand Long-Finned Pilot Whale Identification Catalogue. The mark rate (i.e. proportion of individuals with long-term or permanent dorsal fin notches and/or nicks; 13.4%) and the re-sight rate (31%) for the sampled population were low, with most (82.2%) re-sights occurring at one study location, the Bay of Islands. Patterns of pilot whale occurrence suggest some degree of seasonal site fidelity, possibly influenced by prey availability or the peak calving season. The low re-sight rate suggests either a large population, high transience and/or large individual home ranges.

Social structure analysis was carried out using the program SOCPROG to determine the strength and temporal stability of associations between pilot whales from north-eastern New Zealand. Individuals associated randomly and there was no evidence to suggest the existence of preferred long- or short-term dyadic associations, however, there were differences in individual gregariousness. Some strong dyadic associations were evident, with hierarchical cluster and social network analyses supporting the division of the study population into multiple social clusters of between three and eight individuals. Dyadic associations were irregular, with individuals disassociating on two different time scales. This indicates that pilot whales may have a hierarchical society, where small social clusters form groups of casual acquaintances, as seen in populations elsewhere.

A similar analysis of social structure investigated the possibility of an interspecific social network based on dyadic associations between oceanic bottlenose dolphins

and pilot whales encountered off the Bay of Islands. There was no evidence of temporally stable interspecific associations, most likely due to the small sample size. However, repeat associations between individuals of both species on variable temporal scales suggests that there may be an underlying pattern worthy of future investigation.

This study revealed the value of opportunistic datasets in understanding the demographics and social behaviours of a species that remains poorly-studied in New Zealand and the southern hemisphere in general. Considering that our knowledge of pilot whales in New Zealand waters is largely based on studies of stranded individuals, this research has revealed important information about the lives of free-ranging pilot whales.

Dedication

This thesis is dedicated to my grandfather, Mervyn Peter Meyer. In so many ways, my love and appreciation for learning about our natural world has come from you. Thank you for always encouraging me, loving me and believing in me. I miss you every day.

“It seems to me that the natural world is the greatest source of excitement; the greatest source of visual beauty; the greatest source of intellectual interest. It is the greatest source of so much in life that makes life worth living.”

David Attenborough

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Chapter 1: General introduction

1.1 Group living in social mammals

The formation of social groups is defined by the preferential association of animals, brought together by social attraction (Krause and Ruxton, 2002), where conspecifics are deliberately sought out by individuals (Norris and Schilt, 1988). Social groups are fundamentally different to aggregations of individuals that form when there is an abundance of some important resource (e.g. prey or access to mates; Eisenberg, 1966; Connor, 2000). While social groups are defined by the spatiotemporal proximity between individuals, non-mutualistic aggregations are instead driven by favourable environmental conditions.

From an evolutionary perspective, it is intuitive that group living and social behaviours in mammals could only have developed and persisted over time if all individuals involved benefitted genetically (Eisenberg, 1966; Alexander, 1974). If the benefits of living in a group outweigh the costs at an individual level, only then could natural selection drive the evolution of group living and, subsequently, social behaviours (Eisenberg, 1966; Alexander, 1974).

Two key benefits to group living are the maximisation of foraging efficiency through cooperative hunting (Packer and Ruttan, 1988) and an increase in predator detection, resulting in decreased predation risk (Hamilton, 1971; Norris and Dohl, 1979; Treves, 1999). Cooperative hunting strategies are well-documented in both terrestrial (e.g. Scheel and Packer, 1991; Boesch, 1994; Sand et al. 2006) and marine (e.g. Baird and Dill, 1996; Gazda et al. 2005; Wiley et al. 2011) mammals. Social behaviours in mammals are also important because they can provide both indirect (e.g. Packer and Pusey, 1982; Watts, 1998; Connor et al. 2006; Connor et al. 2010) and/or direct reproductive benefits (e.g. Gilbert et al. 1991; Jarvis et al. 1994; Gero et al. 2009) for members of these social groups. The potential costs associated with group living include an increase in, for example, intraspecific competition, the transmission of parasites and disease, and detectability by prey or predators (Wrangham et al. 1993; Côté and Poulinb, 1995; Janson and Goldsmith, 1995; Krause and Ruxton, 2002). Animal social structure exists on a continuum (Eisenberg, 1966). At one extreme are those animals that live most of their lives in solitude, with the exception of the breeding season and raising of young (for females), and at the other extreme are those that live in complex social groups with stable relationships between individuals

(Eisenberg, 1966). Gaining an understanding of the social structure of a population is vital, since it influences many aspects of its biology, for example, the transfer of information and culture (e.g. McComb et al. 2001; Cantor et al. 2015; Brakes et al. 2019); transmission of diseases (e.g. Krause and Ruxton, 2002; Krause et al. 2007), gene flow and dispersal (e.g. Oremus et al. 2009), and habitat use (e.g. Baird and Dill, 1996). This information can then be used to inform management decisions and conservation initiatives (Sutherland, 1998).

Hinde (1976) developed a conceptual framework for analysing animal societies, consisting of three interacting levels. The framework can be applied to studies of societies with varying degrees of intricacy, from very complex societies such as those found in some primates and cetaceans, to more basic societies such as those found in most rodents (Hinde, 1976; Whitehead, 2008b). At the most fundamental level of the framework are the interactions between individuals (Hinde, 1976). A culmination of the effects of these interactions defines the relationships between individuals, and this characterises the second level of the social structure. These relationships are defined by the content, quality and spatiotemporal patterning of the interactions (Hinde, 1976). Gaining an understanding of the relationships between individuals can give insight into socioecological aspects of an animal population, including cooperative behaviours, dominance and competition (e.g. Whitehead, 1996; Gowans et al. 2007). The final level of Hinde's framework is the social structure of a population. This is defined using a combination of the nature, quality and patterning of the relationships between the individuals in the population. This final level of analysis is arguably the most important, as it has the potential to reveal more complex social properties of a population (Hinde, 1976; Whitehead 2008a).

1.2 Social structure in cetaceans

Cetaceans display a rich diversity of different social structures. Complex societies with stable relationships between individuals tend to be more common in odontocetes compared to mysticetes (Trillmich and Cantor, 2018). In particular, the larger species of odontocetes such as killer whales (*Orcinus orca*), sperm whales (*Physeter macrocephalus*), bottlenose dolphins (*Tursiops* spp.), rough-toothed dolphins (*Steno bredanensis*) and pilot whales (*Globicephala* spp.) have some of the most intricate social structures (Connor et al. 2000; Baird and Whitehead, 2000; Gowans et al. 2007; Baird et al. 2008b; de Stephanis et al. 2008b). These are all large-brained (Connor, 2007; Pearson and Shelton, 2010), long-lived (Jefferson et al. 2015)

cetaceans with slow life histories (Gowans et al. 2008; Jefferson et al. 2015) and complex communication capabilities (e.g. Jensen et al. 2011; Sayigh et al. 2013; Vester et al. 2017; Zwamborn and Whitehead, 2017a, b). All of these characteristics are inter-linked and there are many hypotheses as to how (and why) large brains, in particular, have evolved (see Connor (2007) and Pearson and Shelton (2010) for concise reviews). Slow life histories (e.g. being long-lived, having high maternal investment and prolonged maternal dependence; Deaner et al. 2003; Payne, 2003) are closely associated with large brains in odontocetes, as well as in other mammals such as primates and elephants (*Loxodonta* spp.) (Pearson and Shelton, 2010). It is likely that by having a prolonged period of development, juveniles of these species have more time to learn the complex socioecological skills necessary to become reproductively successful adults (Pearson and Shelton, 2010).

Natal group philopatry is very rare in cetacean societies but is well documented in resident killer whale populations off north-eastern North America (Bigg, et al. 1990; Baird, 2000; Hoelzel et al. 2007). This is where offspring of both sexes remain with their natal group for life and males only leave the group temporarily to mate with outside females, avoiding inbreeding (Bigg, et al. 1990; Baird, 2000; Hoelzel et al. 2007). It has been suggested that populations of long-finned pilot whales (*Globicephala melas*) in the Faeroe Islands and Baird's beaked whales (*Berardius bairdii*) in Japan display the same social structure, living in large groups of extended matriline (Amos et al. 1991; Amos et al. 1993; Kasuya et al. 1988).

In delphinid societies, fission-fusion patterns of association are commonly observed. Depending on the species in question, individuals will form complex social networks and display variable social clustering at different organisational scales (e.g. Connor et al. 2000; Whitehead and Weilgart, 2000; Gowans et al. 2007; Baird et al. 2008a, b; McSweeney et al. 2009; Mahaffy et al. 2015). Associations between individuals are usually hierarchically structured, with the smallest societal unit being the most temporally stable (e.g. Baird and Dill, 1996; Connor et al. 2000; Parra et al. 2011; Augusto et al. 2017a). Larger groups typically consist of multiple smaller social units and tend to be ephemeral (e.g. Connor et al. 2000; Parra et al. 2011; Augusto et al. 2017a; Hunt et al. 2019). The primary advantage of having a social system with varying degrees of flexibility is that group size can be adjusted with the availability of essential resources such as prey and mates.

Interspecific or mixed-species groups are defined by close associations between individuals from two or more species (Stensland et al. 2003). Interspecific associations are the result of deliberate interactions between individuals from different species, which distinguishes them from multi-species aggregations that are formed around concentrated essential resources (Eisenberg, 1966; Stensland et al. 2003; Cords and Würsig, 2014). These types of associations occur across a wide range of taxa (e.g. Krause et al. 1996; Ward et al. 2002; Sridhar et al. 2009; Farine et al. 2012), including in many species of mammals (e.g. Fitzgibbon, 1990; McGraw and Bshary, 2001; Psarakos et al. 2003; Stensland et al. 2003; Cords and Würsig, 2014). Among mammals, such associations are most common in species that are intra-specifically gregarious (Stensland et al. 2003; Cords and Würsig, 2014). As such, theories of group-living that are applied to studies of mono-specific groups (Eisenberg, 1966; Alexander, 1974; Krause and Ruxton, 2002) are also useful for understanding possible drivers of mixed-species groups (e.g. Norris and Schilt, 1988).

1.3 Studying social structure

Photo-identification (photo-ID) is an important tool used in cetacean research (e.g. Hammond et al. 1990; Mann, 2000). When conducting longitudinal studies of populations of long-lived cetaceans (e.g. killer whales, pilot whales, sperm whales, bottlenose dolphins), it is vital to have repeated, reliable identification of individuals to answer questions about their behavioural patterns and life-histories (Würsig and Würsig, 1977; Würsig and Jefferson, 1990; Whitehead and Dufault, 1999; Mann, 2000). Photo-ID methodology therefore forms the foundation of studies focused on understanding social structure in cetaceans (e.g. Baird and Whitehead, 2000; Christal et al. 2001; de Stephanis et al. 2008; Hunt et al. 2019). Although originally developed some time ago (Würsig and Würsig, 1977), photo-ID methodology continues to improve with the advent of the digital camera (e.g. Hillman et al. 2003; Beirão et al. 2014), which has required stricter data-selection criteria to be applied in more recent studies of social structure.

Genetic markers such as genotyping and molecular sex identification are increasingly used to study social structure and can reveal important information about sampled individuals, as well as the group or population as a whole (Whitehead et al. 2000). This includes key aspects such as the identity (Amos and Hoelzel, 1990), sex (e.g. de Stephanis et al. 2008c) and reproductive success of individuals (Ford et al. 2011), as well as whether groups display kinship (e.g. Gero et al. 2008; Oremus et al. 2013),

matrilineal societies (e.g. Gero et al. 2008; Whitehead, 2005; Whitehead et al. 2017), spatial dispersal (Oremus et al. 2013) or segregation of sexes (e.g. Duffield and Wells, 1991), and can therefore provide insight into the mating systems of cetacean species (Whitehead et al. 2000).

Once individuals in a group of cetaceans have been identified, it is possible to undertake more detailed investigations of their social structure using quantitative methods (Whitehead, 1997). By far the most common method of measuring interactions between individuals within social animal groups (including cetaceans) is with the use of association indices (Whitehead, 1995; Whitehead and Dufault, 1999; Webber and Vander Wal, 2019). Since direct observations of interactions between individuals can be difficult to achieve in the marine environment (Chilvers and Corkeron, 2002), spatiotemporal association patterns are used as a proxy (Whitehead, 1997). There are two important underlying assumptions to be aware of when using association indices to study social cohesion in animals (Bejder et al. 1998; Whitehead and Dufault, 1999). First, social affiliation is signified by physical proximity (i.e. when animals are members of the same group or are observed in a number of groups together) and second, the strength of the affiliation is correlated with the amount of time individuals spend together. While there are a few different association indices that may be appropriate for use in studies of animal societies (Cairns and Schwager, 1987; Ginsberg and Young, 1992), the half-weight index (HWI) is used most often (Whitehead, 2008a, b). Calculation of the HWI quantifies the frequency of association among individuals (dyads) in a group and has a range of possible values between zero (two individuals are never seen together) and one (two individuals are always seen together; Cairns and Schwager, 1987). Once the underlying patterns of association are understood, analytical techniques can be used to better reveal the complexity often present in delphinid societies.

1.4 Pilot whales

Pilot whales are one of the largest members of the Delphinidae family and belong to the subfamily Globicephalinae (Olson, 2018). There are two recognised species of pilot whale: long-finned pilot whale (Traill, 1809) and *Globicephala macrorhynchus* (short-finned pilot whale; Gray, 1846).

Short-finned pilot whales are a cosmopolitan species, having a continuous global distribution and inhabiting tropical, sub-tropical and warm-temperate waters (Figure 1.1; Olson, 2018). Regional populations of short-finned pilot whales have

mitochondrial DNA (mtDNA) haplotype frequencies that are strongly differentiated, whilst simultaneously sharing dominant haplotypes across populations in different oceans (Oremus et al. 2009; Van Cise et al. 2016).

There are two recognised subspecies of long-finned pilot whale: *G. m. melas* (North Atlantic) and *G. m. edwardii* (Southern Hemisphere; Davies, 1960). The two subspecies have discrete anti-tropical distributions, inhabiting sub-tropical, temperate and, in the case of *G. m. edwardii*, sub-Antarctic waters (Figure 1.1; Davies, 1960; Olson, 2018). There is also evidence to suggest the existence of a now-extinct population of long-finned pilot whales in Japanese waters (Jefferson et al. 2015; Olson, 2018). Northern and southern hemisphere populations display morphological differences including dissimilar colouration patterns (Davies, 1960) and significant variations in skull morphology (Marina et al. 2018). There is also strongly restricted gene flow between long-finned pilot whale populations in each hemisphere (Oremus et al. 2009).

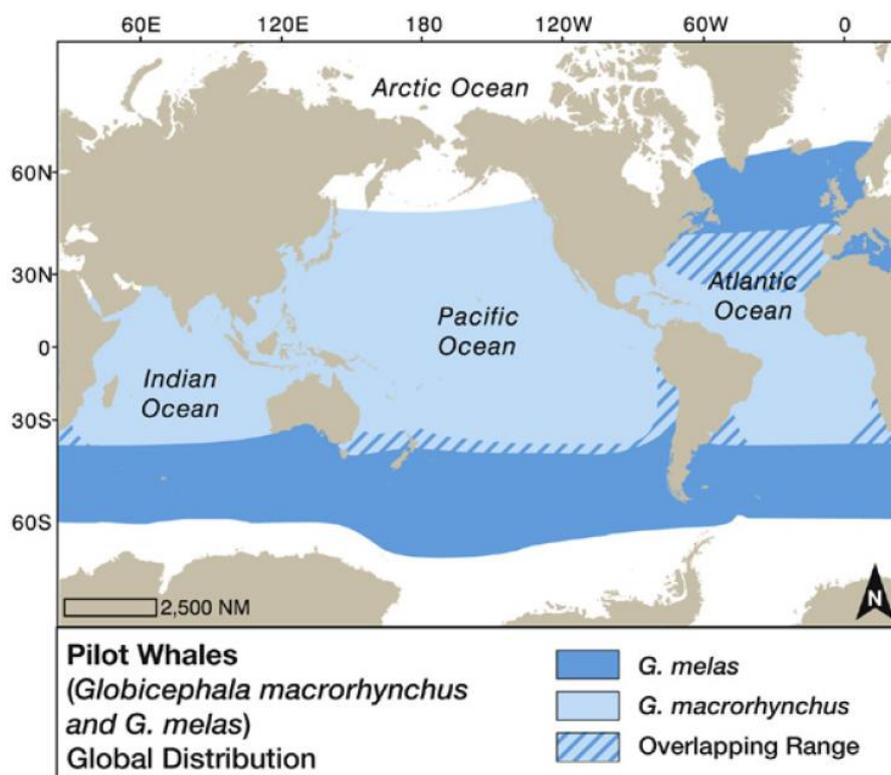


Figure 1.1 Global distribution of *Globicephala* spp. Map from Olson (2018) adapted from Jefferson et al. (2015).

While the global distributions of the two species of pilot whale overlap in parts of the South Pacific, South Atlantic and North Atlantic Oceans (Figure 1.1; Olson, 2018),

both historical and recent phylogenetic analyses support the current species status (Le Duc et al. 1999, McGowen et al. 2008, Oremus et al. 2009; Vilstrup et al. 2011). Importantly, a recent study by Miralles et al. (2016) identified evidence of the first known interspecific hybridisation between long- and short-finned pilot whales in the waters off northern Spain, a region of overlapping ranges for these two species.

The vast majority of pilot whale studies have focused on the northern hemisphere subspecies and populations of *G. m. melas* and *G. macrorhynchus* respectively (e.g. Amos et al. 1991; Ottensmeyer and Whitehead, 2003; Curé et al. 2012; Alves et al. 2013; Miralles et al. 2013; Mahaffy et al. 2015; Augusto et al. 2017a; Alves et al. 2019b). Collectively, the results of these studies confirm that pilot whales have complex social structures (Amos et al. 1993; Ottensmeyer and Whitehead, 2003; de Stephanis et al. 2008c; Augusto et al. 2017a), advanced communication capabilities (Jensen et al. 2011; Sayigh et al. 2013; Vester et al. 2017; Visser et al. 2017; Zwamborn and Whitehead, 2017a, b) and are involved in inter-specific associations and interactions (Shane, 1995; Baraff and Asmutis-Silva, 1998; Ciano and Jørgensen, 2000; Migura and Meadows, 2002; Curé et al. 2012; Zaeschmar, 2014).

Almost all studies of long-finned pilot whales to date have reported the presence of multiple sub-groups within larger groups during encounters, usually spread out over a few square kilometres (Weilgart and Whitehead, 1990, Cañadas and Sagarminaga, 2000; Ottensmeyer and Whitehead, 2003; de Stephanis 2008b, c; Visser, 2014; Augusto et al. 2017a; Curé et al. 2019). However, the methods used to delineate groups and sub-groups while at sea have not yet been standardised, and studies of both species of pilot whale continue to define groups in different ways (e.g. Ottensmeyer and Whitehead, 2003; de Stephanis et al. 2008c; Alves et al. 2013; Mahaffy et al. 2015). Behavioural (de Stephanis 2008c; Servidio, 2014; Visser, 2014; Hartny-Mills, 2015; Mahaffy et al. 2015; Augusto et al. 2017) and genetic (de Stephanis 2008c; Van Cise et al. 2017; Alves et al. 2019b) evidence suggests that sub-groups are representative of socially-cohesive cohorts of individuals in both pilot whale species, with larger groups representing multiple social units, which is similar to patterns of social structure seen in sperm whales (e.g. Whitehead and Weilgart, 2000), bottlenose dolphins (Connor et al. 2000) and killer whales (e.g. Baird and Dill, 1996).

Long-finned pilot whales are listed as “Least Concern” on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Minton et al. 2018),

however they remain data-poor in much of their global range, especially in the southern hemisphere. Recent abundance estimates of long-finned pilot whales from the Northeast Atlantic have indicated that there have been no long-term trends over the period from 1987 to 2015 (Pike et al. 2019). This is despite an annual take of between 700 and 1000 individuals by drive fisheries in the Faeroe Islands and an increasing take of animals from the waters around Greenland (Minton et al. 2018), suggesting a large, wide-ranging population of whales throughout the region.

1.5 Long-finned pilot whales in New Zealand

Stranding records from the New Zealand Whale Stranding Database (NZWSDB; curated by the Department of Conservation (DOC), data extracted on 1 October 2019) indicate that both long- and short-finned pilot whales are found in New Zealand waters; however, long-finned pilot whales are the most frequent mass stranding cetacean on New Zealand's coast (Brabyn, 1991; Thompson et al. 2013; Betty et al. 2020). Consequently, the majority of information available for long-finned pilot whales in New Zealand has come from strandings-related data. Studies of stranded pilot whales in New Zealand have revealed detailed information about their dietary preferences (Beatson et al. 2007; Beatson and O'Shea, 2009), sexually dimorphic traits (Betty, 2019), reproductive parameters (Betty, 2019; Betty et al. 2019) and genetic relatedness (Oremus et al. 2009; Oremus et al. 2013). Gene flow between pilot whales in New Zealand and those in the North Atlantic is strongly restricted (Oremus et al. 2009), which is to be expected considering the anti-tropical distribution of these two sub-species. Patterns of gene flow for long-finned pilot whales throughout the Pacific Ocean remain largely unknown, however, genetic evidence shows that despite the lack of geographical boundaries, there is strong genetic differentiation of populations in New Zealand compared to Tasmania, Australia (Oremus et al. 2009). Individuals in these regions do share common haplotypes, which indicates that there is some mixing of genes and therefore, that populations are genetically linked (Oremus et al. 2009; Oremus et al. 2013). Nevertheless, such strong differentiation is unexpected, especially considering the wide-ranging nature of pilot whales (Bernard and Reilly, 1999; Alves et al. 2019a), but may be influenced by the social organisation of this species (e.g. Whitehead, 1998; Hoelzel et al. 2002). Within New Zealand, pilot whale genetic diversity is low but particular haplotypes are common and widespread, which indicates high levels of mixing of individuals from different regions (Oremus et al. 2009; Oremus et al. 2013).

Mass-stranded groups of pilot whales in New Zealand and Tasmania represent multiple matrilineal groups (Oremus et al. 2013), which suggests that social associations are formed between related and unrelated individuals. Interestingly, there appears to be no correlation in the spatial distribution of strandings among related individuals (Oremus et al. 2013). Additionally, mothers and their calves sometimes strand many metres apart, and in some cases mothers of calves are completely absent from sampled groups (Oremus et al. 2013). It has been suggested that these close kinship bonds are disrupted prior to the occurrence of strandings when multiple groups join together (Oremus et al. 2013), possibly in response to mating opportunities (de Stephanis et al. 2008c; Oremus, 2008). However, this remains speculative, as there have been no studies of free-ranging pilot whales in New Zealand to date.

1.6 Thesis aims and objectives

Considering that long-finned pilot whales are the most numerous species to strand on New Zealand shores and that all of the knowledge we have has come from stranded animals, a study of this species in the wild was warranted. Using a long-term, opportunistically-collected data set, the aims of this study were three-fold. First, to assess the occurrence of living long-finned pilot whales off the east coast of New Zealand. Second, to assess the social structure of long-finned pilot whales off north-eastern New Zealand. Finally, to investigate the interspecific associations between long-finned pilot whales and oceanic bottlenose dolphins (*Tursiops truncatus*).

By conducting this research, I hope to provide novel information concerning the lives of the poorly studied long-finned pilot whales in New Zealand waters, which may help inform both future studies and management decisions.

This thesis is structured in the following way:

Chapter 1 Introduction

Chapter one provides a literature review on group living and social structure in animals, particularly cetaceans. It also gives a general introduction to pilot whales and an overview of the current knowledge of long-finned pilot whales in New Zealand.

Chapter 2 Population Demographics

Chapter two assesses the occurrence of free-ranging long-finned pilot whales off the east coast of New Zealand across six regions spanning ca. 520km in total from the Bay of Islands to Kaikōura, from 2003 to 2019. Demographic parameters including group size, age-class composition, mark rate and re-sight rate of the population were analysed, and a photo-ID catalogue of pilot whales in New Zealand was established.

Chapter 3 Pilot Whale Social Associations

Chapter three describes the social structure of long-finned pilot whales off the north-eastern coast of New Zealand, the area with the highest number of sightings and photo-ID data. More specifically, it looks at the strength of associations between individuals, investigates possible clustering of individuals into social units, and considers the temporal stability of dyadic associations within the population.

Chapter 4 Social Associations between Pilot Whales and Bottlenose Dolphins

Chapter four provides an investigation into the possible existence of an interspecific social network, based on temporally stable dyadic associations of long-finned pilot whales and oceanic bottlenose dolphins encountered off the north-eastern coast of New Zealand.

Chapter 5 General Discussion

Chapter five provides a discussion of the overall findings from this thesis and suggests future directions to enhance our understanding of long-finned pilot whales in New Zealand waters, and global knowledge of the species.

Chapter 2: Population demographics

2.1 Introduction

An understanding of demographic parameters such as species occurrence, population abundance and group structure provide baseline data for comparison to other populations and inform the development of effective management strategies. Baseline information of both terrestrial and aquatic species can be collected by researchers via field surveys, focusing on individual identification and group dynamics. Capture-recapture techniques are an integral part of these studies and rely on the identification of individuals based on different markings (e.g. Pennycuick and Rudnai, 1970; Kelly, 2001; Heilbrun et al. 2003; McMahon et al. 2006; Holmberg et al. 2009; Marshall et al. 2011). These markings can occur naturally as a result of life processes (e.g. Heithaus, 2001; Rosso et al. 2011; Bertulli et al. 2016), by some anthropogenic interaction that results in injury (e.g. Baird and Gorgone, 2005; Denkinger et al. 2013), or may be purposefully applied by researchers (e.g. Godley et al. 2003; Ruiz- Gutiérrez et al. 2012). Using data linked to unique animals facilitates a better understanding of both individuals and populations, for example, through the spatial and temporal occurrence of individuals, their association patterns, reproductive rates, age, sex and social behaviour (Connor et al. 1999; Calambokidis et al. 2008; Holmberg et al. 2009; Saraux et al. 2011; Cantor et al. 2012; Wells, 2014; Augusto et al. 2017a; Brough et al. 2019).

Photo-ID techniques provide information about the demographics of free-ranging cetacean populations (e.g., Würsig and Würsig 1977; Katona et al. 1979; Würsig and Jefferson 1990; Dufault and Whitehead, 1995; de Stephanis et al. 2008b). This technique has been successfully used to study a wide range of cetacean species. For example, bottlenose dolphins (Connor et al. 2000), killer whales (Bigg et al. 1990), pygmy killer whales (*Feresa attenuata*; McSweeney et al. 2009), humpback whales (*Megaptera novaeangliae*; Katona et al. 1979) and sperm whales (Whitehead et al. 1991). Unlike many terrestrial studies, this method of marking does not require the physical capture of individuals (Begon, 1979). Instead, photographs of the unique marking patterns of individuals (which they acquire and accumulate during their lives) can be used to identify animals over periods of months to decades (Würsig and Würsig, 1977; Würsig and Jefferson, 1990).

Photographs can be used for determining the proportion of identifiable individuals in a population (Würsig and Jefferson, 1990; Ottensmeyer and Whitehead, 2003; Baird et

al. 2008a), population abundance (Calambokidis and Barlow, 2004; Balmer et al. 2008), social associations between individuals (Whitehead and Dufault, 1999; Baird and Whitehead, 2000; Connor et al. 2000; Mahaffy et al. 2015), population distributions (Wells, 1991; Evans and Hammond, 2004) as well as survival and reproduction rates (Verborgh et al. 2009; Sears et al. 2013). It is vital that all photographs be quality-controlled to ensure that strict image quality and mark distinctiveness criteria are met. These criteria are designed to include only the best quality images of the most distinctive animals in the data analysis process, ensuring that the images and individual marks are good enough for animals to be re-identifiable, regardless of any mark changes (Wilson et al. 1999; Calambokidis et al. 2001; Stevick et al. 2001). This process is important as it minimises the chances of mis-matches (two or more animals being assigned the same catalogue number) and missed-matches (multiple catalogue numbers being assigned to the same individual), which could otherwise skew the results (Hammond et al. 1990, Würsig and Jefferson, 1990; Wilson et al. 1999; Stevick et al. 2001).

Photo-ID techniques have been successfully used to study pilot whales, with all studies to date being focused on Northern hemisphere populations. For example, the Mediterranean Sea (Cañadas and Sagarminaga, 2000), the Nova Scotian coast, Canada (Ottensmeyer and Whitehead, 2003; Augusto et al. 2017a), the Strait of Gibraltar (de Stephanis et al. 2008c; Verborgh et al. 2009), off Hawai'i (Mahaffy et al. 2015) and Madeira (Alves et al. 2013; Alves et al. 2019b). These studies used dorsal fin markings (nicks and notches) to understand population dynamics and demographics. In general, pilot whales in the northern hemisphere have similar average group sizes and mark rates (i.e. the proportion of individuals with permanent, distinctive dorsal fin markings; Würsig and Jefferson, 1990), show some degree of site fidelity and have complex social structures (Cañadas and Sagarminaga, 2000; Ottensmeyer and Whitehead, 2003; de Stephanis et al. 2008a, c; Alves et al. 2013; Augusto et al. 2017a; Alves et al. 2019b). In contrast, there is little known about southern hemisphere pilot whales.

Studies of long-finned pilot whales in the southern hemisphere have used dead whales from stranding events to investigate prey preferences and foraging ecology in Argentina (Clarke and Goodall, 1994), Chile (Mansilla et al. 2012), New Zealand (Beatson and O'Shea, 2009) and Australia (Beasley et al. 2019), with only a single study focused on live individuals from the Kerguelen Islands (Fontaine et al. 2015). Long-finned pilot whales in the southern hemisphere are known to feed predominantly

on cephalopods, especially arrow squid (*Nototodarus* spp., Clarke and Goodall, 1994; Beatson and O'Shea, 2009; Mansilla et al. 2012; Beasley et al. 2019), and mesopelagic fish species (Fontaine et al. 2015). Studies from Australia have assessed the success of long-finned pilot whale stranding management techniques (Gales et al. 2012), and more recently strandings data have been used to investigate spatial and temporal patterns of long-finned pilot whale strandings in New Zealand (Betty et al. 2020). To date, no studies have used photo-ID to assess demographics of pilot whale populations in the southern hemisphere. In New Zealand, long-finned pilot whales are the most numerous species to mass strand (events involving two or more adult animals), with 120 mass stranding events recorded between 1978 and 2017 (Betty et al. 2020). Strandings-related data have informed diet (Beatson et al. 2007; Beatson and O'Shea, 2009), genetic (Oremus et al. 2009; Oremus et al. 2013) and life history (Betty, 2019; Betty et al. 2019) studies, giving insight into long-finned pilot whales in this region. However, there are no studies on the population dynamics of live long-finned pilot whales in New Zealand. Despite the paucity of data, this species is currently classified as Not Threatened in New Zealand (Baker et al. 2019). This classification reflects our current knowledge of their genetic status where there are high levels of gene flow (Oremus et al. 2009), but does lack important information related to abundance estimates since there is still very limited demographic data available.

This chapter presents an assessment of the occurrence and demographics of live long-finned pilot whales off eastern New Zealand from 2003 to 2019. This includes information on group size, age-class composition, mark rate and the re-sight rate of the population.

2.2 Methods

2.2.1 Study site

The study site was broadly divided into two focal regions: 1) the north-eastern coast of the North Island - Te Ika a Maui, and 2) the north-eastern coast of the South Island - Te Wai Pounamu, New Zealand (Figure 2.1). This included five sampling locations in the North Island: North Cape (NC), Bay of Islands (BOI), Poor Knights Islands (PKI), Hauraki Gulf (HG) and Bay of Plenty (BOP), and one sampling location in the South Island (Kaikōura).

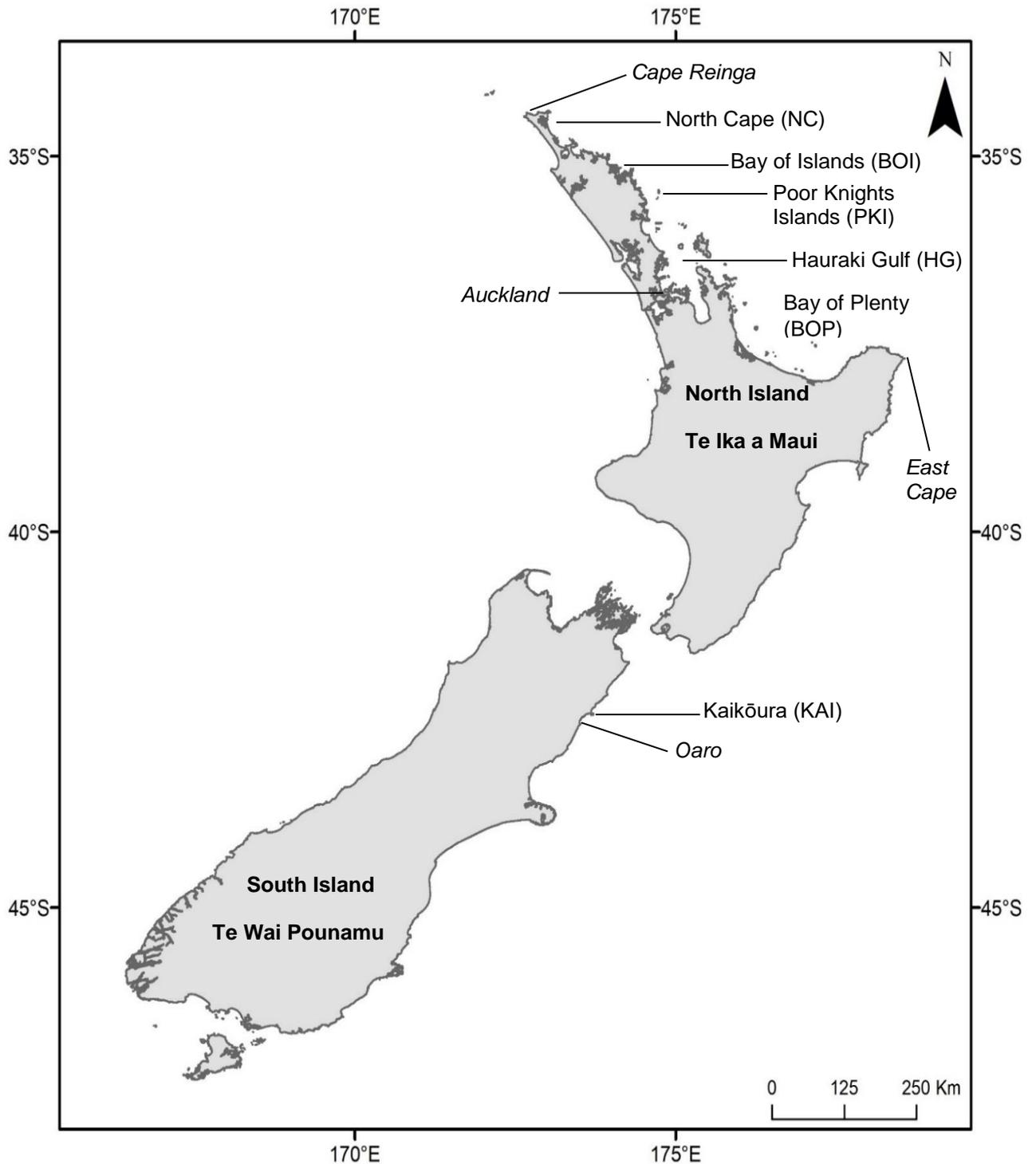


Figure 2.1 Map of New Zealand showing the six study locations spanning ca. 520km in total; five along the north-eastern coast of the North Island and one along the north-eastern coast of the South Island.

The North Island focal region includes a ca. 500 km stretch of the north-eastern coast of New Zealand extending from North Cape (~34°41' S, 173°05' E) down to East Cape (Bay of Plenty, ~37°05' S, 177°4' E). Sea surface temperatures reach 23°C during the

austral summer months (December to February) and fall to 15°C during the austral winter months (June to August; Shears and Bowen, 2017). From December to May, the surface waters off the north-east coast are warmed due to the East Auckland Current (Sutton and Roemmich, 2001; Zeldis et al. 2004). The five North Island study locations are oceanographically diverse, with water depths ranging from < 60m in the Hauraki Gulf to > 600m off North Cape.

The South Island focal region includes a ca. 20km stretch of the south-eastern coast of New Zealand, extending along the Kaikōura Peninsula (~42°52' S, 173°71'E) to Oaro (~42°56' S, 173°51'E). There is a submarine canyon system very close to shore, with the 1000m depth contour coming to within 5km of the shoreline. The unique bathymetry of this submarine canyon has a direct influence on the hydrological system of the south-eastern coastal waters off Kaikōura. The cold, sub-Antarctic, low salinity water that is carried by the Southland Current mixes with the warmer northern water from the East Cape Current, which leads to a local upwelling (Chiswell et al. 2015). The deep nutrient-rich waters brought to the surface by this upwelling cause the area to be highly productive and it is known to be a valuable feeding location for sperm whales (Bradford, 1972; Sagnol et al. 2014; Guerra et al. 2017).

2.2.2 Boat survey methods

2.2.2.1 Pilot whale encounters

While both species of pilot whale are found in New Zealand, 87% (n = 355) of all recorded stranding events were confirmed as long-finned pilot whales, with no mixed groups of long-finned and short-finned pilot whales ever recorded (New Zealand Whale Stranding Database, extracted on 1 October 2019). Based on this knowledge, it was assumed that all groups encountered during the current study were of long-finned pilot whales, hereafter referred to as pilot whales.

For this study, a pilot whale encounter was defined as a sighting event where there were one or more photographs enabling accurate species identification, as well as records of the date, time and GPS coordinates of the encounter. Each encounter was recorded as a day-long event (a single encounter per sampling day), and included all of the individual pilot whales sampled on the day. An encounter ended as a result of worsened weather conditions, loss of daylight hours, operational time pressures, or when the observer(s) lost sight of the animals.

Photo-ID images of pilot whales were collected opportunistically from a combination of commercial tour vessels (during marine wildlife tours) and dedicated research vessels between January 2003 and July 2019. Six tour operators and seven dedicated research vessels provided images and associated metadata from pilot whale encounters (Appendix 1).

Tour vessel encounters with pilot whales were opportunistic, occurring during the operation of tours typically focused on more frequently occurring local species of marine mammal. Pilot whales were encountered by the research vessels during dedicated cetacean surveys primarily looking for false killer whales (*Pseudorca crassidens*). All observers used cues such as splashes, blows, fin sightings and silhouettes of surfacing animals (surface disturbance) to detect pilot whales. Dedicated research surveys also used the presence of foraging bird species that are known to associate with pilot whales, in particular black petrels (*Procellaria parkinsoni*; Gaskin, 2017). This was achieved by employing continuous scanning methodology (e.g. Mann, 1999), using both the naked eye and binoculars. Upon sighting the animals, the vessel was operated following the New Zealand Marine Mammals Protection Regulations (1992) to minimise disturbance to the group. Metadata were collected, and for the purposes of this study only data on species presence, GPS coordinates and water depth were used.

Once closer to the pilot whales, estimated group size and general observations of group composition were recorded. Neonates were distinguished by their small size (approximately half the size of an adult), patchy light-grey colour, presence of dorsoventral foetal folds and, occasionally, a bent-over dorsal fin (Auger-Méthé and Whitehead, 2007). Calves were of a similar size and colour to neonates, but lacked foetal folds and had straightened dorsal fins (Auger-Méthé and Whitehead, 2007). Juveniles were two-thirds of the length of adult whales, and adults were approximately between 4.5 and 5.5m long. Both juveniles and adults had similar dark grey to black colouration, with a prominent white saddle-patch immediately behind the dorsal fin and white post-orbital eye blazes (Auger-Méthé and Whitehead, 2007). Individuals were presumed to be mothers (and therefore females) if they were consistently seen in the company of a calf during an encounter (Whitehead, 1996; Grellier et al. 2003). While at sea, adult males in a group can be distinguished by their larger size and taller, broader dorsal fin, however this information was not collected during field observations.

In any instances where encounter depth data were not available, the reported GPS coordinates were entered into ArcGIS® online (Esri, 2020), while using the “NZ

Bathymetric Data Index” base layer from Land Information New Zealand (LINZ, 2019), to determine water depth at the encounter location.

2.2.2.2 *Groups and group-size estimates*

The typical spatial spread of pilot whale groups encountered between North Cape and the Poor Knights Islands off the north-eastern North Island (Figure 2.1; Zaeschmar, unpubl. data), and the often-opportunistic method used to collect the data, required a group definition that captured all potentially interacting individuals in a particular area (Chapter 1, Section 1.4). Therefore, a group was defined using a 1,000m chain rule, where all pilot whale individuals opportunistically encountered on a single day, in the same location by the research vessel or tour boat, and which were within 1,000m of each other were considered to be members of the same group (Mahaffy et al. 2015). Consequently, every encounter included just a single pilot whale group.

Field observations made from the *Manawanui* research vessel (Appendix 1) during encounters between North Cape and the Poor Knights Islands (Figure 2.1) noted the presence of multiple smaller, more cohesive groupings of pilot whales within larger, widely-spread groups. These were termed “sub-groups” and were defined as cohorts of pilot whales that were showing similar behaviour and had a maximum distance between individuals of less than one body length (approximately 5m; de Stephanis et al. 2008c). This represents a subset of the overall data set, as sub-group information was only collected from this research vessel throughout the study period.

It cannot be confirmed that group sizes were estimated using the same techniques for all encounters, since the data were collated from multiple sources and had been recorded by different observers. Those records that provided just a single value for the group size estimate instead of a minimum, best and maximum were treated as the best estimate of group size. For the purpose of consistency, the best estimate was used from those records that did differentiate. The group size estimates may therefore be biased and possibly over- or under-estimated, but as the data were provided by trained marine mammal tour operators and researchers, the estimates should be reasonably reliable. When pilot whales were encountered in association with other cetacean species, for example offshore bottlenose dolphins and false killer whales, it was termed a mixed-species group (Shane, 1990), and separate group-size estimates were provided for each species.

2.2.3 Comparison to strandings data

The research vessel used to collect the majority of the study data operates on a seasonal basis (see Appendix 1). Therefore, it was not possible to assess the seasonality of pilot whale occurrence in north-eastern New Zealand based solely on data from encounters. To verify any patterns of seasonality, data on long-finned pilot whale strandings that occurred between 2003 and 2018 were sourced from the New Zealand Whale Stranding Database, curated by DOC (Department of Conservation, 2019). The records were filtered to include both single- and mass-stranding events of "*Globicephala melas*" and "*Globicephala* sp." entries that occurred in the "Northland", "Auckland", "Bay of Plenty", "Waikato" and "Canterbury" regions, to correspond with the focal study areas. The Northland, Auckland and Waikato regions were filtered further, to include only strandings that occurred on the east coast. Canterbury was filtered to include only those strandings occurring near Kaikōura. Single-stranding events included just one animal while mass-stranding events included two or more animals stranded together, with the exclusion of mother-calf pairs (Geraci and Lounsbury, 2005).

2.2.4 Photo-identification and photographic data analyses

Standard photo-ID methods (Würsig and Jefferson 1990) were applied to identify individual pilot whales via marks on their dorsal fin. A range of different Digital SLR cameras with auto-focusing lenses were used as photographs were sourced from different tour boats and research vessels over multiple years. During research surveys, individual pilot whale dorsal fins were photographed at random, regardless of their degree of marking, to ensure that every individual had the same probability of being photographically captured (Auger-Méthé and Whitehead, 2007; Verborgh et al. 2009). The photographs taken from the tour vessels were collected opportunistically and therefore biases towards capturing images of distinctive or interactive individuals was more likely. Time constraints, weather conditions or operating limits also resulted in tour operators being less likely to spend enough time with the pilot whales to successfully sample entire groups. Therefore, it has been assumed that at least some of the groups included in this study were not sampled completely and/or randomly.

Primary features used to identify individual pilot whales included notches and nicks on or adjacent to the leading and/or trailing edge of the dorsal fin (Auger-Méthé and Whitehead, 2007). These primary features were used to confirm fin matches. Secondary features such as scars and fresh subdermal wounds from presumed cookie

cutter shark bites (*Isistius* spp.), as well as the unique saddle-patches behind the dorsal fin of the individual were used to aid in identification (Auger-Méthé and Whitehead, 2007). All dorsal fin images of pilot whales from 2003 – 2019 were graded according to the likelihood of successfully re-sighting individuals (Table 2.1).

Photographic quality was determined by the sharpness of the focus, the clarity of the contrast and the angle of the fin relative to the frame. Each image was assigned a quality control grade on a scale of Q1 to Q4 (Table 2.1). Only the best photograph of an individual from each encounter was used. All images scored Q1 and Q2 were then given a distinctiveness score of D1 to D4 based on the size and number of notches on the leading and trailing edges of the fin (Table 2.1). Only individuals with the highest scores, D1 and D2, were included in the analysis.

Table 2.1 Grading system and assessment criteria applied to evaluate image quality (Q1 – Q4) and distinctiveness of marks (D1 – D4) for use in photo identification of long-finned pilot whales off eastern New Zealand. Adapted from Zaeschmar et al. (2014).

Image quality grading	Examples	Assessment criteria
Q1 (<i>excellent</i>)		Image meets all quality criteria. It is in sharp focus with clear contrast and is taken at an angle that allows a distinct profile of both the leading and trailing edge of the dorsal fin.
Q2 (<i>good</i>)		One of the quality criteria is not met, but the information in the image remained intact allowing for identification of <i>very distinctive</i> and <i>distinctive</i> individuals.
Q3 (<i>fair</i>)		One or more quality criteria is/are not met, allowing for identification of <i>very distinctive</i> individuals only.
Q4 (<i>poor</i>)		Two or more quality criteria are not met, preventing successful identification of an individual.

Dorsal fin distinctiveness grading	Examples	Assessment criteria
D1 (<i>very distinctive</i>)		Fin has multiple notches, including large notches and can be identified from all image quality categories.
D2 (<i>distinctive</i>)		Fin has multiple smaller notches or one large notch and can be identified from <i>excellent</i> , <i>good</i> and <i>fair</i> quality images.
D3 (<i>slightly distinctive</i>)		Fin has a few notches and can be identified only from <i>excellent</i> and <i>good</i> quality images.
D4 (<i>not distinctive</i>)		Fin has no notches or other permanent distinguishing features (i.e. clean fin) or has notches that could only be seen in <i>excellent</i> quality images and could only be identified within an encounter, with positive identification between encounters unlikely.

To avoid false positives (when the same catalogue number is assigned to two or more distinct animals) and false negatives (when a single individual is assigned more than one catalogue number), each new dorsal fin image was carefully examined (Hammond et al. 1990; Würsig and Jefferson 1990) and confirmed by two experienced researchers. Mark changes (e.g. when an individual acquires one or more new notches or an existing notch changes in size and/or shape) could be identified by comparing the shape and relative positioning of another two or more identical marks on the dorsal fin.

As there was no existing pilot whale catalogue for New Zealand prior to this research, each newly identified individual was assigned a unique identification number (e.g. NZGme001) and added to the New Zealand Long-finned Pilot Whale Identification Catalogue (NZLFPWIC). To keep a record of the sighting history of each individual captured during the study period, capture histories were created for each catalogued pilot whale (i.e. those individuals that met the analysis criteria). A “1” denoted the presence of an individual on any given sampling day while a “0” denoted its absence.

2.2.5 Mark rate and rate of discovery of individuals

Using only photographs of high quality (Q1 – Q2) and highly distinctive individuals (D1 – D2), the proportion of individual pilot whales sufficiently well-marked to be confidently recognised was assessed by counting the number of marked and unmarked individuals from nine independent encounters between January 2011 and May 2019 (Table 2.2). The mark rate was estimated using the following equation from Ottensmeyer and Whitehead (2003):

$$\frac{\text{\# of good quality fin images (Q1 – Q2) of well-marked individuals (D1 – D2)}}{\text{\# of good quality fin images (Q1 – Q2) of all individuals}}$$

SOCPROG 2.9 (Whitehead, 2009) was used to determine the rate of discovery of marked individuals. This was done by calculating the cumulative number of identified individuals in relation to the number of newly identified whales.

2.3 Results

2.3.1 Boat surveys and stranding records

In total, 81 long-finned pilot whale encounters were recorded in the waters off eastern New Zealand over the 16-year study period between January 2003 and July 2019 (Figure 2.2). Most encounters (88%, n = 71) took place between December and May (Figure 2.3) with pilot whales being encountered most frequently in January (28%, n = 23). One research vessel (Appendix 1), which was used to collect the majority of the data (63%, n = 51 encounters), operates only between October and May, hence there was more survey effort overall during these months each year.

Strandings records for the study regions between 2003 and 2018 showed that pilot whales strand in almost every month, with a total of 27 strandings over the study period (Figure 2.3). Overall, single-stranding events (n = 17), more frequent in October, were

more common than mass-stranding events ($n = 10$) that were more frequent in November (Figure 2.3).

Comprehensive encounter depth data were only available for the north-eastern New Zealand study locations between North Cape and the Hauraki Gulf ($n = 56$, 69.1%). Depth data for the remaining encounters ($n = 25$, 30.9%) were determined using ArcGIS® online. The average encounter depth was 306m (SE = 31.7m, range = 48 – 1464m).

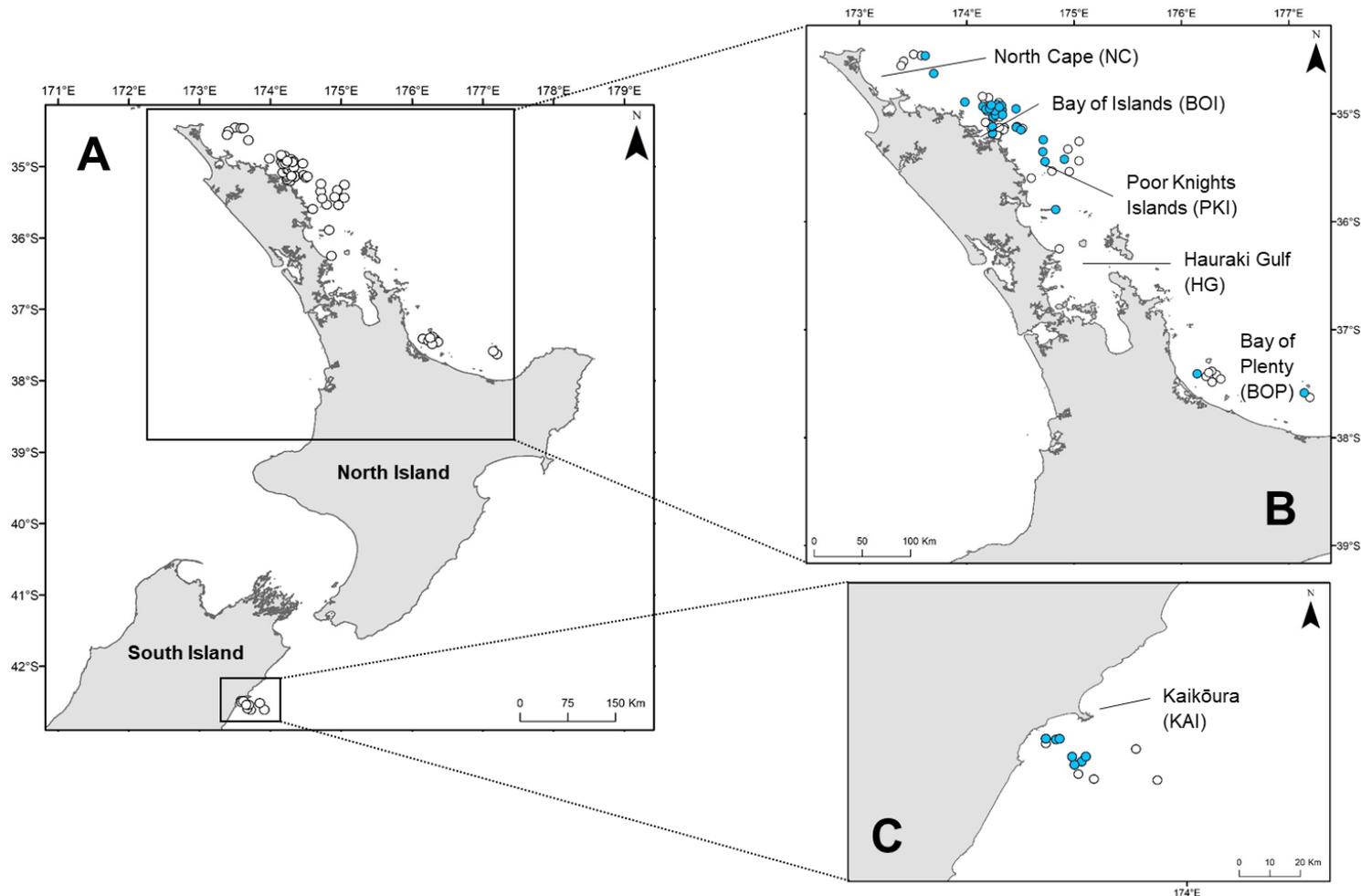


Figure 2.2 Locations of pilot whale encounters between 2003 and 2019 off eastern New Zealand. (A) All encounters ($n = 81$) in white. (B) All encounters off north-eastern North Island ($n = 68$). (C) All encounters off north-eastern South Island ($n = 13$). Blue icons in (B) and (C) indicate encounters where one or more photographs were taken that could be used in photo-ID assessment, $n = 34$ and $n = 7$ respectively.

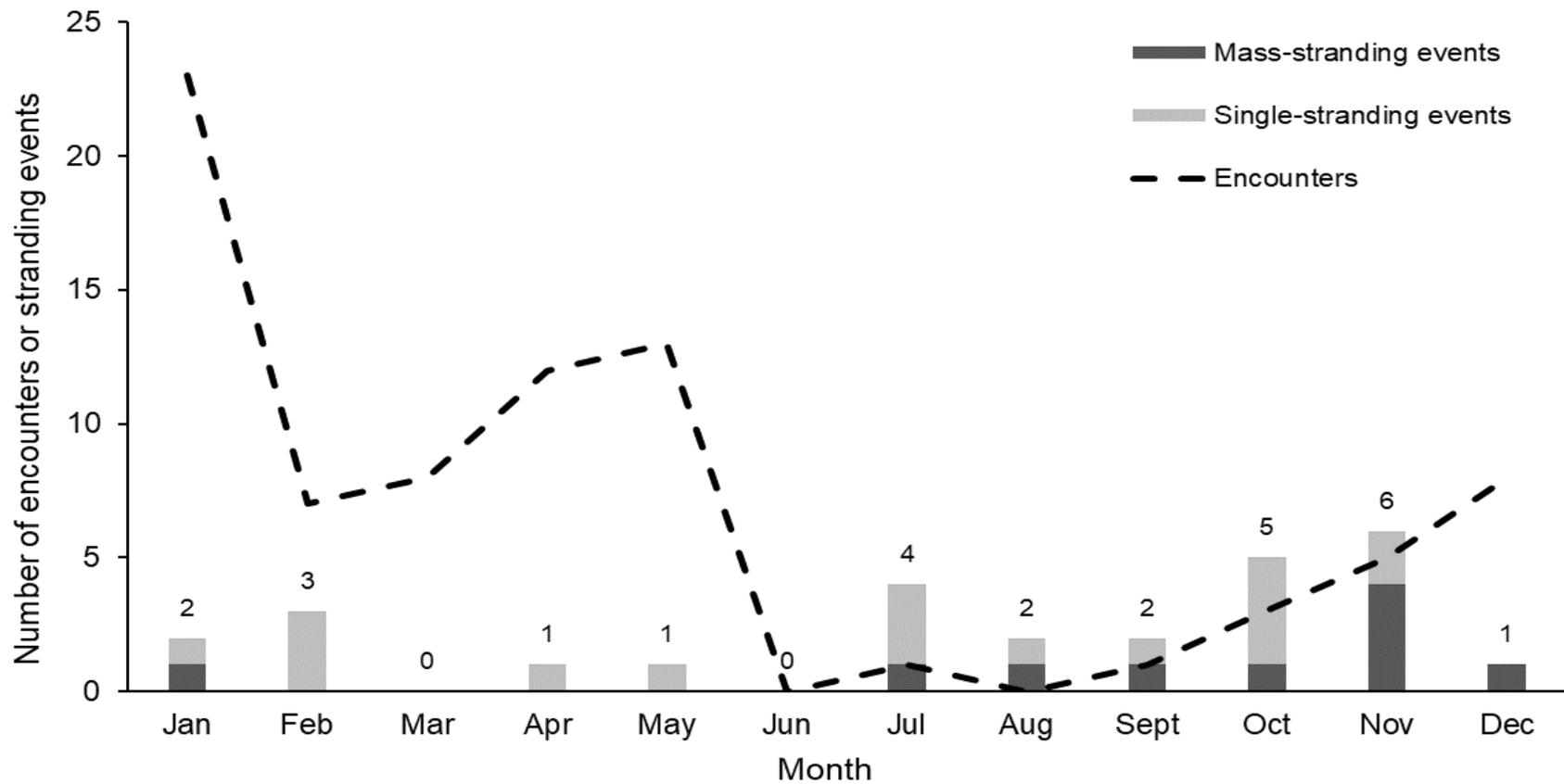


Figure 2.3 Summary of encounters with pilot whales and pilot whale stranding events off eastern New Zealand by month, between 2003 and 2019 (n = 27). Numbers above the bars are total numbers of strandings for each month.

Of the 81 encounter records over the 16-year study period, 79 (98%) had reliable group-size information. The median group size was 50 animals (IQ = 30 – 80, range = 5 – 250, Figure 2.4). Thirty percent (n = 24) of encounters (all from the Bay of Islands study region) included multiple sub-groups of pilot whales, with a median sub-group size of 30 individuals (IQ = 25 – 30, range = 15 – 35).

Reliable age-class data were available for 70 out of 81 encounters (86.4%). Using presence/absence criteria, neonates were present in 25 encounters (30.9%) from December to May and calves were present in 63 encounters (79%) from September to May. A total of 29 recognisable pilot whales (20%) were recorded with a neonate or calf and one of these individuals was observed with a neonate in two different years (Appendix 2).

Pilot whales were observed in single species groups during 17 (21%) encounters. Therefore, the majority of the encounters involved mixed-species groups (Figure 2.5; Figure 2.6), with pilot whales most frequently observed with oceanic bottlenose dolphins (71.6%, n = 58) in almost all locations with the exception of the Hauraki Gulf (Figure 2.6). Mixed-species encounters also included false killer whales (6.2%, n = 5) and southern right whale dolphins (*Lissodelphis peronii*) (1.2%, n = 1) (Figure 2.5; Figure 2.6). Interspecies associations between the pilot whales and oceanic bottlenose dolphins are investigated further in Chapter 4.

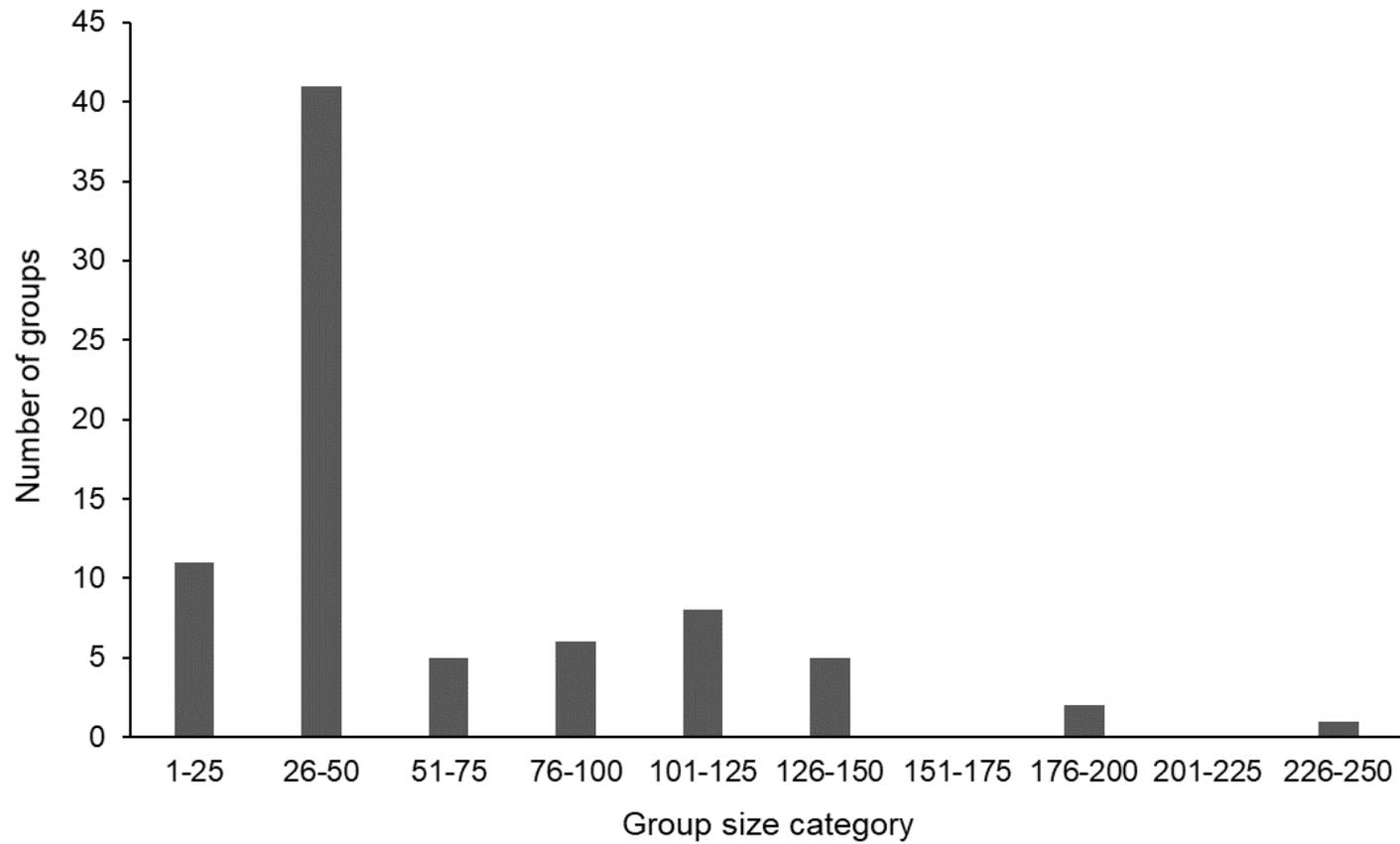


Figure 2.4 Group sizes of pilot whales (n = 79) encountered off eastern New Zealand between 2003 and 2019.

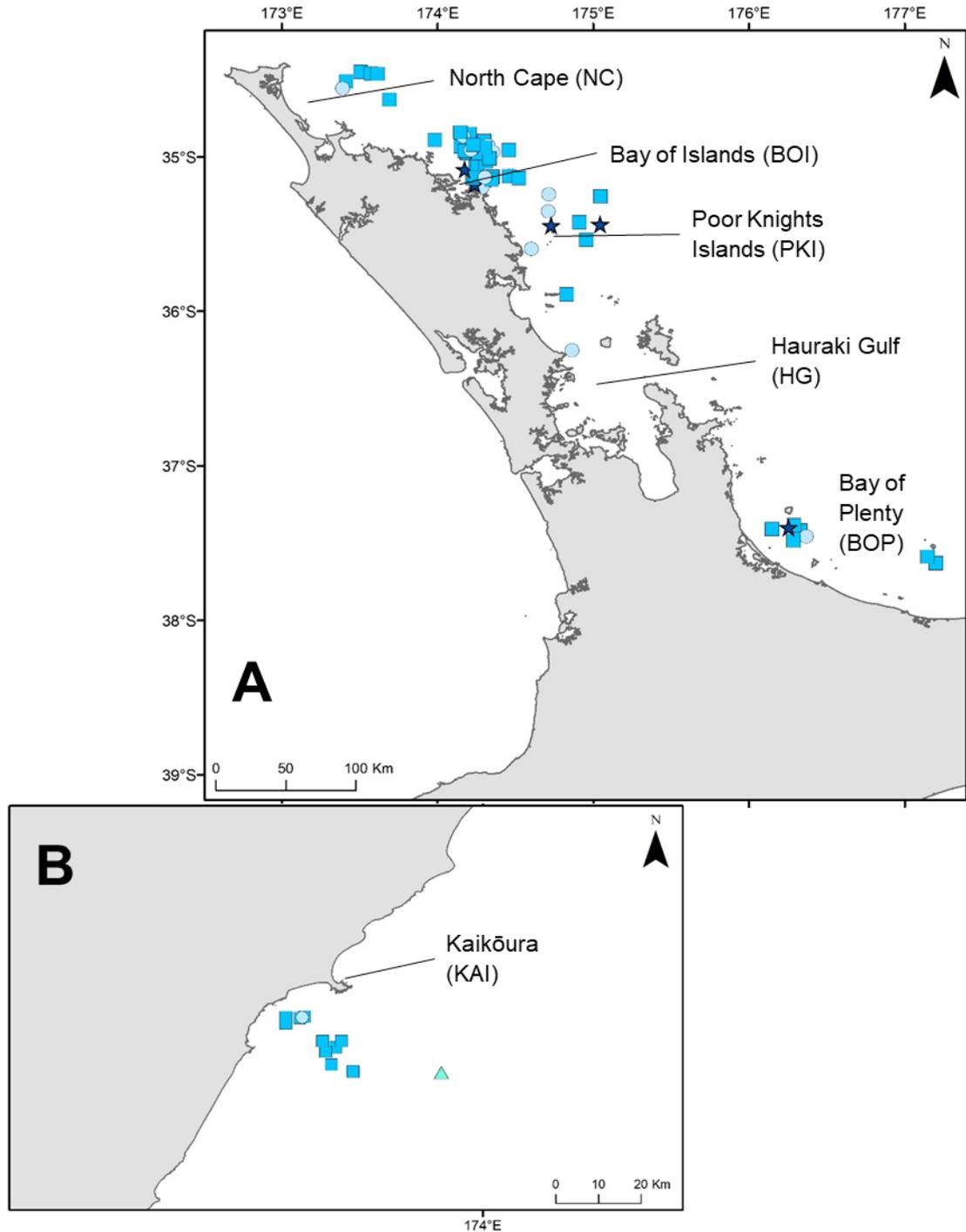


Figure 2.5 Locations of pilot whale sightings between 2003 and 2019 off north-east North Island (A) and north-east South Island, New Zealand (B). Light blue circles indicate groups consisting of pilot whales only ($n = 17$). Dark blue boxes indicate mixed-species groups of pilot whales and oceanic bottlenose dolphins ($n = 58$). The stars indicate mixed groups of pilot whales, oceanic bottlenose dolphins and false killer whales ($n = 5$). The triangle in (B) indicates one encounter of a mixed-species group of pilot whales, oceanic bottlenose dolphins and southern right whale dolphins ($n = 1$).

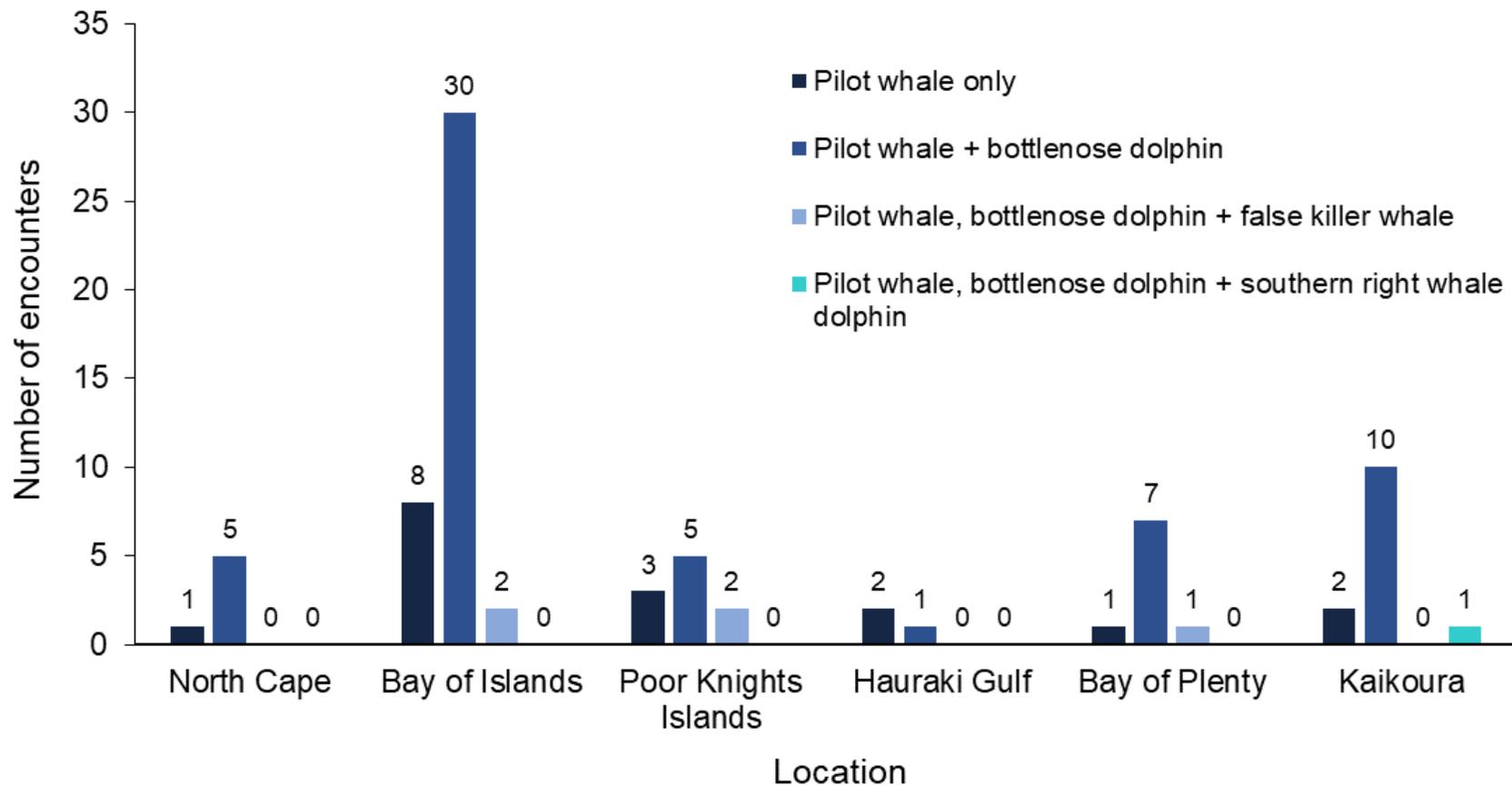


Figure 2.6 Single- and mixed-species pilot whale encounters by location between 2003 and 2019 (n = 81); the number of encounters is given above each bar.

2.3.2 Photo-identification, re-sight rate and site fidelity

A total of 53,857 photographs of pilot whales were taken between January 2003 and July 2019. Out of 2,144 good quality (Q1 – 2) images, there were 104 (4.9%) D1 images, 174 (8.1%) D2 images, 364 (17%) D3 images and 1502 (70%) D4 images. Photo-ID images of dorsal fins that passed quality control (Q1 – 2 and D1 – 2) were obtained during 51% (n = 41) of the 81 encounters. Of these 41 encounters, the majority were in the Bay of Islands (65.8%, n = 27), followed by Kaikōura (17%, n = 7), Poor Knights Islands (7.3%, n = 3), North Cape (4.9%, n = 2) and Bay of Plenty (4.9%, n = 2). In total, 278 good quality photographs (Q1 – 2) of distinctive individuals (D1 – 2) were used for further analysis.

A total of 145 individuals were identified from Q1 – 2 photographs, with 53 (36.6%) D1 (very distinctive) animals and 92 (63.4%) D2 (distinctive) animals (Appendix 3). Of these, 14 individuals were identified from Kaikōura and 131 individuals were identified from the north-eastern North Island. There was a cumulative total of 206 identifications of these 145 individuals ($\bar{x} = 2.5$, SE = 0.3), with the number of individuals identified in each encounter ranging from 1 to 14 whales ($\bar{x} = 5$, SE = 0.5, n = 41). On average, there were 3.5 (SE = 0.5) newly identified individuals and 1.4 (SE = 0.3) re-sighted individuals per encounter.

Of the 145 distinctive pilot whales, 69% (n = 100) were sighted only once and 31% (n = 45) were re-sighted (observed two or more times during the study period), with 14 of those individuals (9.7%) sighted on three or more occasions. Twenty (13.8%) of the 145 individuals were observed across multiple years, with 17.2% (n = 25) of re-sightings occurring in the same year (range = 1 d – 5 yr. 58 d).

Of the 45 pilot whales that were re-sighted, 37 (82.2%) were encountered in one location, with 6 (13.3%) encountered in two locations and two (4.4%) encountered in three locations. Both of these individuals were encountered in Bay of Islands and Bay of Plenty, a distance of approximately 500km, and the longest observed distance between re-sights. There were no re-sights of individuals between the North Island and South Island.

2.3.3 Mark rate

The overall proportion of marked and unmarked individuals (excluding neonates and calves) was calculated using photographs taken during nine encounters (Table 2.2)

where the total number of Q1 – 2 and D1 – 2 photographs was greater than or equal to the estimated pilot whale group size. There was variation in the proportion of marked individuals between encounters, ranging from 7.5% to 20.4% (\bar{x} = 13.4, SE = 1.4, n = 9).

2.3.4 Rate of discovery of uncatalogued individuals

Overall, the proportion of newly identified individuals increased as the rate of re-sightings increased. The discovery curve continued on its upward trajectory throughout the study period (Figure 2.7). Newly identifiable individuals were observed in 44.4% (n = 36) of encounters and re-sights of individuals occurred in 28.4% (n = 23) of encounters.

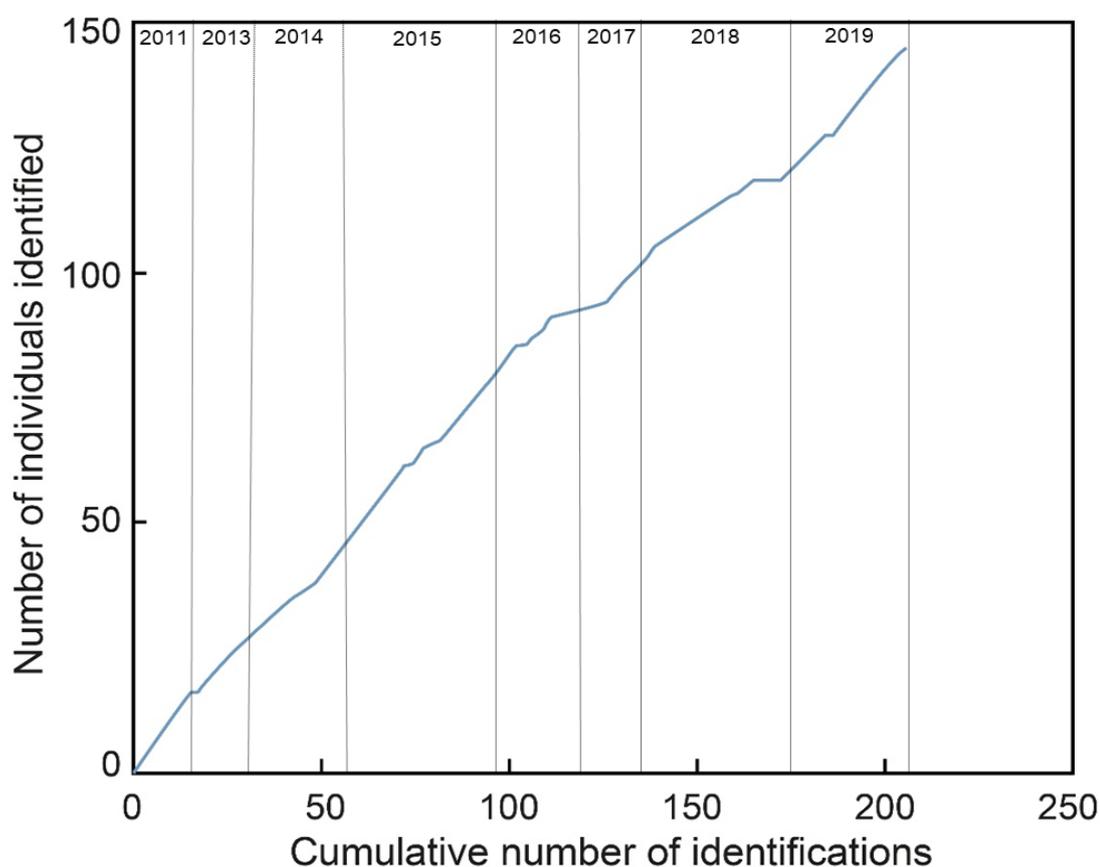


Figure 2.7 Discovery curve of pilot whales encountered off eastern New Zealand between 2003 and 2019. The number of identified individuals is shown in relation to the cumulative number of identifications made (maximum one identification per day). Note only survey years where there was more than one identification of an individual are labelled.

Table 2.2 Pilot whale encounters (n = 9) off north-eastern New Zealand between 2011 and 2019 used for mark rate assessment. Calves and neonates were excluded from the assessment.

Encounter date	Total marked	Total unmarked	Total photographs	Total new ID's	Total re-sighted individuals	Mark rate (%)	Group size estimate
3 Jan 2011	10	45	55	8	0	18.2	30
30 Mar 2014	9	96	105	6	1	8.6	80
8 Apr 2014	7	44	51	3	2	13.7	30
13 May 2014	12	71	83	7	0	14.5	70
6 Jan 2015	10	39	49	7	0	20.4	30
10 Jan 2015	6	28	34	1	2	17.6	30
12 Jan 2015	5	43	48	3	0	10.4	40
3 May 2019	9	88	97	9	0	9.3	90
4 May 2019	13	161	174	8	2	7.5	150
Mean	9	68.3	77.3	5.8	0.8	13.4	61.1

2.4 Discussion

Pilot whales were often sighted in the austral summer and autumn months, and across different oceanographic habitats off the east coast of New Zealand; a finding which reflects stranding records (Betty et al. 2020). Group sizes were generally quite large, although smaller, more cohesive sub-groupings of individuals were frequently observed within larger, wide-spread aggregations. It was uncommon to see pilot whales on their own, instead mixed-species groups of pilot whales and oceanic bottlenose dolphins were most frequently encountered.

2.4.1 Occurrence in New Zealand waters

Sightings of free-ranging pilot whales in New Zealand occur during the warmer months, in both near- and off-shore waters along the eastern coasts of the North and South Islands. This is in-line with previous sighting records, which have reported pilot whales in waters all around New Zealand, including the sub-Antarctic Islands (Berkenbusch et al. 2013). Historical stranding records indicate a year-round presence of this species, however strandings occur more frequently throughout New Zealand during the austral summer months (New Zealand Whale Stranding Database, 2019; Betty et al. 2020). The seasonal and spatial patterns of both sightings and strandings may be a result of long-distance or in-shore migrations by pilot whales during these warmer months, and/or a reflection of seasonal fluctuations in the distribution of prey (Beasley et al. 2019). A lack of survey data has prevented evaluations of pilot whale abundance in New Zealand (Baker et al. 2019). It is likely that offshore waters also represent important habitat for the species, but with the low mark-rate and re-sights of individuals shown in this study, it would be a substantial challenge to gain an accurate abundance estimate.

Long-finned pilot whales were encountered over a wide range of water depths, in both inshore and offshore areas (Figure 2.2), indicating that water depth may not be a key factor influencing their distribution. However, water depth is a good predictor of pilot whale distribution in both the northern hemisphere (e.g. Abend and Smith, 1999; de Stephanis et al. 2008a) and parts of the southern hemisphere (e.g. Fontaine et al. 2015). Both species of pilot whale carry out deep dives of more than 1000m when foraging, although there is diel variation in hunting behaviour of the two species (e.g. Cañadas and Sagarminaga, 2001; Baird et al. 2002; Aguilar de Soto et al. 2008). While the abundance and general movement patterns of pilot whales in New Zealand

remain unknown, it is highly likely that they are linked to pelagic prey resources in some way (Bloch et al. 2003). Long-finned pilot whales in New Zealand feed primarily on cephalopods, predominantly arrow squid, and to a lesser extent common octopus (*Pinnoctopus cordiformis*) (Beatson et al. 2007; Beatson and O'Shea, 2009). Although many species of marine megafauna in New Zealand rely on pelagic cephalopods as prey (e.g. Gaskin and Cawthorn, 1967; Beatson and O'Shea, 2009; Flemming et al. 2013; Lalas and Webster, 2013; Miller et al. 2013), little is known about their movement and distribution in these waters, with most information based on (highly variable) annual catch data for different species (Fisheries New Zealand, 2018). Both species of arrow squid (*Nototodarus* spp.) in New Zealand (Smith et al. 1981) are commercially targeted, with catch and effort data from the mainland fishery (SQU1T) reporting peaks in catch numbers between January and April (Fisheries New Zealand, 2019). This coincides with the high number of pilot whale sightings reported here, as well as peak stranding (Betty et al. 2020) and calving season (Betty, 2019). Both squid species occur over the continental shelf in water up to 500m depth, but are most common in shallower water, at less than 300m depth (Jackson et al. 2000; Fisheries New Zealand, 2018). Long-finned pilot whales in the eastern North Atlantic prefer areas along the edge of the continental shelf (Bloch et al. 2003), and have similar prey preferences to those in New Zealand (Desportes and Mouritsen, 1993; Santos et al. 2014). Furthermore, high catch rates of long-finned pilot whales in the drive fisheries of the Faeroe Islands (Desportes and Mouritsen, 1993; Bloch et al. 2003) had a positive correlation with good squid years in these regions (Betty, 2019), suggesting a relationship between squid and pilot whale numbers. Off Cape Breton, Nova Scotia, large-scale aggregations of long-finned pilot whales are thought to occur as a result of squid migration, although this has not been confirmed (Ottensmeyer and Whitehead, 2003).

Around early December, an increase in the cross-shelf flow of the East Auckland Current (EAUC) brings warm water southward and over the continental shelf adjacent to north-eastern New Zealand (Sharples, 1997). Here, more frequent mixing of the water column creates a strong, nutrient-rich upwelling which enhances productivity within the coastal waters (Chang et al. 2003). The inshore flooding of warmer water during the austral summer and autumn months brings seasonal increases in phytoplankton blooms (Chang et al. 2003; Zeldis et al. 2004) and warm water species in northern waters (Francis and Evans, 1993; Francis, 1996; Duffy and Abbott, 2003). During these months, there are frequent sightings of pilot whales in shallow (<100m)

near-shore waters. As outlined previously, pilot whales in New Zealand predominantly feed on arrow squid and common octopus (Beatson et al. 2007; Beatson and O'Shea, 2009), which typically occur over continental shelf waters (Jackson et al. 2000; Fisheries New Zealand, 2018). Although very little is known about the movement and distribution of arrow squid species in New Zealand (as outlined above), it is possible that squid abundance increases seasonally off the north-eastern North Island as a result of heightened levels of primary productivity in this region. The observed summer peak in pilot whale sightings within relatively shallow coastal waters may therefore be as a result of increased prey availability, driving seasonal inshore movements of this species.

A different set of environmental drivers influences the Kaikōura coast in the eastern South Island where pilot whales were also sighted. The narrow continental shelf drops steeply to a depth of 1,000m just 5km from the coastline, forming the submarine Kaikōura Canyon, a highly productive deep-sea habitat (De Leo et al. 2010). A local upwelling is also generated by the mixing of warm, northern water from the East Cape Current and cooler water from the Southland Current (Garner, 1953; Hart et al. 2008), which brings nutrient-rich water up from the depths of the canyon, leading to high productivity levels. As a result, this is an important foraging ground for a variety of top-predators targeting mesopelagic and demersal prey, including deep-diving cetaceans (e.g. Yen et al. 2004; Moors-Murphy, 2014; Guerra et al. 2017). Some male sperm whales forage in the Kaikōura Canyon year-round, while other individuals (predominately males) are seasonally resident (Childerhouse et al. 1995; Jacquet et al. 2000). Since the diet of pilot whales (Beatson et al. 2007; Beatson and O'Shea, 2009) is similar to that of sperm whales (Gaskin and Cawthorn, 1967; Guerra et al. 2017; Guerra et al. 2020), it is likely that the deep, productive waters of the Kaikōura Canyon provide a rich feeding ground for both of these deep-diving species, however further investigation is required to determine the residency patterns of pilot whales in this region.

At this stage it is unclear whether pilot whales in New Zealand display seasonal movements between offshore and inshore habitats, but there is some evidence of seasonal site fidelity. There were no re-sights of pilot whales between the broader North and South Island study locations, although it is important to note that there were fewer photographs from the South Island. All within-year re-sights and between-year re-sights occurred within the same broad study regions, with some individuals being sighted across multiple North Island sites. Additionally, the longest observed distance

between re-sights was approximately 500km, with two individuals observed in both Bay of Islands and Bay of Plenty. The re-sight rate for individuals was generally low, which likely reflects larger home ranges for pilot whales than that covered in the present study area. Although the lack of re-sights between the North Island study locations and Kaikōura is quite unusual, this is likely as a result of the small sample size of the study. Indeed, genetic studies of pilot whales stranded in New Zealand have shown that there is genetic movement of individuals throughout these waters, as well as between New Zealand and Tasmania (Oremus et al. 2009; Oremus et al. 2013). Therefore, long-distance movements of individuals are almost certainly more common than is suggested by the data presented here.

The low re-sight rate could also indicate a large population of individuals with (at least partially) overlapping home ranges and possibly different patterns of residency. This is supported by the large proportion (69%) of recognisable individuals sighted only once during the study period, as well as the absence of a plateau in the discovery curve of individuals. Furthermore, long-distance movements and variable patterns of site fidelity and/or residency are not uncommon in large offshore delphinids. For example, long-finned pilot whales off Nova Scotia display little residency but some seasonal site fidelity (Ottensmeyer and Whitehead, 2003), while in the Strait of Gibraltar some individuals have a high degree of seasonal residency, being sighted within and between years during the warmer months (Verborgh et al. 2009). Similarly, individuals from the insular population of false killer whales around the Hawaiian Islands display strong site fidelity and have limited home ranges (Baird et al. 2008a; Baird et al. 2010), while false killer whales in New Zealand show strong patterns of seasonal residency and site fidelity during December to May (Zaeschmar et al. 2014). It is likely that the variable movement patterns of each of these social delphinids is closely linked to seasonal fluctuations in prey availability (de Stephanis et al. 2008a, b; Verborgh et al. 2009; Baird et al. 2010; Zaeschmar et al. 2014).

2.4.2 Group size and age-class composition

Group size estimates of pilot whales are similar to some of those reported from other southern and northern hemisphere studies (Table 2.3). Importantly, group sizes from different populations may have been estimated using different definitions of what constitutes as group (Chapter 1), so caution should be taken when directly comparing them. The group size for pilot whales encountered during this study was similar to that reported for stranded whales in New Zealand (Betty et al. 2020; Table 2.3). However,

some of the stranded groups have been significantly larger (Betty, 2019) than any of those reported from at-sea observations. It has been suggested that the very large groups that occasionally strand represent multiple groups that have formed short-term aggregations, possibly due to abundant prey availability (Bradshaw et al. 2006; Oremus et al. 2013) or for breeding purposes (Oremus et al. 2013). Prey availability and preference also influence group size in killer whales, another social delphinid species (Baird and Dill, 1996; Baird and Whitehead, 2000). Northern hemisphere studies of short-finned pilot whales have also suggested that large aggregations may be for breeding purposes (Alves et al. 2013; Servidio, 2014; Mahaffy et al. 2015), which may also cause social disruption (Oremus, 2008) and therefore influence the large numbers of individuals found in some mass stranding events.

Table 2.3 Group size information from northern and southern hemisphere long-finned pilot whale studies. “Type” indicates whether the information is sourced from studies using pilot whale fishery data, strandings data or data from at-sea observations.

Mean	Median	Range	Type	Location	Source
n/a	50	3 – 250	At-sea	New Zealand	Current study
41	n/a	1 – 350	At-sea	Alboran Sea	Cañadas and Sagarminaga, 2000
14	10	2 – 150	At-sea	Strait of Gibraltar	de Stephanis et al. 2008c
10	11	1 – 30	At-sea	Norway	Visser et al. 2017
53	n/a	1 – 300	At-sea	Kerguelen Islands	Fontaine et al. 2015
59	n/a	2 – 135	At-sea	Cape Breton Is.	Ottensmeyer and Whitehead, 2003; Augusto et al. 2017a
n/a	46	2 – 600	Stranding	New Zealand	Betty et al. 2020
149	110	1 – 1000	Fishery	Faeroe Islands	Zachariassen, 1993

One third of at-sea observations of pilot whales off the north-east North Island reported multiple smaller sub-groups of individuals, dispersed over a wide area, likely changing in both size and membership during encounters. These fission-fusion dynamics indicate that larger groups may not be temporally stable, but instead represent short-term aggregations, driven by feeding and/or mating opportunities (Alves et al. 2013; Chapter 1, Section 1.2). This has also been documented in social delphinids (e.g. Connor et al. 2000; Baird et al. 2008b; Connor, 2007; Parra et al. 2011). As mentioned previously, pilot whale mass strandings in New Zealand include individuals from multiple matrilineal lines (Oremus et al. 2013), which may indicate the presence of more than one social unit. Therefore, the smaller sub-groups observed during at-sea encounters may be indicative of more cohesive social units that persist over longer time periods, similar to those reported in northern hemisphere pilot

whales (e.g. de Stephanis et al. 2008c; Augusto et al. 2017a; Visser et al. 2016), while large aggregations occur infrequently and likely include different social units (Mahaffy et al. 2015; Augusto et al. 2017a) as well as multiple matrilineal units (Oremus et al. 2013).

As outlined above, many studies of both species of pilot whale populations have observed the presence of multiple sub-groups during encounters (e.g. Ottensmeyer and Whitehead, 2003; de Stephanis et al. 2008c; Alves et al. 2013; Hartny-Mills, 2015; Mahaffy et al. 2015; Augusto et al. 2017a; Visser et al. 2016), with the suggestion that large groups are breeding or feeding aggregations. However, it is also possible that a few sub-groups of individuals (representing socially cohesive cohorts) remain loosely associated over long periods of time, travelling between foraging grounds together to ensure safety from possible predation. Pilot whales are large animals but it is likely that they would be most threatened by killer whales or large sharks. Killer whales have been observed attacking adult false killer whales (a similar-sized delphinid to pilot whales) and eating a calf, off the north east coast of New Zealand (Visser et al. 2010). Multiple studies have reported abrupt changes to pilot whale behaviour in response to both actual killer whale calls (de Stephanis et al. 2014) and those that are played back during research experiments (Curé et al. 2012; Curé et al. 2019). In most instances, multiple sub-groups of pilot whales in one area were observed aggregating and then moving towards the killer whale group or sound source (Curé et al. 2012; de Stephanis et al. 2014; Curé et al. 2019). This has been suggested to be intimidation behaviour, meant to ward off conspecifics and/or potential predators, a tactic which relies on larger group numbers.

Northern hemisphere studies of long- and short-finned pilot whales have found that group age-class composition varies seasonally, with larger groups including immature whales observed during warmer months and smaller groups consisting only of mature individuals observed in cooler months (e.g. Cañadas and Sargarminaga, 2000; de Stephanis et al. 2008b; Hartny-Mills, 2015; Mahaffy et al. 2015). These patterns may be driven by prey availability (Shane, 1995; de Stephanis et al. 2008a), as well as breeding (Heimlich-Boran, 1993; Cañadas and Sargarminaga, 2000; Alves et al. 2013) and calving (Hartny-Mills, 2015) behaviour. The data used in this study did not allow for seasonal trends in group composition to be investigated, however, the majority of groups encountered during September – May contained neonates and/or calves. This was unsurprising given that the peak calving season for pilot whales in New Zealand is during the austral summer months (Betty, 2019).

Furthermore, two births were observed on separate occasions in the Bay of Islands area in January (Zaeschar, pers. comm.). This suggests that groups including pregnant females, neonates and young calves may be using shallower, more coastal habitats during this time of the year, which may be related to differences in foraging behaviour and/or preferred prey of groups with young whales. For example, sperm whales have been observed to leave calves at the surface while carrying out deep foraging dives (Whitehead, 1996; Gero et al. 2009). Similar to other large cetacean species (Gibson et al. 2013; Thompson et al. 2013; Hartman et al. 2014), female pilot whales caring for young calves may prefer to use nearshore waters for foraging in the warmer months, allowing them to make shallower, less time-consuming dives; which may simultaneously provide increased protection from predators (e.g. Dungan et al. 2012). This supports the finding that New Zealand pilot whale strandings peak in austral summer (Betty et al. 2020), indicating that the animals are likely spending more time inshore during this season. Similar patterns are observed in Gray's beaked whales (*Mesoplodon grayi*) off north-east New Zealand (Thompson et al. 2013), a species that also feed on squids and mesopelagic fishes. Interestingly, unlike the beaked whales there is no evidence to suggest a temporal trend in the incidence of pilot whale strandings including calves and neonates (Betty et al. 2020).

2.4.3 Mark rate

The mark rate of 13% for pilot whales in New Zealand is certainly low when compared to other large, social delphinids, including other pilot whale populations (Table 2.4). It is important to acknowledge that no standardised method of calculation was used to estimate the mark rate of the different populations reviewed here, which can affect the accuracy of direct comparisons. Bottlenose dolphins are frequently considered to be the standard for expected mark-rate in delphinid populations, but often have very distinctive fins compared to most other species (e.g. Shark Bay, Nicholson et al. (2012) and Sarasota Bay, Wells (2014)), and even when compared to similar sized dolphins (e.g. spinner dolphins, Tyne et al. 2014), indicating that they may be outliers rather than the norm. This is likely as a result of high rates of aggressive interactions and/or competitive mating behaviour between bottlenose individuals, as conspecific tooth rake marks are particularly common in some populations (e.g. Scott et al. 2005; Marley et al. 2013). The reasonably high mark rates observed in northern hemisphere pilot whale populations indicate that the low mark rate observed for pilot whales in New Zealand may be unusual, but since this species is poorly-studied in the southern

hemisphere, possible drivers of these differences remain unclear and require further research.

Table 2.4 Comparison of mark rates of selected large delphinid species. While mark-rate calculations were not uniform across studies, all relied on notches and nicks to determine the distinctiveness of individuals.

Species	Mark-rate (%)	Location	Reference
Long-finned pilot whale	51.0	Cape Breton Is., Nova Scotia	Augusto et al. 2017a
	33.1 – 40.2	Strait of Gibraltar	Verborgh et al. 2009
Short-finned pilot whale	51.0	Madeira	Alves et al. 2013
	80.5	Hawaiian Islands	Mahaffy et al. 2015
False killer whale	72.7	New Zealand	Zaeschmar et al. 2014
	73.7	Hawaiian Islands	Baird et al. 2008a
Bottlenose dolphin	68	Moray Firth, Scotland	Wilson et al. 1999
	72	Bay of Islands, New Zealand	Tezanos-Pinto et al. 2013
Pygmy killer whale	73.7	Hawaiian Islands	McSweeney et al. 2009

2.4.4 Interspecies groups

The high incidence (79%, n = 64) of pilot whale encounters that included other species is interesting, although such interspecies associations are common amongst social delphinids (Stensland et al. 2003; Cord and Würsig, 2014). There are a few studies reporting on the frequency of pilot whale associations with other species (e.g. Kraus and Gahr, 1971; Polacheck, 1987; Baraff and Asmutis-Silvia, 1998; Zaeschmar, 2014), and it appears that associations between bottlenose dolphins and pilot whales are particularly common (e.g. Norris and Prescott, 1961; Kraus and Gahr, 1971; Kenney, 1990; Kasuya and Marsh, 1984). There have been many accounts of mixed-species groups of cetaceans (e.g. Psarakos et al. 2003; Frantzis and Herzing, 2002; Baird et al. 2008a), however, there are very few studies that have focused on the possible drivers behind long-term interspecies associations (e.g. Stensland et al. 2003; Zaeschmar et al. 2014; Elliser and Herzing, 2016). One example of this is

research from north-eastern New Zealand, which has shown that oceanic bottlenose dolphins and false killer whales are part of a very large interspecific social network that has persisted over many years, and hunt, feed and socialise together (Zaeschar et al. 2014). Notably, it is the same oceanic bottlenose dolphin individuals that have been found to be associating with pilot whales in New Zealand; this occurrence is further explored in Chapter 4.

2.4.5 Study limitations

It is important to consider the limitations that arise due to the opportunistic nature of the majority of data analysed in this study. The apparent predominant occurrence of pilot whales in northern New Zealand waters is due to insufficient effort in other areas as they do occur in many places (Berkenbusch et al. 2013; Betty et al. 2020). Additionally, the seasonality of occurrence may be the result of inconsistent sampling effort, restricted to a few relatively small, discontinuous study regions that are not completely representative of the species' habitat. Likewise, uneven sampling effort may have influenced re-sight rates, including the lack of re-sights between North and South Island study regions. The overall heterogeneity of the data collection process has meant that data quality would be further compromised if results were stratified. Therefore, the study has focused more on the robust broad scale spatial and temporal trends; largely omitting fine-scale analysis.

2.4.6 Summary

At-sea observations presented here indicate that pilot whales in New Zealand are infrequently encountered by tour and research vessels that predominantly operate in near shore waters. Pilot whale occurrence in shallower northern waters may be seasonally variable, possibly influenced by prey availability or the peak calving season, with sightings being highest during austral summer and autumn months. Pilot whales may display some degree of seasonal site fidelity off the eastern coasts of both North and South Islands, however more data are needed to reveal any true patterns. Additionally, the low re-sight rate observed in this study suggests either a large population, high transience and/or large ranges of pilot whales in New Zealand. Group sizes appear to be similar to those documented for the species in most other regions, varying with age-class composition. It is likely that large aggregations of individuals are infrequent events, consisting of smaller sub-groups that represent cohesive social units, a topic further explored in Chapter 3.

Chapter 3: Pilot whale social associations

3.1 Introduction

Revealing the social structure of animals influences our understanding of many aspects of their population biology. For example, the transfer of information between individuals (McComb et al. 2001; Lusseau et al. 2003), culture (Rendell and Whitehead, 2001; Garland et al. 2011; Cantor and Whitehead, 2013), disease transmission (Krause and Ruxton, 2002; Krause et al. 2007), genetics (Storz, 1999; Oremus et al. 2013; Whitehead et al. 2019), and habitat use (Baird and Dill, 1996; Connor et al. 2001) have all been linked to the social structure of animal populations. Consequently, both the ecology and evolution of a population are influenced by its social structure (Whitehead, 2008a). This means that knowledge about social structure is not only important for theoretical reasons, but also for guiding conservation and management decision-making and initiatives (Sutherland, 1998; Chilvers and Corkeron, 2001; Frère et al. 2010; Brakes et al. 2019).

Examples of cognitively advanced mammals with complex social systems include many cetacean species, chimpanzees (*Pan* spp.) and elephants (e.g. Wittemyer et al. 2005; Connor, 2007; Mitani, 2009; Cantor and Whitehead, 2013; Goldenberg et al. 2016). A robust framework is required to describe variation in social structure between populations, and in turn understand the diverse and specific ecological forces acting on different populations (Whitehead, 1995; Whitehead and Dufault, 1999; Pearson and Shelton, 2010; Cantor et al. 2012). Hinde (1976) developed a framework for the purpose of studying social structure (Chapter 1, Section 1.1.), which has since been applied to socially complex animals. Relationships between dyads are defined by the content, quality and patterning of interactions between individuals in the population. Further to this, social structure is defined by the nature, quality and patterning of these dyadic relationships (Hinde, 1976). It is therefore essential for studies of social structure to collect data on the associations and/or interactions between individuals, since they form the foundation on which dyadic relationships, and hence entire animal societies, are built.

Social structure and group dynamics of animal populations are tightly interlinked and are underpinned by the same ecological theories, suggesting that studies of these processes should consider them simultaneously. Group living in mammals is thought to be fostered by ecological variables such as predation risk (Hamilton, 1971; Treves, 1999), the availability of resources (MacDonald and Kays, 1998) and access to mates

(Packer and Pusey, 1982; Watts, 1998; Connor et al. 2006; Connor et al. 2010). The potential benefits of living in groups usually come with associated costs (Chapter 1, Section 1.1). Consequently, it can be advantageous for group-living animals to employ a compromise by adopting a flexible social system, one that can be frequently in flux, much like the environments in which they are found (Connor et al. 2000). The dynamic nature of fission-fusion societies (Chapter 1, Section 1.2.) enables individuals to maximise the benefits of group living while simultaneously minimising the associated costs (Connor et al. 2000). Such flexible social systems are commonly seen in primate (e.g. van Schaik et al. 1983) and delphinid (e.g. Connor, 2007; Parra et al. 2011; Pearson et al. 2017) populations.

Cetaceans typically surface only briefly when they need to breathe, which limits researchers' ability to identify individuals, collect information about group structure and determine interactions between individuals. Consequently, the associations between two individuals in a population (i.e. dyads) are used to investigate social structure with the assumption that the large majority of interactions occur when two individuals are in close proximity to each other (Whitehead and Dufault, 1999; Whitehead, 2009). Dyadic associations can be defined in various ways (Whitehead, 2008a, b; 2009) and data about these associations are collected using photo-ID methods (Chapter 2), which allow individuals to be identified from their unique, natural markings (Würsig and Würsig, 1977; Würsig and Jefferson, 1990). In particular, long-term studies are important for understanding the social structure of different cetacean populations. Over the years, this approach has been applied to produce a number of detailed descriptions of cetacean social systems, for example: pilot whales (Ottensmeyer and Whitehead, 2003; de Stephanis et al. 2008c; Mahaffy, 2012; Servidio, 2014; Hartny-Mills, 2015), bottlenose dolphins (Connor et al. 2000; Daura-Jorge et al. 2012; Hamilton, 2013; Baker et al. 2018), sperm whales (Cantor and Whitehead, 2015; Cantor et al. 2015) and false killer whales (Baird et al. 2008a; Zaeschmar, 2014; Martien et al. 2019).

Group-living cetaceans display a rich diversity of different social structures, ranging from highly fluid to stable societies. Classic fission-fusion societies are formed by individuals associating in sub-groups of fluctuating size and composition (Connor et al. 2000). The well-studied coastal bottlenose dolphin populations of Shark Bay, West Australia and Sarasota Bay, Florida, USA are known to have highly-complex societies, with males forming temporally variable alliances of varying stability (Wells 2014; Connor and Krützen, 2015). In Shark Bay, males form a very large social

network (> 400 individuals), termed a “super-alliance”, which has two nested levels comprising of certain individuals with long-term stable alliances, and others with labile alliances (Connor and Krützen, 2015). This is indicative of a population with high variability in dyadic association indices, i.e. high social differentiation (Whitehead, 2008a).

At the opposite end of the continuum of social structure are completely stable societies, where all individuals have homogenous relationships (Whitehead, 2008a). This is characteristic of some populations of sperm whales (e.g. Christal and Whitehead, 2001) and killer whales (e.g. Bigg et al. 1990; Baird and Whitehead, 2000) that live in small, stable units (pods) of mixed sex and age classes, where individuals have high association rates and spend most of their time together. Multiple stable units may coalesce, forming larger cohesive groups that remain casually associated for several days (Baird and Whitehead, 2000; Christal and Whitehead, 2001). Intermediate forms of social structure also exist, displaying aspects of both fluid and stable societies. For example, Risso’s dolphins (*Grampus griseus*) in the Azores live in strongly associated pairs organised into units (pods), that are strongly stratified by age and sex classes, but some individuals in the population have no long-term stable associations (Hartman et al. 2008).

Long-finned pilot whale social structure has been studied in the Faeroe Islands, Cape Breton Island, Canada and the Strait of Gibraltar (Amos et al. 1991, 1993; Ottensmeyer and Whitehead, 2003; de Stephanis et al. 2008c; Augusto et al. 2017a). Genetic data collected from the Faeroe Islands have suggested that pilot whales live in strictly matrilineal groups and display bisexual natal group philopatry (Amos et al. 1991; 1993; but see also Connor, 2000), with the latter being a rare occurrence in social mammal populations, where males disperse from the group only for breeding purposes. Photo-identification studies of pilot whales in Cape Breton Island (Ottensmeyer and Whitehead, 2003; Augusto et al. 2017a) and the Strait of Gibraltar (de Stephanis et al. 2008c) have found that both of these populations have hierarchically structured societies, with evidence of both long- and short- term associations between individuals. Short-finned pilot whales, the more tropical congener of the long-finned species, have a similar social structure (Heimlich-Boran, 1993; Mahaffy, 2012; Alves et al. 2013; Servidio, 2014; Hartny-Mills, 2015; Mahaffy et al. 2015).

In the southern hemisphere, studies of free-ranging long-finned pilot whale social structure are lacking, with most research focused on dead, stranded animals (Clarke and Goodall, 1994; Beatson and O’Shea, 2009; Oremus et al. 2013; Mansilla et al. 2012; Betty et al. 2020; Kraft et al. 2020). In New Zealand and Tasmania, Australia there are multiple matriline (indicated by multiple mtDNA haplotypes) present in the majority of pilot whale mass strandings (Oremus et al. 2013), suggesting that social associations in southern hemisphere long-finned pilot whales may be formed between genetically unrelated groups of individuals as well as some related individuals.

Understanding pilot whale social structure, especially in terms of associations within and between social units, as well as the temporal patterning of dyadic associations, is important for socially complex animals (Whitehead and Rendell, 2001; Croft et al. 2017). Establishing studies that form the baseline for future work can be valuable for future conservation management decisions. As such, the aim of this chapter is to determine the social association patterns between individual long-finned pilot whales off the north-eastern coast of New Zealand.

3.2 Methods

3.2.1 Surveys and photo-identification

Opportunistic data were collected between December 2003 and July 2019, following the methods described in Chapter 2.2.

3.2.2 Data selection: Encounters and groups

During an encounter, a group was defined using a 1,000m chain rule, where all pilot whale individuals opportunistically encountered on a single day by the research vessel or tour boat that were within 1,000m of each other were considered to be members of the same group (Mahaffy et al. 2015), and thus assumed to be associated at some level (“gambit of the group”; Whitehead and Dufault, 1999). As outlined in Chapter 2 (Section 2.2.2.2), the presence of smaller, more cohesive sub-groups of individuals was recorded in the field-notes of observations by the *Manawanui* research vessel during encounters between North Cape and the Poor Knights Islands, ca. 170km apart (Figure 2.2). These were termed sub-groups, being defined as cohorts of pilot whales that were showing similar behaviour and had a maximum distance between individuals of less than one body length (approximately 5 m; de Stephanis et al. 2008c). However, details of group membership and fine-scale

photo-ID data were not explicitly collected, and therefore these sub-groups have not been considered during the investigations of pilot whale social structure.

When studying social associations in delphinids, photo-identification of all individuals within a group is preferred in order to avoid negatively biased association indices (AIs) (Parra et al. 2011). It is also important to ensure equal opportunity for all individuals to be photographed (i.e. no bias toward well-marked individuals). Common practice is to remove any groups from the social association analysis where less than 50% of the individuals are successfully photo-identified (e.g. Ottensmeyer and Whitehead, 2003). However, due to the low mark rate (13.4%; Chapter 2, Section 2.3.2) of pilot whales in New Zealand and the opportunistic nature of the data, applying such criteria would have excluded all groups from the analysis. Therefore, the coverage calculation method described by Ottensmeyer and Whitehead (2003) was modified to account for limitations in the data set. Each encounter was assigned a photographic coverage score based on the number of good and excellent quality photographs (Table 2.2) that were taken of individuals in the group, taking into account group size. Only those encounters with a group photographic coverage score of 0.5 or more were included in the social association analysis. Group photographic coverage scores were calculated using the following equation, modified from Ottensmeyer and Whitehead (2003):

$$\frac{\text{Sum of Q1 and Q2 fin images from encounter}}{\text{Estimated group size}}$$

Another common practice in association work is to include only those individuals encountered on four or more occasions in the analysis (Whitehead, 2008a). This represents a compromise between limiting bias that is created by the misidentification of individuals and including as many individuals as possible in the analysis (Bejder et al. 1998; Parra et al. 2011). Applying this restriction to the data would have once again excluded all individuals from further social association analyses. Previous cetacean studies have altered the criteria to include individuals encountered on three or more (e.g. Bouveroux et al. 2019), or two or more (e.g. McSweeney et al. 2009; Hamilton 2013; Azzellino et al. 2016) occasions when investigating social structure, acknowledging this as a limitation when interpreting results. Therefore, the criteria were adjusted for the current study to include all individuals identified on two or more occasions in the social association analyses.

3.2.3 Data analysis

Unless stated otherwise, all social analyses of data collected during the study period were carried out using SOCPROG 2.9, a social association analysis software (Whitehead, 2009).

3.2.3.1 Dyadic association indices

Association indices are used to estimate the proportion of time that two individuals spend associating, and so may not always be reflective of the true pattern of social relationships in a population (Cairns and Schwager, 1987; Whitehead, 2008a, b). Associations between individuals were based on group membership for the analysis (Section 3.2.2) and, to increase the power of permutation tests (Section 3.2.7) to detect preferred associations, the sampling period was set to four days (Hamilton, 2013). For those populations where a number of groups are encountered within a single day, setting a sampling period of one day is appropriate to detect preferred associations. However, when only a single group is found in the study area in a day (as is the case with the current study), permutation tests have very little power (Whitehead, pers. comm. in Hamilton, 2013).

The strength of dyadic associations of pilot whales in New Zealand was measured using the half-weight index (HWI). The HWI is recommended for situations where only some proportion of individuals within the sampling period are identified and is designed to compensate for undocumented associates within groups (Cairns and Schwager, 1987; Whitehead, 2008a, b). A value of 0 indicates the absence of any association between individuals and 1 indicates that the pair are always associated. Therefore, the greater the AI value, the greater the level of association between individuals (Bejder et al. 1998). The HWI is calculated using the following equation:

$$\frac{X}{X+Y_{ab}+\frac{1}{2}(Y_a+Y_b)}$$

Where, X is the number of sampling periods where individuals A and B are considered to be associated (observed together in the same group); Y_a is the number of sampling periods where only individual A is seen (without B); Y_b is the number of sampling periods where only individual B is seen (without A); and Y_{ab} is the number of sampling periods where individuals A and B are both identified but are not associated (Cairns and Schwager, 1987).

A Pearson's correlation coefficient (r) between the true AIs (the proportion of time a pair are actually associated) and the estimated AIs was calculated, and used to determine how accurately the true social structure of the population was modelled by the association data. An r value of 1 indicates that the data provides an excellent representative pattern of social structure, 0.8 a good representation and approximately 0.4 a somewhat representative pattern (Whitehead, 2008a, b).

Social differentiation (S) is a measure used to indicate the relative homogeneity of dyadic association indices within a social system. To investigate this, the estimated coefficient of variation (CV) of the true association indices was calculated (Whitehead, 2008a, b). Relatively homogenous societies are indicated by S values between 0.0 and 0.3, well-differentiated societies are indicated by S values greater than 0.5 and extremely differentiated societies are indicated by S values greater than 2.0 (Whitehead, 2008a, b).

The HWI of association (Section 3.2.5) estimated both the r and S values, with the standard error calculated using the likelihood method with 1,000 bootstrap replicates and a resolution of integration equal to 0.001 (default in SOCPROG).

After calculating social differentiation, an estimated mean number of observed associations per dyad (G) needed to obtain a 'somewhat representative view' (at $r = 0.4$) and 'highly representative view' (at $r = 0.8$) of the population social structure was determined using Table 3.1 (Whitehead, 2008a). Although the study population of pilot whales is expected to violate the assumption that effort is equally concentrated across all dyads included in the analysis, the last equation in Table 3.1 still provides a useful indication of the amount of data required to draw meaningful conclusions about the social structure (Mahaffy, 2012).

Table 3.1 Criteria used to estimate the quantity of data required to obtain reliable information about population social structure, sourced from Whitehead (2008a; pg. 84).

Social differentiation (S)	Mean number of observed associations per dyad (G)		Mean observed associations per individual (g') for probable rejection of null hypothesis of no preferred/avoided companionship
	For "somewhat representative" picture of social structure; $r = 0.4$	For "good" representation of social structure; $r = 0.8$	
0.05	76.19	711.11	2000
0.2	4.76	44.44	125
0.8	0.3	2.78	7.8
2.5	0.03	0.28	0.8
10	0.002	0.02	0.05

3.2.3.2 Community division and social network analysis

An agglomerative hierarchical cluster analysis using average-weight linkage was implemented with the use of SOCPROG 2.9, producing a dendrogram to visually display the relationships between individuals using AI. It is important to note that dendrograms can be misleading and must be interpreted with caution (Whitehead, 2008a), as they can suggest complex social structures when none truly exist. A cophenetic correlation coefficient (CCC) was used to statistically test the validity of the dendrograms as a representation of the population social structure (Wittemyer et al. 2005; Whitehead 2008b). The CCC measures the correlation strength between the dyadic association values in the association matrix and their position within the dendrograms. CCC values range from 0, indicating a poor correlation with the data, through to 1, indicating that the dendrogram correlates to the association matrix perfectly (Whitehead 2008b, 2009). CCC values of 0.8 and above signify that the dendrogram is an acceptable representation of the association indices of the study population (Whitehead, 2008a, 2009).

Further analysis was necessary to determine the relative significance of each given social unit. Modularity (Q) was used as a statistical measure to ascertain the level at

which groups of individuals were considered distinct social entities (Newman 2004; Whitehead, 2008a). Modularity values range from 0, indicating a poor division or randomly formed clusters, through to 1, indicating closed communities/clusters with no shared associations between them (Newman, 2004; Whitehead, 2008a). Acceptable social divisions of the population are indicated by Q values of 0.3 and above (Newman, 2004).

The Q value was calculated using two different methods available in SOCPROG 2.9 (Whitehead, 2009). The first uses a modification to Newman's (2006) test for modularity (Lusseau, 2007) which maximises modularity through a series of tests along the dendrogram. It provides a corresponding AI at the maximum modularity which indicates the stopping point. Any clusters formed at association values above this stopping point indicate meaningful social divisions within the study population.

The second is based on Newman's eigenvector modularity method. This uses a social network analysis approach, utilising a divisive method to assign individuals to clusters. Here, all individuals within the study population are initially contained within one large cluster, which is then progressively divided until a desired stopping point (i.e. maximum modularity) is reached. This is achieved when any additional divisions would reduce modularity (Whitehead, 2008a). The Modularity-G test (Lusseau, 2007) was used for both methods, which calculates expected proportions while accounting for previous sighting history and controlling for gregariousness by focusing on association preference.

The null hypothesis that the rates of association between and within defined clusters are similar was then tested by performing a Mantel test (Schnell et al. 1985) with 1,000 permutations. A matrix correlation coefficient was calculated, with a positive t-value, large *P*-value (> 0.95) and positive coefficient value indicating that within-cluster association rates are significantly higher than between-cluster association rates (Whitehead, 2009). This testing was carried out for each of the possible community structures determined from the two methods outlined above.

It has been suggested that the eigenvector-based method is preferable for dividing populations into social clusters compared to delineating across the entire dendrogram using maximum modularity (Whitehead, 2008a). Following this suggestion, the associations among identified pilot whales were visualised using the social network visualisation tool, NetDraw 2.160 (Borgatti, 2002) based on the social clusters delineated using the eigenvector-based method in SOCPROG 2.9. A 'spring-

embedded' layout was selected which places more connected nodes (individuals) in the centre of the diagram and those with fewer connections around the periphery.

3.2.3.3 Preferred or avoided associations

While the strength of a dyadic relationship can be appropriately measured using AIs, this result gives no indication of whether these are preferred or avoided associations, or whether all individuals in the population associate randomly. Modified permutation tests (Manly, 1995; Bejder et al. 1998; Whitehead, 2008a, b) tested the null hypothesis that all individuals associated with the same probability (i.e. individuals do not have preferred or avoided companions). The permutation tests were performed in SOCPROG 2.9 (Whitehead, 2009) and required the association data to be randomised while important features of the data were held constant (Bejder et al. 1998).

There were three methods available to run permutation tests in SOCPROG, each with its own assumptions: 1) permute all groups, 2) permute groups within samples and 3) permute associations within samples (Whitehead, 2009). The first method, 'permute all groups' was not suitable for use in this analysis as the data collected here did not meet any of the necessary criteria (Whitehead, 2009). The latter two options were better suited to the data set and used to test the null hypothesis of random associations between individuals.

The 'permuting groups within samples' approach uses a group by individual matrix to test the null hypothesis by accounting for the number of groups each individual is seen in during the sampling period (Whitehead, 2009). It is useful for testing for both long-term (between sampling periods) and short-term (within sampling periods) preferred/avoided associations, by examining the standard deviation (SD) and mean of AIs. The existence of long-term preferred companions in the population is indicated by significantly higher ($p > 0.95$) SD and CV values of the real (observed) association indices (HWI values) compared to the permuted data (Whitehead 2008b, 2009). The existence of short-term preferred companions is indicated by a significantly low ($p < 0.05$) mean of the real (observed) association indices compared to the permuted data (Whitehead, 2009). The "permute groups within samples" test is also used to determine whether individuals show a preference for particularly large or small groups (degree of gregariousness). A high SD of typical group size and a large corresponding p -value ($p > 0.95$) indicates that some individuals are always found in large or small groups.

The 'permute associations within samples' approach uses a symmetric association matrix to test the null hypothesis by accounting for the number of associations each individual had within every sampling period, and keeping it constant (Whitehead, 2009). This is a useful method of testing the null hypothesis as it has fewer assumptions, controls for gregariousness (unlike the previous method) and accounts for the fact that not all individuals may be present during each sampling interval due to births, deaths, emigration and immigration (i.e. demographic effects) (Whitehead, 2008a, b, 2009). This method tests only for long-term preferred or avoided associations, hence two different methods were used to evaluate both long- and short-term pilot whale associations (Whitehead, 2009). Similar to the previous approach, a significantly high SD or CV value of the real association indices compared to the permuted data set indicates the existence of long-term preferred associations (Whitehead, 2009). For both tests, a significantly smaller proportion of non-zero HWIs in the observed (real) data set compared to the random (permuted) data would indicate avoided companions (Whitehead, 2008a, b).

The results of these permutation tests produce a distribution of test statistics for HWI values and from this, a p -value can be calculated. However, the p -value can be considered to be conservative, and the results positively-biased because each new generation of a data matrix is always generated from the previous one and so the results are not independent (Manly, 1995). To ensure that the results were not biased, the number of permutations was increased sequentially by 1,000, until all of the p -values stabilised (Bejder et al. 1998; Whitehead et al. 2005). This was achieved when there was < 0.001 variance between the values and when the overall p -values remained constant across three runs of the same number of permutations.

After each random permutation of the data, the HWI was calculated for every dyad in the data set. Preferred associations among dyads were determined by comparison of the observed dyadic association indices to the mean association index of the study population (average HWI of all permutations) (Lusseau et al. 2003). Following Durrell et al. (2004) and Gero et al. (2005), those dyadic associations with an AI greater than or equal to twice the mean AI of the study population were considered "preferred associations," and those that fell below this threshold were considered "acquaintances."

3.2.3.4 Temporal patterns of associations

An important aspect of social structure is the temporal patterning of relationships between individuals within a population that reveal the long-term nature of relationships (Hinde, 1976). To investigate long-term dyadic associations, the lagged association rate (LAR) and null lagged association rate (NLAR) were determined for all identified pilot whales (Whitehead, 1995). The LAR estimates the probability that if two individuals are associated at a known time (i.e. beginning of the study period), they will still be in association several time lags later (Whitehead, 1995). In contrast, the NLAR is representative of the expected value if dyadic associations are random (i.e. no preferred associations). Both the LAR and NLAR were standardised due to the fact that it is unlikely for all members of a group to have been identified during the sampling period, and therefore unlikely that all true associations were recorded (Parra et al. 2011; Whitehead, 1995). Standardisation is achieved by accounting for the number of associates an individual is seen with at each specific time lag. The standardised rate estimates the probability that if two individuals (A, B) are associated at a given time, following some chosen time lag (τ) a randomly-chosen associate of A will be B (Whitehead, 1995).

To determine whether the temporal patterning of associations between individuals were significant, the standardised lagged association rate (SLAR) was compared to the standardised null lagged association rate (SNLAR). The SLAR was calculated using all well-marked individuals (D1 – 2) captured in good-quality images (Q1 – 2) (Chapter 2.2.4), irrespective of photographic coverage of the group or sightings history, since those individuals with only a few captures have a small impact on the outcome of the LAR (Whitehead, 2008a). Additionally, the inclusion of all individuals in this part of the analysis avoided the possibility of positively-biasing the SLAR (Baird and Whitehead, 2000; Lusseau et al. 2003). Here, the sampling period was set to one day to ensure interpretable results (Whitehead, pers. comm. in Hamilton, 2013).

The observed temporal association pattern for all individuals (the SLAR) and SNLAR were then plotted against a time lag of 1200 days and standard errors were calculated using jack-knife methods (Efron and Gong, 1983). There are four exponential mathematical models available in SOCPROG that can be fitted to the SLAR (Table 3.1) to investigate the types of associations within the population. All of the models were run simultaneously, being fitted to the SLAR curve using maximum likelihood and binomial loss. Model selection was executed using the Quasi-Akaike Information Criteria (QAIC), as this approach corrects for over-dispersion in the count data and is

considered more accurate when choosing the best fitting model i.e., the minimum QAIC (Whitehead, 2007; Whitehead, 2009). However, a difference of less than two units in the QAIC score between the best fit model and any other model(s) indicated support for the competing model, meaning that it should not be dismissed (Whitehead, 2007; Whitehead, 2008a).

Table 3.2 Models available in SOCPROG 2.9 that can be fitted to the SLARs and LARs using maximum likelihood and binomial loss methods. Possible model interpretations are also given.

Model description	Possible model interpretation
Constant Companions (CC)	Permanent, stable associations over periods of time. May be indicative of closed, non-interacting units.
Casual Acquaintances (CA)	Irregular associations between individuals that disassociate and then may re-associate at a later stage.
Casual Acquaintances and Constant Companions (CA + CC)	A combination of the previous two explanations. Associations may stabilise at a lower level after the disassociation and re-association process.
Two levels of Casual Acquaintances	Irregular associations between individuals that disassociate on two different time scales (at two different rates).

3.3 Results

3.3.1 Data selection: Encounters and groups

A total of 145 photo-identified adult pilot whales were sighted at least once during the 2011-2019 study period (Appendix 3). Once the data had been restricted to include only those individually identified pilot whales seen on two or more occasions and only those encounters with a minimum photographic coverage score of 0.5, there were 27 individuals (18.6%) from 14 encounters (34.1%, all from north-eastern New Zealand) included in the social structure analysis. These restrictions on the data set were not applicable in the evaluation of the SLAR, and therefore all 145 identifiable individuals were included in that portion of the analysis.

3.3.2 Dyadic association indices

The data were of sufficient quality to detect the true social system within sampled pilot whale individuals, with $r = 0.52$ (SE = 0.04), and the social differentiation value $S = 0.78$ (SE = 0.07) indicating a well-differentiated population, with some individuals having preferred associates. This indicates that the data provide a 'somewhat representative' pattern of the social relationships (Table 3.1; Whitehead, 2008a, b).

The observed average HWI for well-marked (D1 – 2) pilot whales was 0.20 (SD = 0.09, range = 0.02 – 0.32), showing that the overall rates of association between individuals in the study population were very low. Out of a possible 351 dyadic associations, 67% (235 dyads) showed no association (AI = 0.00) (Figure 3.1A, Figure 3.1B), which suggests a high degree of fission-fusion in the individuals sampled. The average association index for non-zero entries (116 dyads) was 0.59 (range = 0.33 – 1) and the observed average maximum HWI was 0.91 (SD = 0.15, range = 0.50 – 1.00; Figure 3.1C), indicating that all 27 well-marked individuals were captured with one other individual at least 50% of the time. This suggests that while the overall associations within the study population are low (Figure 3.1B), there are also some strong dyadic associations (Figure 3.1C). Individuals included in the analysis also differed in the number of other individuals with whom they were associated (mean = 6.11, SD = 2.41); membership ranged from 1.50 to 9.23, suggesting some differences in individual gregariousness (Figure 3.1D).

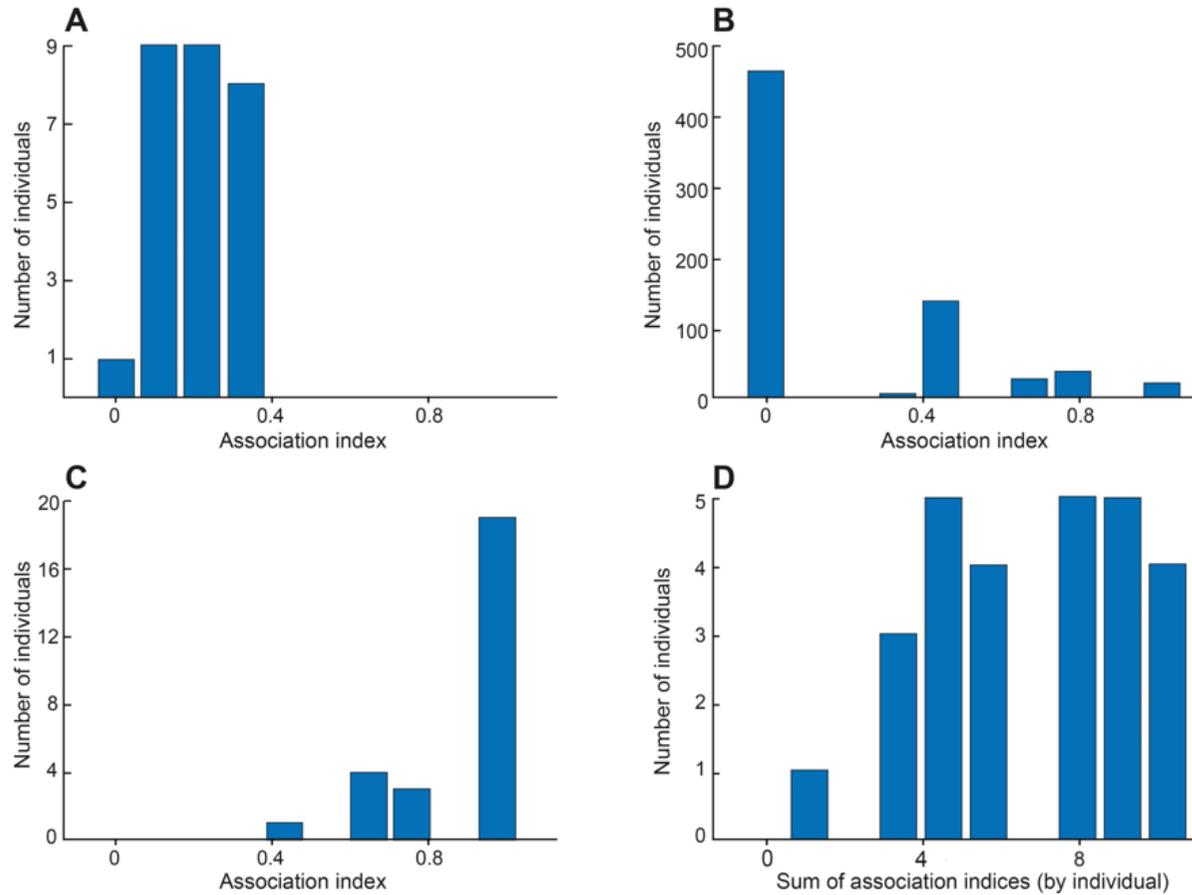


Figure 3.1 Distribution of the half-weight association indices for distinctive pilot whales encountered on at least two occasions off New Zealand between 2011 and 2019 ($n = 27$). Distribution of A) mean association indices by individual, B) overall association indices for all individuals, C) maximum association indices by individual and D) sum of association indices by individual, including diagonal elements. Note the different scales on the x- and y-axes.

3.3.3 Social network analysis and community division

There was a high correlation between the actual dyadic AI in the association matrix and the levels of clustering in the HWI dendrogram ($CCC = 0.855$), indicating an effective representation of population social structure (Figure 3.2). Both the hierarchical cluster analysis and the social network analysis supported the division of the study population into multiple clusters (maximum modularity-G using cluster analysis: $Q = 0.395$, $AI = 0.267$ and $Q = 0.390$ respectively). Both Q values meet the threshold of 0.3 (Newman, 2004) and therefore indicate an acceptable division of clusters. However, both are still low enough to suggest that within-cluster associations are not much higher than would be expected in a society of random associates.

Hierarchical cluster analysis resulted in the division of the study population into six clusters of variable size and association strength (Figure 3.2). Community division using Newman's (2006) eigenvector-based method resulted in five clusters, with cluster membership ranging from three to eight individuals (Figure 3.3; Appendix 4). Visualisation of the social clusters (NetDraw 2.158; Borgatti, 2002), revealed the existence of a core social network of 22 individuals consisting of four associated sub-clusters and a satellite cluster of five individuals (Figure 3.3).

Overall, both the HWI dendrogram (Figure 3.2) and the social network analysis (Figure 3.3) represent similar social structures. For the hierarchical cluster analysis, the levels of association of individuals within clusters (mean $AI = 0.70$, $SD = 0.18$, range = 0.52 – 1.00) were significantly higher (Mantel permutation test t -value = 13.46, $p = 1.00$) than those between clusters (mean $AI = 0.09$, $SD = 0.07$, range = 0.00 – 0.27), indicating that the divisions within the study population determined by maximising modularity were supported. Similarly, for the social network analysis, the levels of association of individuals within clusters (mean $AI = 0.63$, $SD = 0.21$, range = 0.40 – 0.87) were significantly higher (Mantel permutation test t -value = 12.20, $p = 1.00$) than those between clusters (mean $AI = 0.10$, $SD = 0.10$, range = 0.00 – 0.56). Both methods produced large, positive matrix correlation coefficients of 0.75 and 0.65 respectively.

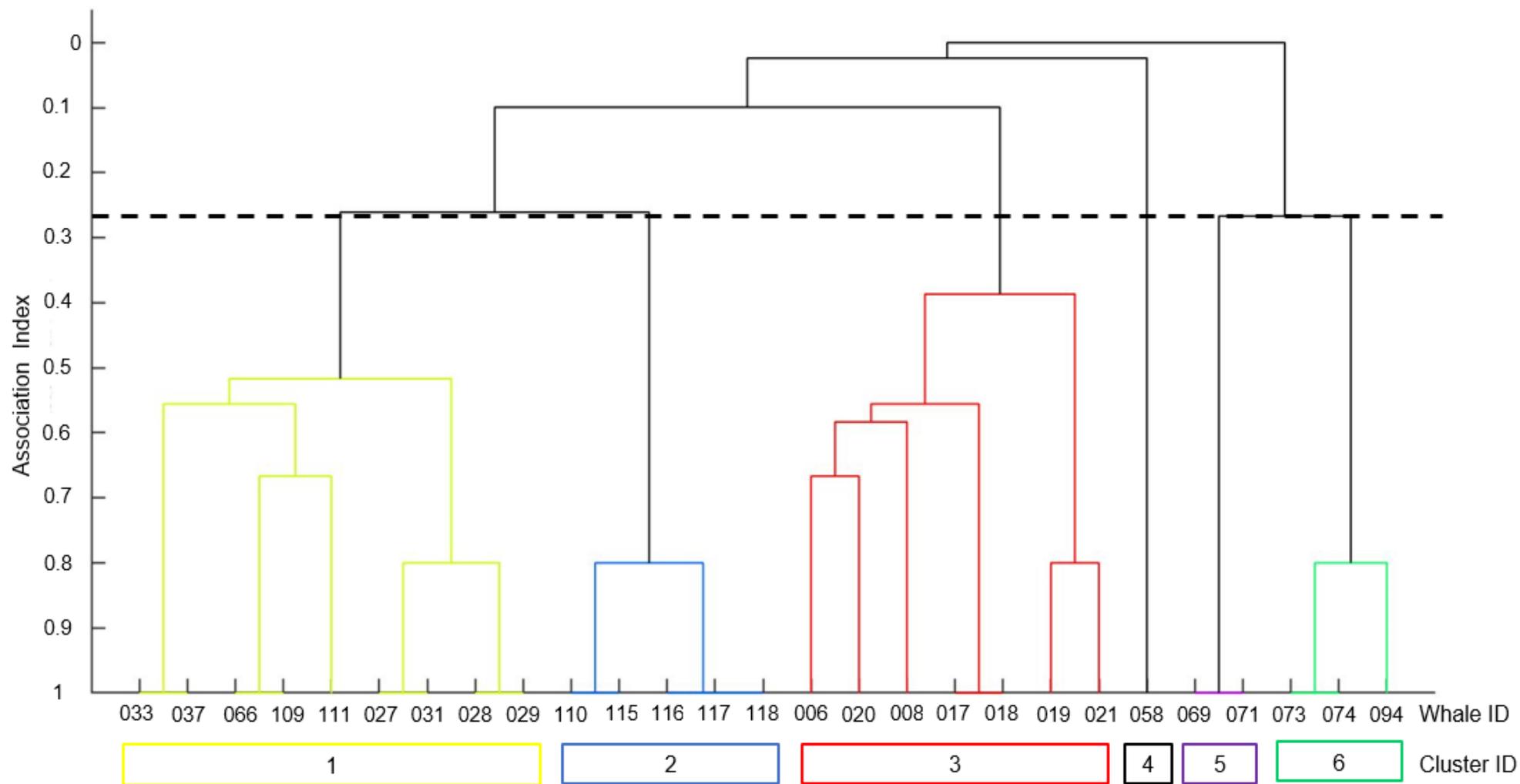


Figure 3.2 Half-weight index dendrogram drawn based on an average-linkage hierarchical cluster analysis showing associations between 27 individual pilot whales. The dashed line indicates the point at which clusters were delineated using modularity-G.

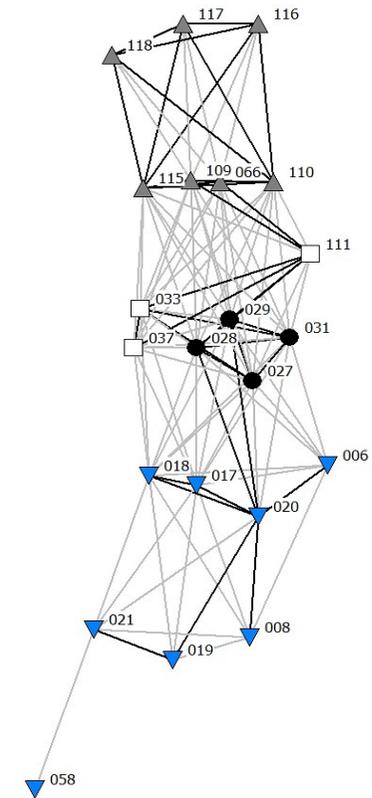
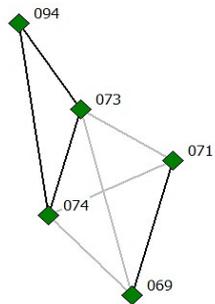


Figure 3.3 Social network diagram showing the associations between 27 distinctive or very distinctive individual pilot whales seen on more than two occasions. The nodes in the network represent individual pilot whales (with ID numbers, Appendix 3), with the colour and shape of the node representing membership to social clusters as delineated by Newman’s eigenvector method ($Q = 0.390$). Ties between nodes represent associations between dyads, where darker coloured ties indicate stronger HWI associations. Ties where the HWI was less than 0.59 (the average HWI for non-zero entries in association matrix) are coloured grey and those above this value are black. A spring-embedding algorithm with Gower scaling in NetDraw 2.158 (Borgatti, 2002) was used to determine the layout of the network, plotted with geodesic distances.

3.3.4 Preferred or avoided associations

There were no significant differences in the relevant test statistics (SD and CV) for either of the permutation tests (Table 3.3), indicating that there is no evidence of long-term preferential associations between individuals. There was no difference in the proportion of non-zero AIs in the real data compared to the permuted data for both tests, which indicated that there was no evidence of long-term avoidance of individuals either (Table 3.3). Additionally, for groups permuted within samples, the similar values of the observed and permuted means of the AIs indicated that there were no short-term preferential associations between individuals. Individuals had significant differences in gregariousness ($p = 0.95$), with some individuals found in consistently small or large groups. P -values stabilised at 40,000 random permutations for associations permuted within samples and at 50,000 for groups permuted within samples (with 1,000 trial flips per permutation for each).

Only a single dyad (NZGme019 and NZGme021) showed a significantly high AI ($p > 0.95$), greater than twice the mean HWI for the population (dyadic AI = 0.8 > mean AI = 0.2). Inspection of the association matrix for all 27 individuals revealed an additional 86 dyads (out of a possible 351, 24.8%) with AIs greater than twice the population mean HWI, however none of these were considered significant and were therefore not reliable (Appendix 5). This indicates that the large majority of the population can be considered acquaintances, having dyadic AIs of less than twice the population mean.

Table 3.3 Tests for non-random associations among 27 individual pilot whales. Permutation tests in SOCPROG 2.9 were used to test for short-term (indicated by asterisk) and long-term preferred or avoided associations and for differences in individual gregariousness. P-values \geq 0.95 are considered significant. HWI = Half-weight Index; AI = Association index; NA = Not applicable; SD = Standard deviation; CV = Coefficient of variation; Prop. = Proportion.

	Test 1: Permute groups within samples (short-term* and long-term test)			Test 2: Permute associations within samples (long-term test)		
	Observed	Permuted	P-value	Observed	Permuted	P-value
Mean AI HWI*	0.1966	0.1963*	0.2632	NA	NA	NA
SD of HWI	0.2981	0.2937	0.9171	0.2981	0.2950	0.8751
CV of HWI	1.5162	1.4960	0.8874	1.5162	1.5010	0.8753
Prop. Non- zero of HWI	0.3362	0.3421	0.9006	0.3362	0.3406	0.8863
SD of typical group size	2.4273	2.3505	0.9477	NA	NA	NA

3.3.5 Temporal patterns of associations

The SLAR for all 145 individually identified pilot whales increased sharply within approximately 50 days and then began a gradual decline which continued until day 1400 (Figure 3.5), which indicates a marked disassociation of individuals. The initial decline is relatively steep, with the SLAR falling from 0.07 to 0.05 over approximately 300 days. The second decline is more gradual, with the SLAR falling from 0.05 to 0.02 over approximately 800 days. The error bars of the SLAR intersected with the NSLAR twice; once around day 1025 and again at day 1400, indicating that the dyadic associations within this population may become random at these time lags. The large error bars indicate uncertainty throughout the study period, most likely due to the large number of individuals in the data set that were only sighted once (69%, $n = 100$).

The 'two levels of casual acquaintances' model gave the lowest QAIC value, suggesting that it was the best fit to the data, but the level of support for the 'casual acquaintances' model was very similar ($\Delta\text{QAIC } 0.80$), indicating that these two models are indistinguishable (Table 3.4 and Figure 3.4). As the SLAR curve falls with little evidence of stabilising over any time lag, the model description of two levels of casual acquaintances is supported. Neither of the best-fitting models fit the data precisely, with both models underestimating the SLAR most of the time. This is most likely the result of the large number of individuals that were sighted only once during the study period (69%, $n = 100$), and this potential bias requires caution when interpreting the results.

If the LAR is standardised, the reciprocal of the number of casual acquaintances of a randomly chosen individual is represented at the level at which the expected SLAR crosses the y-axis. The value of the best-fitting model for short time periods at time 0 was 0.0163.

Following the model for 'two levels of casual acquaintances,' the typical group size (gregariousness; Jarman, 1974) of the study population was estimated at 61 individuals ($1/a$). Scaling this up to account for non-identifiable individuals (mark rate = 0.134; Chapter 2), plus 1 to account for the individual itself (i.e. $(61 \times 0.134) + 61 + 1$), gives an overall typical group size estimate of 70 individuals (group size typically experienced by a member of the population; Whitehead, 2008a). Associations between individuals were estimated to persist for 20 days ($1/a_1$, $a_1 = 0.05$) under the 'two levels of casual acquaintances' model and for 1,000 days ($1/a_1$, $a_1 = 0.001$) under the 'casual acquaintances' model.

Table 3.4 Fit of, and relative support for, exponential social-system models to the standardised lagged association rate for individual pilot whales in New Zealand. Associations were defined as individuals grouped within an encounter; the lowest Δ QAICc value indicates the best-fit model.

Description of model	Model formula	Maximum likelihood values for parameters (SE)	QAICc	Δ QAICc	Model support
Constant Companions	$g' = a_1$	$a = 0.04 (0.03)$	226.61	6.01	Little support
Casual Acquaintances	$g' = (a_2 \cdot e^{-a_1 \tau})$	$a_2 = 0.06 (0.43)$ $a_1 = 0.001(1.974)$	221.40	0.8	Good support
Constant Companions & Casual Acquaintances	$g' = a_2 + a_3 \cdot e^{-a_1 \tau}$	$a_2 = 0.04 (0.04)$ $a_1 = 1.27(11.88)$ $a_3 = -0.01 (25881.95)$	230.61	10.01	Little support
Two levels of Casual Acquaintances	$g' = a_3 \cdot e^{-a_1 \tau} + a_4 \cdot e^{-a_2 \tau}$	$a_4 = 0.08 (1.34)$ $a_2 = 0.001(0.259)$ $a_3 = -0.06 (81.35)$ $a_1 = 0.05 (48.99)$	220.61	0	Best

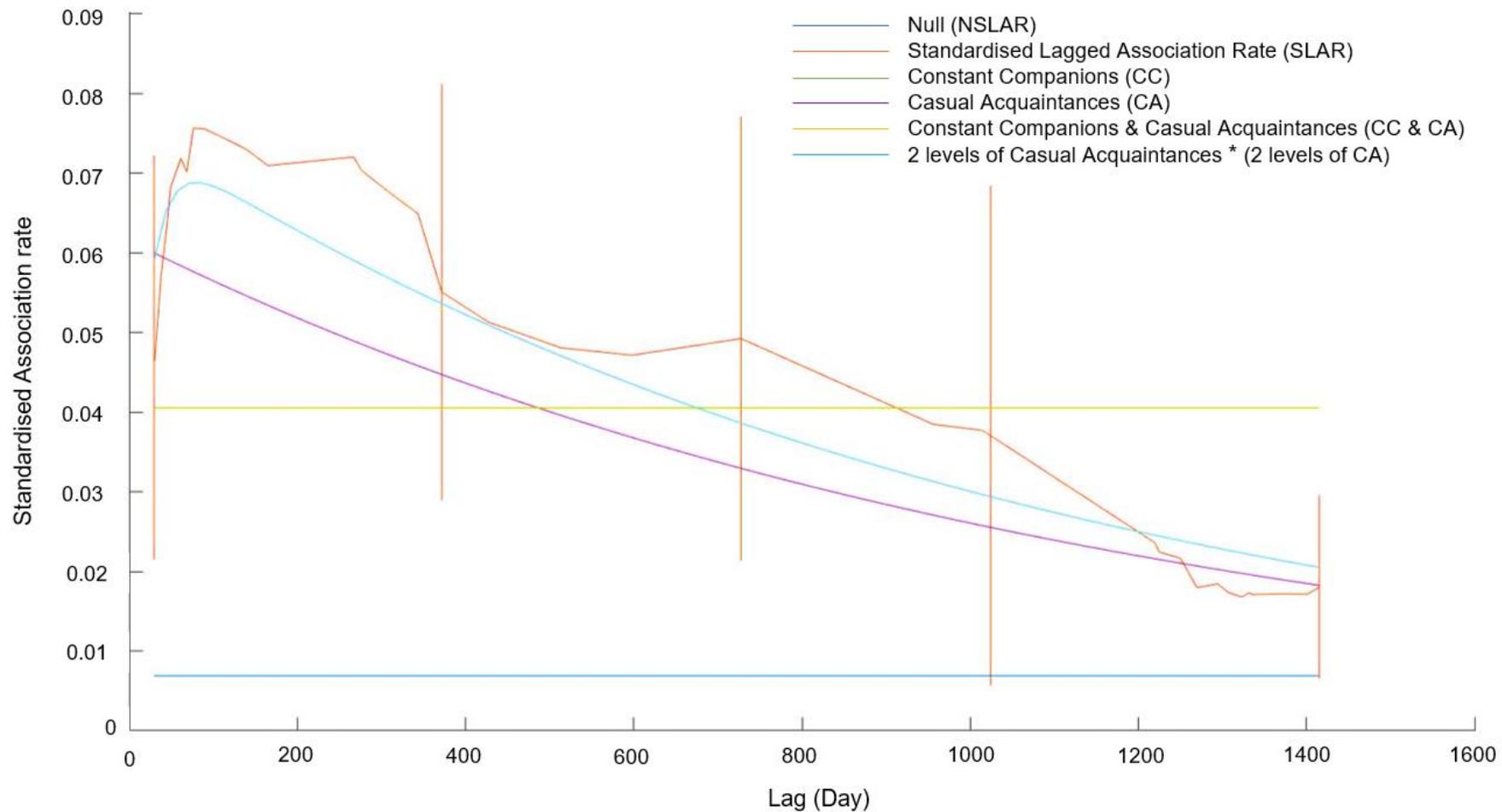


Figure 3.4 Standardised lagged association rate (SLAR) for all distinctive pilot whale individuals captured between 2007 and 2019, using a moving average of 1200 associations and with approximate standard errors bars (produced by jack-knife on each sampling period). Asterisks denotes best-fit model. Note 'CC' and 'CC & CA' models are identical (poor) fits to the data and therefore only one line (yellow) is shown on the graph.

3.4 Discussion

The long-finned pilot whales in north-eastern New Zealand waters appear to be characterised by a well-differentiated, fission-fusion society where large groups of individuals most likely represent ephemeral aggregations, containing multiple smaller but more persistent social units. The large majority of dyadic associations within groups are weak and short-lived, with casual acquaintances disassociating over two different time scales. However, evidence also suggests the existence of strong relationships between some individuals within these groups, which are likely reflective of different cohesive social units. There is some caution required in interpreting these findings (Section 3.4.2) but further research should reveal the complexities of pilot whale social structure in time.

3.4.1 Social structure

3.4.1.1 Individual associations and gregariousness

The association patterns of pilot whales off north-east New Zealand indicate a well-differentiated society, where dyadic relationships within the population are varied. There was no evidence of preferential or avoided long- or short- term bonds between individuals (Table 3.5) and the overall AI for the sample population was low. However, an evaluation of the sightings history for all individuals revealed evidence of strong, long-term associations between some group members (Appendices 4 and 5). This suggests that while the majority of pilot whales have casual, short-term associations, there are likely some dyadic bonds that are temporally stable, which is characteristic of hierarchically structured societies of delphinids (e.g. Connor et al. 2000; McSweeney et al. 2009; Parra et al; 2011; Alves et al. 2013; Augusto et al. 2017a; Hunt et al. 2019). Unlike the current study, long- and short-term preferential associations were found amongst long-finned pilot whales off the coast of Nova Scotia (Ottensmeyer and Whitehead, 2003; Augusto et al. 2017a) and in the Strait of Gibraltar (de Stephanis et al. 2008c) (Table 3.5). Similarly, short-finned pilot whale societies in the Canary Islands (Servidio, 2014), and the archipelagos of Hawai'i (Mahaffy et al. 2015) and Madeira (Alves et al. 2013) are all characterised by both long- and short-term preferential associations between individuals (Table 3.5). These differences are likely an artefact of using a small, restricted dataset in the current study as other aspects of the analysis (Section 3.3.2) indicate that persistent dyadic associations are present in the population.

Individual pilot whales in New Zealand also displayed differences in gregariousness, with some animals consistently found in large or small groups. Interestingly, the same pattern of variable gregariousness has not been documented elsewhere (Ottensmeyer and Whitehead, 2003; de Stephanis et al. 2008c), suggesting that individuals in other pilot whale populations are typically found in similar sized groups. This could indicate a key difference in the social structures of the two long-finned pilot whale sub-species, however more research is needed to determine the extent of these differences. It may also be an artefact of the data used in this study, as detailed information about the stability of sub-group membership was not available. It is possible that the observed sub-groups represent stable social units of a similar size, with very large groups representing ephemeral aggregations, but the combination of a small data set, low mark rate and low re-sight rate make this difficult to test at present. Short-finned pilot whales also demonstrate differences in gregariousness (Servidio, 2014; Hartny-Mills, 2015; Mahaffy et al. 2015). Possible reasons for this variation remain speculative, but are thought to be linked to specific age and/or sex classes (as seen in chimpanzees; Pepper, 1999) or serve as an indicator of individual social standing within the population (Servidio, 2014; Mahaffy et al. 2015). Association based on age and sex class could not be investigated here, as no genetic analysis was available to support field observations, but this would be a valuable addition to future studies.

3.4.1.2 Detecting and understanding community structure

Pilot whales in New Zealand may exhibit a hierarchical social structure. Social network analysis supported the division of individuals into five socially meaningful clusters of varying size and association strength. The mean AI within clusters was relatively high, which provides support for the existence of multiple, persistent social units within the study population. The low mean association rate in addition to the very low mean AI between social clusters indicate that individuals across different clusters are not forming strong, long-term bonds with one another. Once again, this is typical of hierarchically structured fission-fusion societies of delphinids, where individuals tend to form the strongest bonds within their own social units (e.g. Connor et al. 2000; Parra et al. 2011; Hunt et al. 2019). The lack of social links between individuals in the core network and those in the satellite cluster suggests that these animals are never in association. However, this may be an artefact of the strict quality control criteria applied to the data (Section 3.2.2), which may have excluded linking individuals. Relaxing these criteria would almost certainly have resulted in misleading

interpretations of the data. It is also possible that individuals in the satellite cluster represent members with different degrees of site fidelity to those in the core network (Section 3.4.1.3), however more directed research is required to elucidate the true patterns of residency in this population.

The typical group size (gregariousness) was slightly higher (70 animals) than the observed median group size from at-sea encounters (50 animals). Notably, the mean number of individuals assigned to each delineated social cluster (5 animals) was considerably smaller than the observed median group size (50 animals). However, scaling this up to account for unmarked individuals (mark rate = 13.4%, Chapter 2) gives a true cluster size of 37 animals, which reflects the median group size more closely. The within-cluster mean association indices were relatively high, suggesting that social clusters are indicative of reasonably cohesive units. Therefore, it is likely that the clusters are representative of meaningful divisions of pilot whale society. The large groups typically observed at sea may have consisted of multiple smaller, stable social clusters of pilot whales in temporary association. This appears to be the general trend amongst longitudinal studies of other pilot whale societies with populations of both long- and short-finned pilot whales showing hierarchical structuring and social complexity (e.g. Heimlich-Boran, 1993; Ottensmeyer and Whitehead, 2003; de Stephanis et al. 2008b; Alves et al. 2013; Servidio, 2014; Hartny-Mills, 2015; Mahaffy et al. 2015; Augusto et al. 2017; Van Cise et al. 2017).

The smallest societal division of any pilot whale population (typically referred to as a unit, sub-cluster or clan; Table 3.5) is considered the most temporally stable (de Stephanis et al. 2008c; Alves et al. 2013; Servidio, 2014; Hartny-Mills, 2015; Mahaffy et al. 2015; Augusto et al. 2017a) consisting of a relatively small number of socially cohesive individuals (Table 3.5). These units probably represent closely related individuals of both sexes which have formed lifelong associations, although this has only been confirmed for a few populations (de Stephanis et al. 2008c; Alves et al. 2013; Van Cise et al. 2017). In New Zealand, the mean number of individuals in a 'cluster' is similar to that of 'units' and 'line units' from other long-finned pilot whale studies, but is seemingly smaller than the 'units' and 'sub-clusters' reported for short-finned pilot whales (Table 3.5).

Clusters (also referred to as 'pods'; de Stephanis et al 2008c) of pilot whales typically represent the next level of association in a population. Clusters tend to be larger than units on average, with more variable associations between individuals (e.g. de

Stephanis et al. 2008c; Servidio, 2014; Hartny-Mills, 2015; Mahaffy et al. 2015), that may or may not be related (Van Cise et al. 2017). Clusters may form when familial units grow too large, eventually undergoing fission; splitting into multiple, smaller units that are highly labile within the cluster, and include individuals of both sexes (e.g. de Stephanis et al. 2008c; Augusto et al. 2017a). In general, genetic studies of pilot whale social structure have found that relatedness is higher within clusters compared to between clusters (de Stephanis et al. 2008c; Alves et al. 2013; Van Cise et al. 2017). Similar processes of fission of large matrilineal units are well-documented in other highly social mammals, for example killer whales (Williams and Lusseau, 2006) and African elephants (Archie et al. 2006), usually following the death of a matriarch. It would therefore be useful to conduct genetic analyses on live pilot whales in New Zealand to determine whether the social clusters delineated here represent closely related individuals of both sexes, which may then be more aptly termed units.

Based on the relatively large mean group sizes of long-finned pilot whales encountered at-sea (Table 3.5), it has been suggested that multiple, possibly unrelated clusters join together to form groups with variable temporal stability (Ottensmeyer and Whitehead, 2003; de Stephanis 2008c; Augusto et al. 2017a). Indeed, every study of long-finned pilot whale populations to date has noted the presence of smaller sub-groups within larger groups of up to 350 individuals (Weilgart and Whitehead, 1990, Cañadas and Sagarminaga, 2000; Ottensmeyer and Whitehead, 2003; de Stephanis 2008b, c; Visser, 2014; Augusto et al. 2017a). Sub-groups display fission-fusion dynamics during encounters, as reported here (Chapter 2, Section 2.3.1). The median size of sub-groups (30 individuals) was similar to the core social network delineated from social structure analysis (22 individuals). Therefore, it seems reasonable that these sub-groups could represent clusters of socially cohesive individuals that associate on a short-term basis with other clusters, likely for breeding and/or feeding purposes (see Chapter 5).

While average group size and average social unit size are markedly different in long-finned pilot whale populations, the same trend is not observed for short-finned pilot whales (Table 3.5). This disparity may indicate a fundamental difference in the social structure of these sympatric species, with larger groups of short-finned pilot whales possibly being representative of entire social clusters of related individuals (e.g. Van Cise et al. 2017). However, it may also be reflective of differences in populations rather than entire species (Mahaffy, 2012). All of the short-finned pilot whale studies included here have focused primarily on the social structures of island-associated

individuals (Heimlich-Boran, 1993; Alves et al. 2013; Servidio, 2014; Hartny-Mills, 2015; Mahaffy et al. 2015; Van Cise et al. 2017), which will likely be influenced by different ecological drivers (e.g. prey availability) compared to oceanic (offshore) populations. Similarly, studies of other large, social delphinids have shown that while group size and social structure are interlinked, these patterns can vary widely amongst populations. For example, sympatric groups of resident and transient killer whales are both strictly matrilineal (Bigg et al. 1990; Baird, 1994), but associations between unrelated groups of the same type occur on very different temporal scales, with varying pod sizes (Bigg et al. 1990; Baird and Dill, 1995; 1996). Around the main Hawaiian Islands, a small insular population of false killer whales consists of multiple cohesive social clusters, which all belong to one social network (Baird et al. 2008a), and while the offshore population is thought to be much larger (Barlow and Rankin, 2007) individuals may also form close social associations (Baird et al. 2008a). Populations of inshore bottlenose dolphins are known to live in hierarchically structured fission-fusion societies, where associations between individuals may vary in their level of temporal stability (e.g. Hamilton, 2013; Wells 2014; Connor and Krützen, 2015), however, the social structure of offshore populations remains largely unknown (Gowans et al. 2007).

Table 3.5 Comparison of long- and short-finned pilot whale population social structures, based on studies using only photo-ID methods or a combination of photo-ID and genetic methods (denoted by a single asterisk). LFPW = long-finned pilot whale, SFPW = short-finned pilot whale, CA = casual acquaintances, CC = constant companions, double asterisk denotes studies that report a median group size.

Species	Location	Smallest societal divisions assigned	Mean size of smallest societal divisions (range)	Mean or median** group size (range)	Non-random long-term associates	Non-random short-term associates	Best-fit model of social structure	Reference
LFPW	New Zealand	Clusters	5 (3 – 8)	50** (3 – 250)	No	No	Two levels of CA	Current study
LFPW*	Cape Breton Is., Nova Scotia	Units	7 (3 – 29)	59 (2 – 135)	Yes	Yes	CA	Ottensmeyer and Whitehead, 2003; Augusto et al. 2017a*
LFPW*	Strait of Gibraltar	Line units	3 (2 – 5)	14 (2 – 150)	Yes	Yes	CC	de Stephanis et al. 2008c*
SFPW	Hawaiian Archipelago	Sub-clusters	12 (8 – 18)	21 (1 – 53)	Yes	Yes	CA	Mahaffy et al. 2015
SFPW	Canary Islands	Units	17 (3 – 33)	16 (1 – 70)	Yes	Yes	Both CA and CC	Servidio, 2014
SFPW	Tenerife	Clusters	7 (3 – 13)	9 (1 – 41)	Yes	No	CC	Hartny-Mills, 2015
SFPW*	Madeira	Clans	15 (4 – 29)	18 (2 – 60)	Yes	Yes	CC	Alves et al. 2013*

3.4.1.3 Community structure and site fidelity

For many populations of large delphinids, social cohesiveness of individuals is closely linked to site fidelity (e.g. Baird et al. 2008a; Parra et al. 2011; Hunt et al. 2019). This pattern has been observed in northern hemisphere populations of both species of pilot whale. For example, a resident population of long-finned pilot whales known to inhabit the deeper parts of the Strait of Gibraltar year-round, represent a society that is characterised by non-random close companionships (de Stephanis et al. 2008a, b, c). Conversely, long-finned pilot whales off Cape Breton, Nova Scotia display some seasonal site-fidelity and represent a population of casual acquaintances where the overall association index is low, but with some persistent dyadic associations within social units (Ottensmeyer and Whitehead, 2003). A more complex example is found in short-finned pilot whales around the Madeiran Archipelago, where resident, visiting and transient individuals all constitute a large social network with varying levels of association, although residents form the strongest bonds with other residents, and satellite clusters that are not connected the main network are mostly made up of transients (Alves et al. 2013). Similar patterns of site fidelity and social cohesion have also been found in short-finned pilot whales from the Hawaiian Archipelago (Mahaffy et al. 2015; Van Cise et al. 2017) and Tenerife (Hartny-Mills, 2015).

At this stage, there is a paucity of data concerning pilot whale site-fidelity in New Zealand waters. However, evidence from sightings records of individuals (Chapter 2) suggests that some may have seasonal site-fidelity, specifically in the study regions off the north-eastern coasts of New Zealand's North and South Islands.

Approximately one-third of individuals were re-sighted, with re-sightings always taking place within the same broad study regions (Chapter 2). The majority of individuals were only sighted once during the study period, which suggests that there may be different 'communities' (Alves et al. 2013) of pilot whales using the waters around New Zealand during the austral summer months. Furthermore, the social structure analysis presented here suggests the existence of a core social network and one satellite cluster of individuals. As outlined previously, this may be due to the restrictions applied to the data, but it may also be a true (albeit very limited) representation of pilot whale social structure. Indeed, this would provide support for there being individuals with varying degrees of site fidelity, and therefore residency patterns. For example, individuals within the satellite cluster may be similar to the 'visitors' or 'transients described by the studies mentioned above, utilising the area at particular times of the year for feeding or mating purposes, while those within the core

network may represent 'residents' of New Zealand that are found in the same region year-round. This is also supported by the two best-fitting temporal analysis models. While the 'two levels of casual acquaintances' model predicts that associations between individuals persist for just 20 days (suggesting short-term social bonds within the study population) the 'casual acquaintances' model predicts that individuals only disassociate after 1,000 days (approximately 2.7 years), suggesting that temporally stable dyadic associations also exist. It is therefore possible that pilot whales with different degrees of site-fidelity and residency patterns are associating in the focal study regions, and then dissociating at different rates depending on their respective dyadic relationships, as has been documented elsewhere (e.g. Alves et al. 2013; Servidio, 2014; Mahaffy et al. 2015). However, more research is required to determine whether this is the case.

3.4.2 Study limitations

Interpretations of some aspects of the social structure analysis presented here should be made with caution. The opportunistic nature of the data has meant that some individuals have not been photographed. Combined with the low mark and re-sight rates of the population, it is reasonable to assume that the majority of possible associations between individuals were not documented. Furthermore, applying strict quality-control criteria has meant that only well-photographed encounters have been included in the analysis, ensuring reliable and interpretable results. This conservative approach excluded a large majority of encounters and may have biased the analysis towards smaller groups (which typically have higher photographic coverage).

Additionally, applying these restrictions resulted in only encounters from the North Island (particularly the Bay of Islands) being used in delineating social units, which means that the results may not be reflective of all pilot whales, as historical sightings (Berkenbusch et al. 2013) and strandings (Betty et al. 2020) report their presence in waters all around New Zealand. Using only well-marked individuals in the analysis further limited the useable subset of data, excluding all immature animals (neonates, calves, juveniles) and all poorly marked individuals. Therefore, the sizes of social units and social clusters presented here are likely to be very conservative, as only a small number of catalogued individuals (18.6%), and the possible associations within and between them, have been used to make general inferences about particular aspects of pilot whale social structure. Additionally, the inclusion of so few individuals in the social structure analysis has meant that an evaluation of lagged identification

rate, and therefore a comprehensive analysis of site fidelity, was not possible. Finally, as previously outlined (Section 3.2.2 and Chapter 2, Section 2.2.2.2), one-third of the encounters from the study period included multiple sub-groups of pilot whales that were observed to join together and separate again, over short time periods. However, fine-scale data for these sub-groups were not consistently available and therefore this analysis of pilot whale social structure has been limited to broader groupings of individuals, which may not be a complete, accurate representation of free-ranging groups. Given these limitations, the current study is best considered a preliminary investigation into the social structure of pilot whales in New Zealand, providing baseline data and a solid foundation on which to build when undertaking more dedicated data collection in the future.

3.4.3 Summary

This analysis of pilot whale social structure has revealed that individuals likely constitute a hierarchical society, where small social clusters form groups of casual acquaintances. This is similar to northern hemisphere populations of both species of pilot whale. There was no statistical evidence to suggest the existence of preferred long- or short-term dyadic associations, however, individuals did show differences in gregariousness. Visual inspection of the data suggests that more directed research efforts may reveal strong, temporally stable bonds (close associations) between individuals in the population. Importantly, highly gregarious species such as long-finned pilot whales are known to also form persistent associations with other cetacean species (Chapter 2), and in particular with bottlenose dolphins, a topic which is further explored in Chapter 4.

Chapter 4: Social associations between pilot whales and bottlenose dolphins

4.1 Introduction

Interspecific or mixed-species groups are comprised of individuals from two or more species that are in close association. Mixed-species groups occur across a wide range of taxa, having been described in avian assemblages (Sridhar et al. 2009; Goodale and Beauchamp, 2010; Farine et al. 2012), fish communities (Krause et al. 1996; Ward et al. 2002), and in both marine and terrestrial mammals (Stensland et al. 2003). Among mammals, studies of interspecies associations have focused largely on primates (e.g. Waser, 1982; Chapman and Chapman, 2000; McGraw and Bshary, 2001; Cord and Würsig, 2014), savannah ungulates (Fitzgibbon, 1990; Stensland et al. 2003) and cetaceans (e.g. Psarakos et al. 2003; Melillo et al. 2009; Kiszka et al. 2011; Cords and Würsig, 2014). To date, there is little published research on cross-taxon mixed-species groups (e.g. Newton, 1989; Minta et al. 1992; King and Cowlshaw, 2009; Kiffner et al. 2014; Heymann and Hsia, 2015). Interspecies associations occur more commonly between species that are inherently gregarious (Stensland et al. 2003), forming large groups with conspecifics that will sometimes consist of smaller species-specific sub-units (e.g. Zaeschmar, 2014).

While the topic of interspecific groups is well-canvassed in both terrestrial and aquatic environments, the possible functions of these associations have continued to interest researchers for many decades (e.g. Morse, 1977; Stensland et al. 2003; Cords and Würsig, 2014). Identifying the causative factors behind mixed-group associations can be quite difficult due to the significant range of potential costs and benefits for each particular species (Cords and Würsig, 2014), the effects of which may be unevenly experienced by group participants (e.g. Newton, 1989; Coscarella and Crespo, 2008; Heymann and Hsia, 2015). Theories relating to group-living (Eisenberg, 1966; Alexander, 1974; Krause and Ruxton, 2002) that are typically applied to studies of single-species groups, also underpin investigations of possible drivers of mixed-species groups (e.g. Norris and Schilt, 1988). Groups are typically viewed as having potential advantages for participating group members, which are not afforded to non-joiners. Costs and benefits associated with groups are usually categorised as having an effect on individual fitness, through direct or indirect mechanisms (Eisenberg, 1966; Alexander, 1974; Connor, 2000). Further to this, groups can be categorised by their degree of complexity and duration, ranging from short-term aggregations where

individuals are attracted to a mutually important resource, e.g. food/prey (Cords and Würsig, 2014), to the intricate, long-term associations observed in many eusocial animal societies (e.g. Jarvis et al. 1994). In general, the primary benefits suggested for the majority of mixed-species groups align with those for single-species groups. In particular, predator avoidance and/or improved foraging opportunities are considered important functional advantages, and therefore likely drivers of group living in animals (Stensland et al. 2003; Cords and Würsig, 2014), with the possibility that some associations are influenced by social factors as well (Norris and Schilt, 1988; Kutsukake, 2009).

In the case of cetaceans, the difficulties associated with studying groups in the marine environment has meant that there are very few studies that directly test hypotheses for possible drivers of interspecies associations. Instead, most accounts of mixed-species groups provide descriptive information about encounters (e.g. Shane, 1995; Baraff and Asmutis-Silvia, 1998; Psarakos et al. 2003; Frantzis and Herzing, 2002). The few publications that have focused on possible functionality of these groups have found some plausible evidence for predator-avoidance strategies (e.g. Kiszka et al. 2011), and advantages to foraging and/or social elements (Stensland et al. 2003; Zaeschmar et al. 2014; Elliser and Herzing, 2016). In general, mixed-species groups involving social delphinids (e.g. false killer whales, bottlenose dolphin, Atlantic spotted dolphins; *Stenella frontalis* and striped dolphins; *Stenella coeruleoalba*) are not uncommon and may form stable cohorts in some cases (e.g. Frantzis and Herzing, 2002; Zaeschmar et al. 2014; Cords and Würsig, 2014; Elliser and Herzing, 2016). Pilot whales are social delphinids with a few studies reporting on their associations with other species (e.g. Kraus and Gahr, 1971; Polacheck, 1987; Baraff and Asmutis-Silvia, 1998; Zaeschmar, 2014). Associations between pilot whales and bottlenose dolphins in particular appear to be common in many regions (e.g. Faeroe Islands: Kraus and Gahr, 1971; the North Pacific: Norris and Prescott, 1961; north-eastern United States: Kenney, 1990; and Japan: Kasuya and Marsh, 1984). However, the possible functions of these groups are poorly understood and remain speculative (Connor et al. 2000).

New Zealand's waters are frequented by two forms of the bottlenose dolphin; coastal and oceanic with both genetically confirmed as *Tursiops truncatus* (Tezanos-Pinto et al. 2009; Baker et al. 2010). Individuals of the oceanic form are morphologically different to their coastal counterparts; generally, more robust with a prevalence of oval-shaped fresh wounds and/or scarring on the body, presumably inflicted by the

cookie cutter shark (Constantine, 2002; Dwyer and Visser, 2011). The New Zealand coastal form generally have fewer cookie cutter shark scars, primarily inhabit near-shore waters (Constantine, 2002; Dwyer et al. 2016) and are well-studied in comparison to the oceanic form, for which there is little information available. Pods of oceanic bottlenose dolphins have been documented in the deeper waters of the study area off north-eastern New Zealand (Chapter 2, Figure 2.2) for many years (Zaeschmar, 2014), and they are not considered part of the coastal population, although there may be some genetic mixing (Constantine, 2002; Tezanos-Pinto, 2009).

Previous work (Zaeschmar et al. 2014) has shown that long-finned pilot whales, oceanic bottlenose dolphins (hereafter referred to as bottlenose dolphins) and false killer whales off north-east New Zealand occasionally form mixed-species groups. In particular, false killer whales and bottlenose dolphins belong to a single large social network, which suggests that their associations are temporally stable (Zaeschmar et al. 2014; Zaeschmar, 2014). Improved foraging opportunities has been suggested as a plausible driver of their association, since both species have similar foraging ecologies, and social factors may also be important in maintaining the interspecific bonds (Zaeschmar et al. 2014). Mixed-species groups of pilot whales and bottlenose dolphins were commonly encountered during this study, while encounters also including other species were uncommon (Chapter 2; Section 2.3.1). Additionally, there were no observations of pilot whales and another species (false killer whales or southern right whale dolphins) in the absence of oceanic bottlenose dolphins. This suggests that long-term associations may exist between pilot whales and bottlenose dolphins in New Zealand, which warrants further investigation. This chapter aims to investigate the possible existence of an interspecific social network based on dyadic associations between oceanic bottlenose dolphins and long-finned pilot whales encountered off north-eastern New Zealand.

4.2 Methods

4.2.1 Surveys

Opportunistic data were collected between December 2003 and July 2019, following the methods described in Chapter 2, Section 2.2. Based on the results from Chapter 3 (Section 3.3.1), only data collected from surveys in north-eastern New Zealand were included in this analysis.

4.2.2 Encounters, groups and photo-identification

The pilot whale photo-ID data (Chapter 2) were refined to include only those encounters where both pilot whales and bottlenose dolphins were present simultaneously, forming mixed-species groups. The bottlenose dolphins in the encounters used for this study were confirmed as the oceanic ecotype by an experienced onboard observer. A mixed-species group was defined in a similar way to Chapter 2 (Section 2.2.2.2), where all individuals (of either species) within 1,000m of each other were considered to be part of the same group (Mahaffy et al. 2015).

All encounters had previously been assigned group photographic coverage scores for pilot whales (Chapter 3, Section 3.2.2), to meet the criteria for social association analyses. Therefore, only those mixed-species encounters that had already met the 0.5 score threshold were processed further.

Following the photo-ID and photographic data analyses outlined in Chapter 2 (Section 2.2.4), bottlenose dolphin photo-ID data from encounters were quality-controlled according to both image quality (Q1 - highest to Q4 - lowest) and dorsal fin distinctiveness (D1 - highest to D4 - lowest; Table 2.1). Primary features used to identify individual bottlenose dolphins included notches and nicks on, or adjacent to the leading and/or trailing edge of the dorsal fin (Würsig and Jefferson, 1990). Other secondary features used to aid in identification of individuals included the shape of the dorsal fin, tooth rake marks, other wounds, scratches or scars (Würsig and Jefferson, 1990).

To ensure consistency and comparability of results, a group photographic coverage score was then assigned to groups of bottlenose dolphins from each of the mixed-species encounters (see below; Chapter 3, Section 3.2.2). As with the pilot whales, only those bottlenose dolphin groups with a photographic coverage score of 0.5 or more were included in the social association analysis. Additionally, all of those individuals encountered on two or more occasions were included in the analysis as applying stricter criteria would have reduced the data to the point of being unusable (Chapter 3, Section 3.2.2). Group photographic coverage scores were calculated using the following equation, modified from Ottensmeyer and Whitehead (2003):

$$\frac{\text{Sum of Q1 and Q2 fin images from encounter}}{\text{Estimated group size}}$$

The best photograph of each bottlenose dolphin individual from each encounter was matched to the existing New Zealand Oceanic Bottlenose Dolphin Identification Catalogue (NZOBDC, Zaeschmar et al. unpubl. data) using the program finFindR (National Marine Mammal Foundation and Western EcoSystems Technology, 2018), to see if the individual had been previously sighted in New Zealand. The catalogue, initiated in 2005, includes the best quality photograph(s) of 478 identifiable dolphins. Dorsal fin images that were not matched correctly by finFindR were checked by manual matching and confirmed by two independent assessors. If both assessors were unsuccessful in matching the individual to the catalogue, it was determined to be a new individual and was assigned a temporary ID code for analysis purposes. Capture histories were created for each of the catalogued dolphins, as well as the newly added individuals. The presence of an individual on any given sampling day was denoted with a “1” and its absence with a “0”.

4.2.3 Data analysis

Unless stated otherwise, all social analyses of data collected between 2011 and 2019 were carried out using SOCPROG 2.9, a social association analysis software (Whitehead, 2009).

4.2.3.1 Dyadic association indices

To determine whether there were associations between individual pilot whales and bottlenose dolphins or not, all individuals of both species sighted on two or more occasions were included in a single data sheet and run in SOCPROG 2.9 as if they were one species. Following the methods for analysing social association outlined in Chapter 3 (Section 3.2.3), the strength of dyadic associations between pilot whales and bottlenose dolphins were measured using the half-weight index (HWI) (Cairns and Schwager, 1987; Whitehead, 2008a). Associations between individuals of both species were based on group membership for the analysis (Section 4.2.2) and a sampling period of four days was used to increase the power of permutation tests to detect preferred associations between individuals (Section 3.2.3; Whitehead, pers. comm. in Hamilton, 2013). The HWI can be calculated using the following equation:

$$\frac{X}{X+Y_a+\frac{1}{2}(Y_a+Y_b)}$$

Where, X is the number of sampling periods where individuals A and B are considered to be associated (observed together in the same group); Y_a is the number

of sampling periods where only individual A is seen (without B); Y_b is the number of sampling periods where only individual B is seen (without A); and Y_{ab} is the number of sampling periods where individuals A and B are both identified but are not associated (Cairns and Schwager, 1987).

To determine how accurately the true social structure of the population was modelled by the association data, a Pearson's correlation coefficient (r) between the true association indices (AIs) and the estimated AIs was calculated. As outlined previously (Chapter 3, Section 3.2.3), an r value of 1 indicates that the data provides an excellent representative pattern of social structure, 0.8 a good representation and approximately 0.4 a somewhat representative pattern (Whitehead, 2008a, b).

To measure the relative homogeneity of the dyadic associations within the social system (social differentiation, S), the estimated coefficient of variation (CV) of the true association indices was calculated (Whitehead, 2008a, b). Relatively homogenous societies are indicated by S values between 0.0 and 0.3, well-differentiated societies are indicated by S values greater than 0.5 and extremely differentiated societies are indicated by S values greater than 2.0 (Whitehead, 2008a, b).

Both the r and S values were estimated using the HWI of association (Section 3.2.3), with the standard error being calculated using the maximum likelihood method with 1,000 bootstrap replicates and a resolution of integration equal to 0.001 (default in SOCPROG). Thereafter, the estimated mean number of observed associations per dyad needed to form a somewhat representative view and highly representative view of the interspecies social structure was calculated (Chapter 3, Table 3.1).

4.2.4.2 Social network analysis and community division

A visual representation of the relationships between individuals based on estimated association indices was achieved by producing a dendrogram using an agglomerative hierarchical cluster analysis (Chapter 3, Section 3.2.3.2). The cophenetic correlation coefficient (CCC; Chapter 3, Section 3.2.3.2) was used to statistically test the validity of the dendrogram as a representation of the population social structure (Wittemyer et al. 2005; Whitehead 2008b). CCC values range from 0, indicating a poor correlation with the data, through to 1, indicating that the dendrogram correlates to the association matrix perfectly (Whitehead, 2008a, 2009). CCC values of 0.8 and above signify that the dendrogram is an acceptable representation of the association indices of the study population (Whitehead, 2008a, 2009).

To determine the relative social significance of each suggested cluster, modularity (Q) was used as a statistical measure to ascertain the level at which groups of individuals were considered distinct social entities (Newman 2004; Whitehead, 2008a). Values range from 0 to 1, with 0 indicating poor community division (randomly formed clusters) and 1 indicating closed communities or clusters with no shared associations (Newman, 2004; Whitehead, 2008a). Acceptable cluster divisions of the population are indicated by Q values of 0.3 and above (Newman, 2004). For detailed methods in calculating the Q value, see Chapter 3, Section 3.2.3.2.

Based on the social clusters delineated using the eigenvector-based method in SOCPROG 2.9, the associations among identified pilot whales and bottlenose dolphins were visualised using the social network visualisation tool, NetDraw 2.160 (Borgatti, 2002). A 'spring-embedded' layout was selected which places more connected nodes (individuals) in the centre of the diagram and those with fewer connections around the periphery.

4.2.3.3 Preferred or avoided associations

Modified permutation tests (Manly, 1995; Bejder et al. 1998; Whitehead, 2008a, b) tested the null hypothesis that all individuals in the study population associated with the same probability (i.e. there were no preferred or avoided associates of either species). Only two of the three available permutation tests were run in SOCPROG: 'permute groups within samples' and 'permute associations within samples' (Whitehead, 2009). For detailed information and methods regarding permutation testing, see Chapter 3, Section 3.2.3.3.

4.2.3.4 Temporal patterning of associations

To reveal the long-term nature of dyadic associations between individuals in the mixed-species groups, the temporal patterning of relationships was investigated (Hinde, 1976). The standardised lagged association rate (SLAR) and standardised null association rate (SNLAR) were determined for all well-marked pilot whales and bottlenose dolphins captured in good-quality images, regardless of how many times they had been sighted during the study period (Whitehead, 1995). Here, a sampling period of one day was used, to ensure that results were interpretable (Whitehead, pers. comm. in Hamilton, 2013). The standardised rate estimates the probability that if two individuals (A, B) are associated at a given time, following some chosen time lag (τ) a randomly-chosen associate of A will be B (Whitehead, 1995). In contrast, the

SNLAR is representative of the expected value if dyadic associations are random (i.e. no preferred associations).

The observed temporal association pattern for all individuals (the SLAR) and SNLAR were plotted against a time lag of 2000 days and standard errors were calculated using jack-knife methods (Efron and Gong, 1983). Thereafter, all four exponential mathematical models available in SOCPROG were run simultaneously, being fitted to the SLAR curve using maximum likelihood and binomial loss methods (Chapter 3, Section 3.2.3.4, Table 3.2) to investigate the types of associations within the population. Model selection was executed using the Quasi-Akaike Information Criteria (QAIC), as this approach corrects for over-dispersion in the count data and is considered more accurate when choosing the best fitting model i.e., the minimum QAIC (Whitehead, 2007; Whitehead, 2009). However, a difference of less than two units in the QAIC score between the best fit model and any other model(s) indicated support for the competing model, meaning that it should not be dismissed (Whitehead, 2007; Whitehead, 2008a). For detailed information and methods regarding temporal patterning of associations, SLAR, SNLAR and model selection, see Chapter 3, Section 3.2.3.4.

4.3 Results

4.3.1 Encounters, groups and photographic analyses

Overall, there were 81 long-finned pilot whale encounters recorded off eastern New Zealand during the 16-year study period between January 2003 and July 2019. A total of 145 distinguishable pilot whale individuals were identified during these encounters, establishing the NZLFPWIC (Chapter 2, Section 2.3.2). The majority (71.6%, $n = 58$) of the encounters involved mixed-species groups of pilot whales and oceanic bottlenose dolphins (Chapter 2, Section 2.3.1, Figure 2.6).

Pilot whale group-size data were available for 79 out of 81 encounters (98%). Of these 79 encounters, 16 (20%) were single-species groups of pilot whales and 57 (72.2%) were mixed-species groups of pilot whales and bottlenose dolphins. Pilot whale group size was significantly smaller (Mann – Whitney, $U = 192$, $p < 0.001$) during single-species encounters (median = 25, IQ = 20 – 34, range = 15 – 50; $n = 16$) compared to during mixed-species encounters (median = 50, IQ = 30 – 85, range = 3 – 200; $n = 57$). Group size data for bottlenose dolphins were available for 50 out

of 57 (87.7%) mixed-species encounters, with an average group size of 86 individuals (SE = 13, range = 15 – 500).

Ten mixed-species encounters (all in the Bay of Islands from 2011 – 2019) had a group photographic coverage score of 0.5 or higher for both species (Table 4.1) and met the criteria for inclusion in the social association analyses.

From these 10 encounters, there were 732 good quality (Q1 – 2) photographs of highly distinctive (D1 – 2) oceanic bottlenose dolphins in total. Of these, finFindR detected 149 individuals from the existing NZOBDC and missed 17 matches which were subsequently manually matched to the catalogue. There were 71 new individuals identified which were assigned temporary ID numbers for inclusion in further analyses. These new dolphins were provided to the NZOBDC curators for inclusion into the catalogue. Overall, there were 237 identifications of oceanic bottlenose dolphins over the eight-year period.

Thirty-nine (16.5%) identifiable bottlenose dolphins had repeat associations with 19 (13.1%) of the 145 pilot whales included in the photo-ID analysis. Of these, six (15.4%) bottlenose dolphins were re-encountered with at least one of the same six (31.6%) pilot whale individuals on two occasions in more than one year (Table 4.2). Furthermore, 84.6% of dolphins (n = 33) and 47.4% of whales (n = 9) were observed together on two or more occasions within the same year (Table 4.2).

Table 4.1 Independent group photographic coverage scores and number of identified pilot whales and bottlenose dolphin individuals from 10 mixed-species encounters off the Bay of Islands, between 3 January 2011 and 4 May 2019.

Date	Group photographic-coverage score		Number of identified pilot whales	Number of identified bottlenose dolphins
	Pilot whales	Bottlenose dolphins		
03 Jan 2011	1.83	0.50	8	14
30 Mar 2014	1.31	0.52	7	55
01 Apr 2014	1.29	0.51	14	31
08 Apr 2014	1.70	0.50	5	9
09 Apr 2014	0.89	0.63	6	42
03 May 2015	0.82	1.00	8	4
23 Mar 2017	0.69	0.51	3	10
26 Jan 2018	0.82	0.53	14	34
26 Mar 2018	1.14	1.04	7	7
04 May 2019	1.16	0.53	10	24

Table 4.2 Repeat associations between individual bottlenose dolphins and pilot whales off the Bay of Islands between 2011 and 2019. Individuals observed together on two or more occasions and during a) more than one year (grey background) or b) within a single season are shown. Note letters are temporary IDs of new individuals to be added to the New Zealand Oceanic Bottlenose Dolphin Catalogue.

Whale ID	Dolphin ID	3 Jan 11	30 Mar 14	1 Apr 14	8 Apr 14	9 Apr 14	26 Jan 18	26 Mar 18	04 May 19
NZGme	NZOTt								
006	220, 226, 239	x	x						
008	220, 226, 240	x	x						
019, 021	475		x						x
033, 037	469					x		x	
017, 018	045, 220, 474, 480, 498, 515		x	x		x			
017, 018	111, 226, 239, 466, 467, 470, 485, 488, 489, 491, 504, 508, 514, 518, 527		x	x					
017, 018	242, 271, 468, 495, 543		x			x			
017, 018	520, M			x		x			
020	045, 111, 220, 226, 239, 242, 271, 466, 467, 468, 470, 474, 480, 485, 488, 489, 491, 495, 498, 504, 508, 514, 515, 518, 520, 527, 543		x	x					
027	220, M			x	x				
033	220, 580, M, Q, P				x	x			
066, 109, 100, 115	AU						x	x	

4.3.2 Association indices

A total of 237 photo-identified adult bottlenose dolphins and 145 adult pilot whales were sighted at least once during the 2011-2019 study period. After the data set had been restricted to bottlenose dolphins and pilot whales seen on two or more occasions, and in encounters with a minimum photographic coverage score of 0.5, a total of 58 animals - 39 oceanic bottlenose and 19 pilot whales - were included in the analysis.

The data were not of sufficient quality to detect the true social system within the pilot whale and bottlenose dolphin mixed-species encounters, $r = 0.00$ (SE = 0.284). All subsequent analyses of social structure should be interpreted with an awareness of this limitation, but there were some interesting patterns for future exploration and worthy of presenting here. The social differentiation value ($S = 0.001$, SE = 0.255) indicated a relatively homogenous society, where dyadic association indices are similar across the multi-species study population. The mean number of observed associations per dyad was 0.70, while the mean number of observed associations per individual was 23.07, which indicates a scarcity of data. To achieve a meaningful r -value of 0.4 or above and enable the rejection of the null hypothesis (i.e. no preferred or avoided companionship), requires 76.19 observed associations per dyad and 2000 observed associations per individual, as well as a minimum S -value of 0.05.

The observed average HWI for well-marked pilot whales and bottlenose dolphins was 0.41 (SD = 0.16, range = 0.04 – 0.58), showing that the overall associations between individuals were low. Out of a possible 741 interspecific dyadic associations, 45.5% (337 dyads) showed no association (AI = 0.00) (Figure 4.1A, Figure 4.1B), which suggests a high degree of fission-fusion in mixed species groups of pilot whales and bottlenose dolphins. The average AI for non-zero entries (404 dyads) was 0.61 (range = 0.4 – 1) and the observed average maximum HWI was 0.97 (SD = 0.11, range = 0.50 – 1.00). This suggests that while the overall associations within the study population are low (Figure 4.1B), there are also some strong dyadic associations (Figure 4.1C). Individuals included in the analysis also differed in the number of other individuals with whom they were associated (mean = 24.51, SD = 9.00); membership ranged from 3.40 to 34.07, suggesting some differences in individual gregariousness (Figure 4.1D).

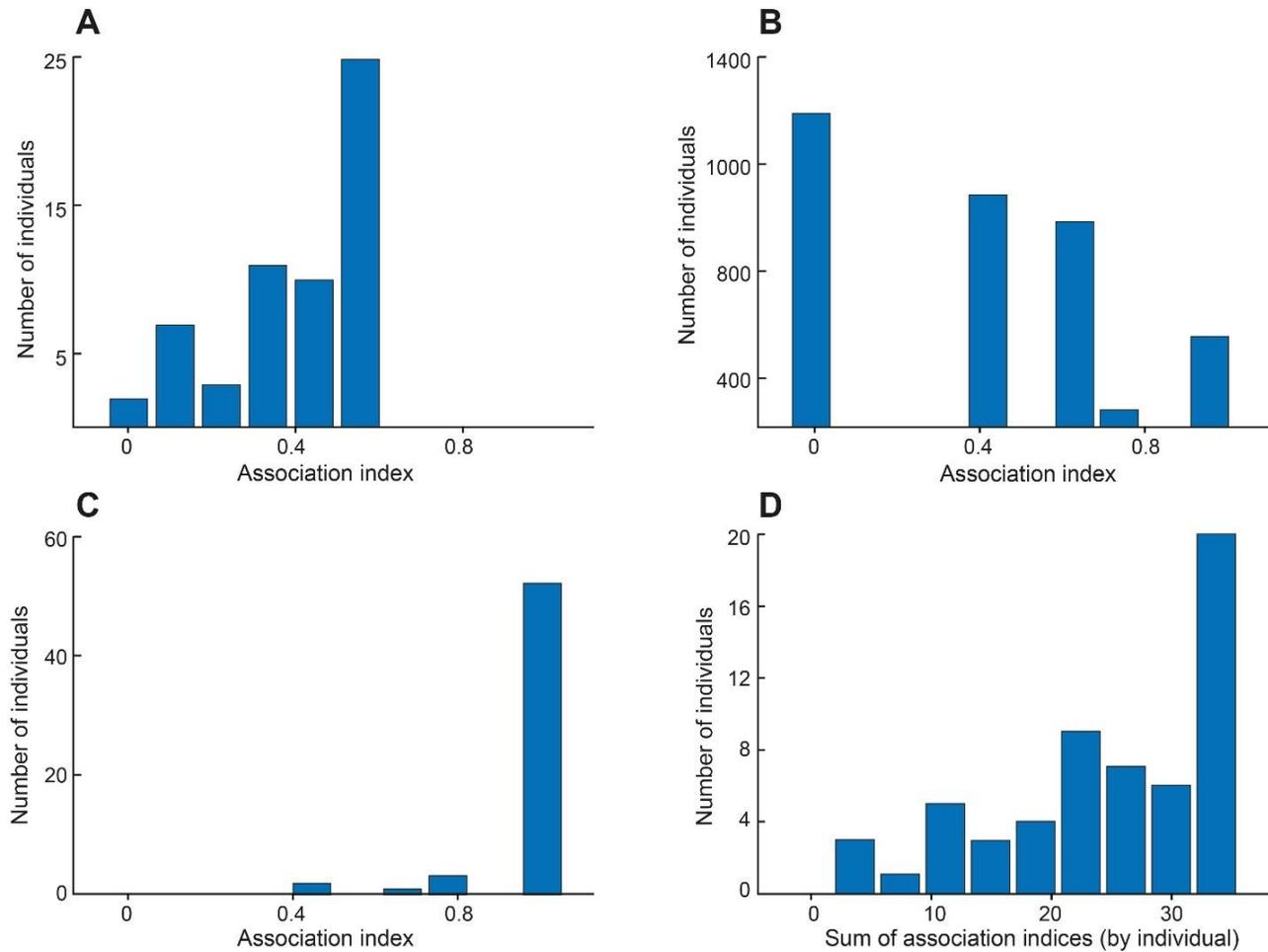


Figure 4.1 Distribution of the half-weight association indices for distinctive pilot whales and bottlenose dolphins encountered on at least two occasions off the Bay of Islands between 2011 and 2019 (n = 58). Distribution of A) mean association indices by individual, B) overall association indices for all individuals, C) maximum association indices by individual and D) sum of association indices by individual, including diagonal elements. Note the different scales on the x- and y-axes.

4.3.3 Social network analysis and community division

There was a high correlation between the actual dyadic AIs in the association matrix and the levels of clustering in the HWI dendrogram (CCC = 0.819), indicating an effective representation of population social structure (Figure 4.2). However, neither the hierarchical cluster analysis nor the social network analysis supported the division of the study population into multiple clusters (maximum modularity-G using cluster analysis: $Q = 0.138$, $AI = 0.276$ and $Q = 0.187$ respectively). Neither of the Q values meet the threshold of 0.3 (Newman, 2004), therefore indicating that within-cluster associations are not much higher than would be expected in a society of random associates. Hence, the following results should be interpreted with caution as they may not reflect the true clustering patterns of mixed-species groups of pilot whales and bottlenose dolphins.

Hierarchical cluster analysis resulted in the division of the study population into four clusters of variable size and association strength (Figure 4.2). Community division using Newman's (2006) eigenvector-based method also resulted in four clusters, with cluster membership ranging from 2 to 24 animals (Figure 4.3). Visualisation of the social clusters (NetDraw 2.158; Borgatti, 2002), revealed that all 58 individuals included in the analysis are linked by varying levels of association in one large, interspecies social network (Figure 4.3).

Overall, both the HWI dendrogram (Figure 4.2) and the social network analysis (Figure 4.3) represent similar social structures. For the hierarchical cluster analysis, the levels of association of individuals within clusters (mean $AI = 0.68$, $SD = 0.13$, range = 0.57 – 1.00) were significantly higher (Mantel permutation test t -value = 11.39, $p = 1.00$) than those between clusters (mean $AI = 0.17$, $SD = 0.10$, range = 0.00 – 0.28), indicating that the divisions within the study population determined by maximising modularity were supported. Similarly, for the social network analysis, the levels of association of individuals within clusters (mean $AI = 0.73$, $SD = 0.16$, range = 0.55 – 0.87) were significantly higher (Mantel permutation test t -value = 20.67, $p = 1.00$) than those between clusters (mean $AI = 0.28$, $SD = 0.14$, range = 0.00 – 0.47). Both methods produced large, positive matrix correlation coefficients of 0.72 and 0.62 respectively, which further supported this conclusion.

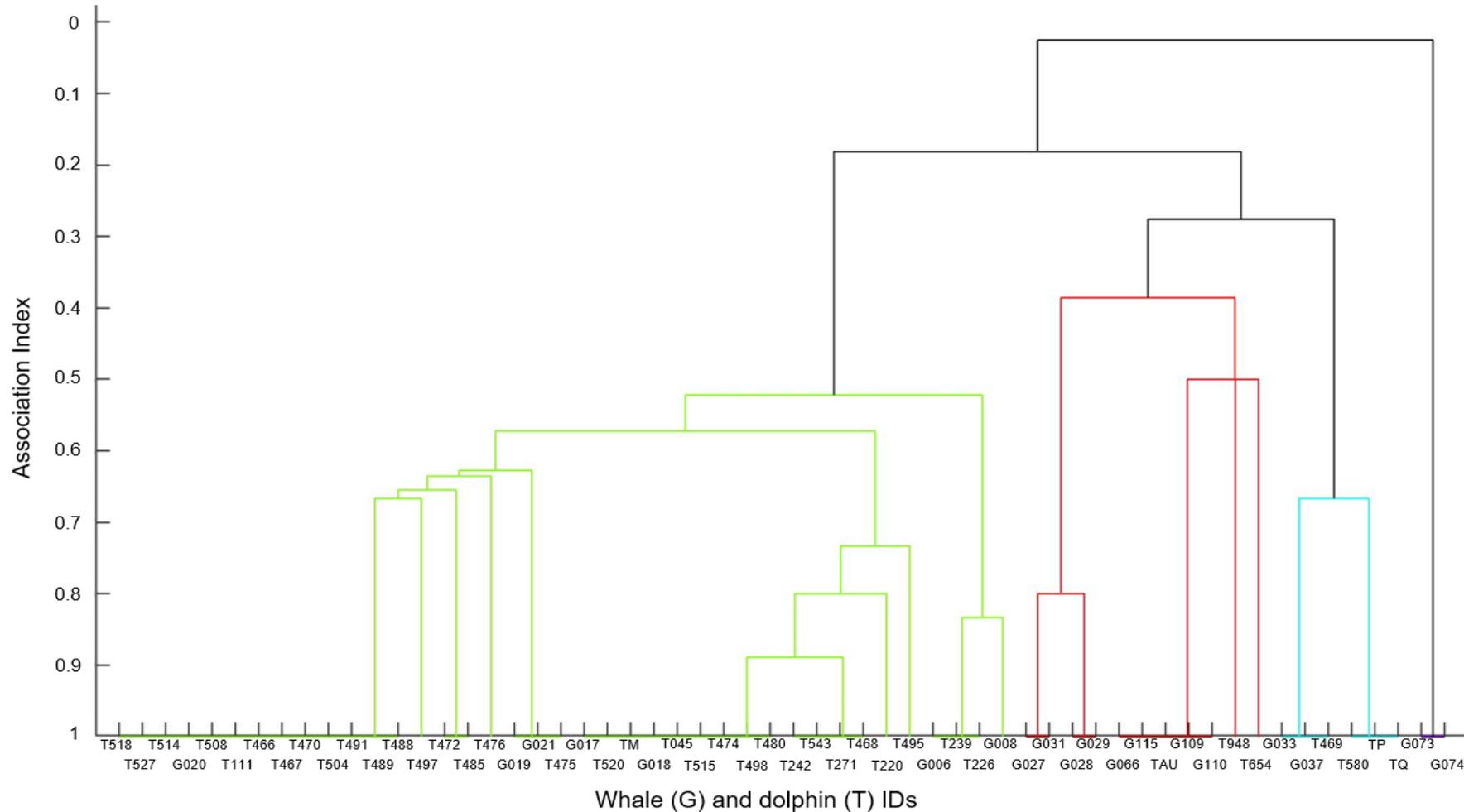


Figure 4.2 Half-weight index dendrogram drawn based on an average-linkage hierarchical cluster analysis showing associations between 19 individual pilot whales (denoted with ‘G’) and 39 individual bottlenose dolphins (denoted with ‘T’). Individual ID numbers are staggered on the Y-axis for ease of reading. The dashed line indicates the point at which clusters were delineated using modularity- G.

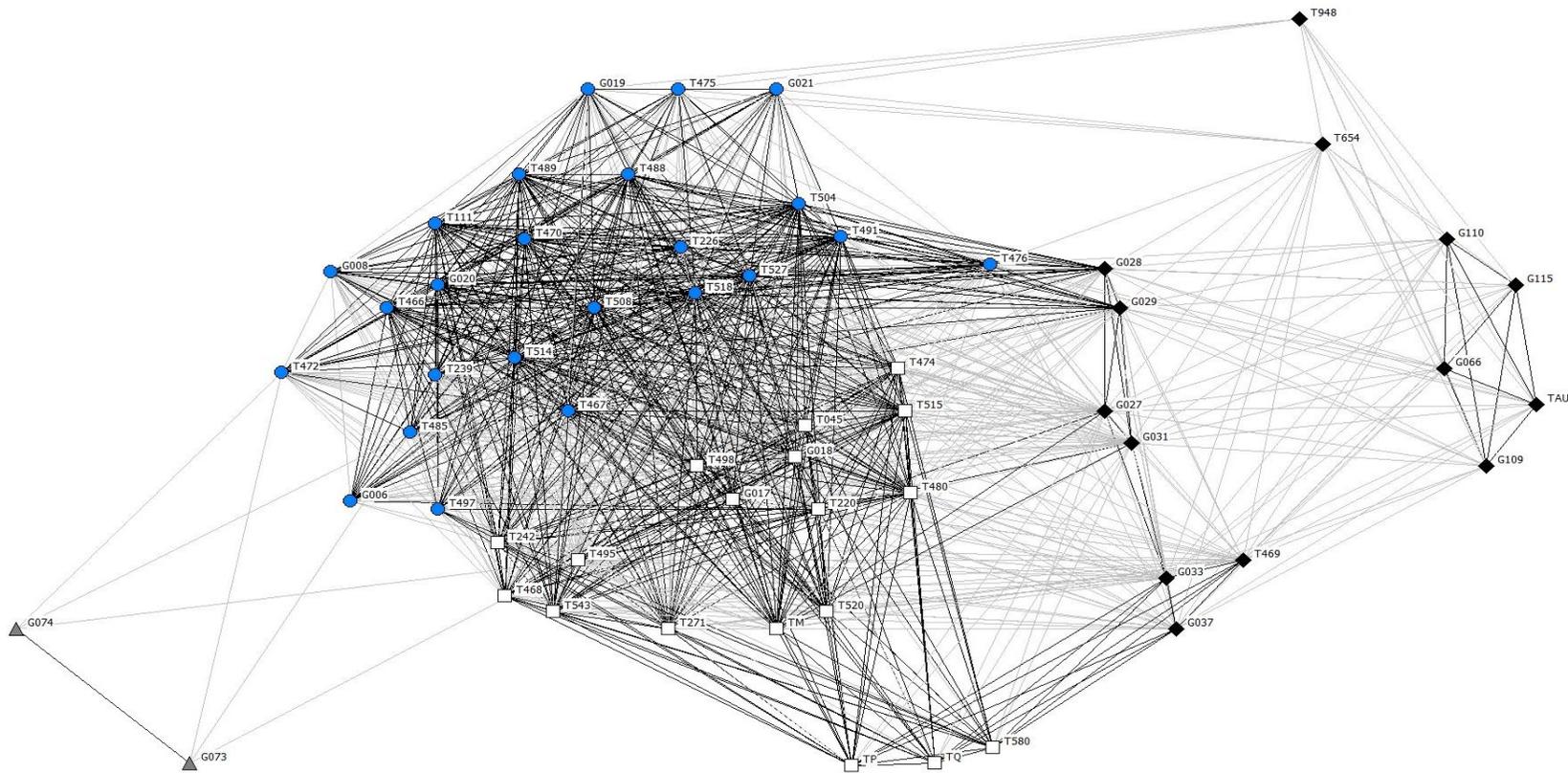


Figure 4.3 Social network diagram showing the associations between 27 individual pilot whales and 45 individual bottlenose dolphins off the Bay of Islands. The nodes in the network represent individual pilot whales (denoted by 'G') and bottlenose dolphins (denoted by 'T'), with the colour and shape of the node representing membership to possible social clusters. Ties between nodes represent associations between dyads, where darker coloured ties indicate stronger HWI associations. Ties where the HWI was less than 0.61 (the average HWI for non-zero entries in association matrix) are coloured grey and those above this value are black. A spring-embedding algorithm with Gower scaling in NetDraw 2.158 (Borgatti, 2002) was used to determine the layout of the network, plotted with geodesic distances.

4.3.4 Preferred or avoided associations

Associations between pilot whales and bottlenose dolphin individuals were random for both short-term and long-term companionship (Table 4.3). Results from both permutation tests suggest that long-term preferential associations between individuals do not exist (Table 4.3). There was no difference in the proportion of non-zero AIs in the real data compared to the permuted data for both tests, which indicated that there was no evidence of long-term avoidance of individuals (Table 4.3). Additionally, for groups permuted within samples, the similar values of the observed and permuted means of the AIs indicated that there are no short-term preferential associations between individuals (Table 4.3). Individuals did not have significant differences in gregariousness ($p = 0.90$). P - values stabilised at 60,000 random permutations for both permutation tests, with 1,000 trial flips per permutation.

There were no interspecies dyads that showed a significantly high AI ($p > 0.95$). Inspection of the association matrix for all 58 individuals (19 pilot whales and 39 bottlenose dolphins) revealed 46 dyads (out of a possible 741, 6.2%) with AIs greater than twice the overall mean HWI (AI = 0.41), however none of these were considered as significant and were therefore not reliable. This indicates that the large majority of the population can be considered “acquaintances”, having dyadic association indices of less than twice the population mean.

Table 4.3 Tests for non-random associations among 27 individual pilot whales and 45 individual bottlenose dolphins captured off the Bay of Islands between 2011 and 2019. Permutation tests in SOCPROG 2.9 were used to test for short-term (indicated by asterisk) and long-term preferred or avoided associations and for differences in individual gregariousness. *P*-values ≥ 0.95 are considered significant. HWI = Half-weight Index; AI = Association index; NA = Not applicable; SD = Standard deviation; CV = Coefficient of variation; Prop. = Proportion.

	Permute groups within samples (short-term* and long-term test)			Permute associations within samples (long-term test)		
	Observed	Permuted	<i>p</i> - value	Observed	Permuted	<i>p</i> - value
Mean AI HWI*	0.3199	0.3194	0.2203	NA	NA	NA
SD of HWI	0.3522	0.3501	0.8907	0.3522	0.3517	0.7921
CV of HWI	1.1011	1.0962	0.7993	1.1011	1.0993	0.8032
Prop. Non-zero of HWI	0.4865	0.4879	0.7156	0.4865	0.4877	0.8656
SD of typical group size	9.5477	9.4048	0.9014	NA	NA	NA

4.3.5 Temporal patterning of associations

The SLAR for all 382 individually identified pilot whales ($n = 145$) and bottlenose dolphins ($n = 237$) remained above the NSLAR only very briefly between time lags of 50 to 75 days, and thereafter dropped below the NSLAR and continued to decline to zero before day 500 (Appendix 7). This indicated that the data for the dyadic associations between species was not sufficient to use in any further analyses and modelling of the SLAR, as it would not provide meaningful results. The graphed SLAR, NSLAR and fitted models can be found in Appendices 7 and 8 respectively.

4.4 Discussion

In this chapter there is an assessment of possible long-term interspecific social associations between long-finned pilot whales and bottlenose dolphins off the Bay of Islands, north-east New Zealand. The extensive analysis produced limited results, preventing a comprehensive evaluation of the true social structure of mixed-species groups. While it appears that individuals of both species constitute a single, large social network of dyads with varying levels of association, the social clusters delineated during the analysis are likely not an accurate reflection of these complex relationships. While there were no statistically significant dyadic associations, an analysis of individual sightings history suggests the existence of some non-random long- and short-term associations between pilot whales and bottlenose dolphins making this an interesting investigation for future studies.

4.4.1 Interspecific associations and group structure

Pilot whale group sizes were significantly larger in mixed-species associations with oceanic bottlenose dolphins compared to single-species encounters. Although data from single-species encounters of bottlenose dolphins were not available, reports from at-sea observations suggest that group size for this species may also be considerably larger during these mixed-species associations. This is interesting as it suggests that either one or both species is likely benefitting from forming associations with heterospecific individuals. As outlined below (Section 4.4.2), it is hypothesised that both pilot whales and bottlenose dolphins may obtain increased foraging advantages and/or protection from potential predators when forming large, mixed-species groups. However, further research is needed to determine whether these are factors driving the observed interspecific associations.

The average group size of 86 individuals for oceanic bottlenose dolphins encountered off the Bay of Islands is considerably larger than that of the coastal population of this species in the same region, where groups include around 25 individuals on average (Hamilton, 2013; Hartel et al. 2014). This may reflect the diverse ecological factors influencing these populations as a result of their different habitats, with the larger size of oceanic groups being driven by a combination of increased predation pressure and the uneven distribution of prey in deeper, offshore waters (Scott and Chivers, 1990; Gygax, 2002).

The high frequency of associations of bottlenose dolphins and pilot whales, including repeat associations between particular individuals of both species spanning more than five years, suggests that these associations are likely not random. However, there was no evidence to suggest the presence of any strong, long- or short-term interspecific dyadic associations. The low mean AI for all individuals in the interspecies association matrix suggested that members of mixed-species groups exhibit fission-fusion dynamics, associating over short time scales. Based on notes from field observations, when pilot whales were members of mixed-species groups, they tended to maintain tight cohesiveness with sub-groups of conspecifics throughout encounters (Zaeschar, unpubl. data). Bottlenose dolphin individuals were more fluid in their associations with conspecifics and pilot whale group members, with frequent fission-fusion occurring, including movement between sub-groups of pilot whales that could be spread out over a few thousand metres (Zaeschar, unpubl. data).

These observations are consistent with the respective social structures reported for each species. Coastal bottlenose dolphin fission-fusion societies are highly complex and are well-documented (e.g. Shane et al. 1986; Connor et al. 2000). In contrast, the relatively few studies of long-finned pilot whale social structure suggest a complex hierarchical society, where smaller groups are more cohesive and temporally stable, becoming less so as they increase in size (Ottensmeyer and Whitehead, 2003; de Stephanis et al. 2008c, Augusto et al. 2017a; Chapter 3 of this study).

The mean maximum AI for all individuals was high enough to suggest that there may also be some longer-term interspecific dyadic associations between individuals of the two species. Inspection of the sightings history of each individual included in the analysis supported this, with particular individual pilot whales and bottlenose dolphins encountered together on multiple occasions, possibly indicating non-random dyadic associations. Additionally, social network analysis indicated that all identified members of mixed-species groups are linked by association in one large social network. While some clustering was apparent, this was likely the result of incomplete sampling (Section 4.4.3).

At this stage, it remains unclear whether the general patterns of association between pilot whales and bottlenose dolphins are non-random, as there are other possibilities for repeated encounters with mixed-species groups that should be acknowledged. For example, short-term associations in particular may be the result of both species

travelling through the same area at the same time, seeking a common food resource (Stensland et al. 2003; Cords and Würsig, 2014). It is also possible that the individuals included in the analysis are part of a much broader meta-group, including members of both species, and that the application of quality-control criteria (Section 4.2.3) has caused them to appear more closely associated than they are in reality. More systematic data collection in future surveys would help to elucidate the true patterns of these interspecific associations.

Importantly, some of the same bottlenose dolphin individuals included in this study are part of a large, mixed-species social network with false killer whales in the Bay of Islands area (and elsewhere in north-eastern New Zealand), including persistent dyadic associations (Zaeschmar, 2014; Zaeschmar et al. 2014). On occasion, mixed species groups of false killer whales, bottlenose dolphins and long-finned pilot whales are encountered in north-eastern New Zealand (Zaeschmar, 2014; Figure 2.6). During these encounters, pilot whales only remain associated with the other two species for relatively short periods of time (Zaeschmar, unpubl. data), while mixed-species groups of just pilot whales and bottlenose dolphins may remain associated for entire days (Zaeschmar, unpubl. data). Furthermore, false killer whales and pilot whales have not been observed in mixed species groups together without bottlenose dolphins present (Zaeschmar, unpubl. data). Overall, this evidence suggests that there are likely quite complex processes underlying these multi-species associations, with bottlenose dolphin individuals possibly serving as intermediaries, facilitating interactions between the two larger delphinid species. However, what those underlying processes may be remains speculative, suggesting that further research should be undertaken to better understand these interspecific associations.

4.4.2 Possible drivers of mixed-species groups

While mixed-species associations are common amongst cetacean species (e.g. Jefferson et al. 2006; Smultea et al. 2014; Koper and Plön, 2016), most of these appear to be ephemeral (e.g. Herzing and Johnson, 1997; Psarakos et al. 2003; Kiszka et al. 2011). There are only a few examples of long-term interspecific associations between individuals of different cetacean species (Cords and Würsig, 2014), with the majority of those records pertaining to singletons of one species associating with groups of another species (e.g. Bearzi, 1996; Baraff and Asmutis-Silvia, 1998). There are even fewer examples of studies investigating the possible drivers behind such temporally stable associations, although mixed-species groups

are more likely to form between individuals of species that are inherently gregarious (Stensland et al. 2003).

The relatively high frequency of association between pilot whales and bottlenose dolphins raises interesting questions as to its possible function(s). Both long- and short-finned pilot whales associate with other delphinids (e.g. Polacheck, 1987; Baraff and Asmutis-Silvia, 1998; Zaeschmar, 2014), in particular with the bottlenose dolphin (e.g. Kraus and Gahr, 1971; Norris and Prescott, 1961; Kenney, 1990; Kasuya and Marsh, 1984). However, the possible functions of these interspecific associations remain largely un-investigated, but may include increased predator avoidance and/or improved foraging success (Norris and Schilt, 1988; Stensland et al. 2003; Cords and Würsig, 2014), with social factors possibly playing a role as well (Norris and Schilt, 1988; Kutsukake, 2009).

Mixed-species groups may experience increased foraging benefits, especially in open ocean habitats (Norris and Schilt, 1988) where prey is abundant but uneven in its occurrence. Detection of food resources may therefore be easier with the formation of mixed-species associations. This has been suggested as a likely driver of associations between smaller delphinid species (e.g. Quéroil et al. 2008) as well as larger ones (e.g. Zaeschmar et al. 2013). Although no observations of feeding were made during this study, it is possible that mixed-species groups of pilot whales and bottlenose dolphins are driven by improved foraging opportunities, for either one or both species. While pilot whales in New Zealand feed almost exclusively on cephalopods (Beatson and O'Shea, 2009), bottlenose dolphins are known to be more generalist predators with prey preferences that vary widely both within and between habitats as well as between populations (e.g. Rossbach and Herzing, 1999; Lewis and Schroeder, 2003; Gazda et al. 2005; Hastie et al. 2006; Sargeant and Mann, 2009). Both species of pilot whale are able to forage at variable depths depending on the distribution of their preferred prey species (Baird et al. 2002; de Stephanis et al. 2008b; Quick et al. 2017; Owen et al. 2019). Although not much is known about the feeding patterns of offshore bottlenose dolphins, evidence suggests that their diet may include a large proportion of pelagic cephalopods (e.g. Mead and Potter, 1995; Barros et al. 2000) and may be able to conduct relatively long, deep foraging dives (e.g. Klatsky et al. 2007). Therefore, the foraging ecologies of these two delphinid species likely overlap. It is not known whether intraspecific cooperative hunting takes place in pilot whale groups, but it is possible that the dolphins may either hunt alongside (and possibly cooperatively with) the pilot whales (Kraus and Gahr, 1971) or

take advantage of a known food source by scavenging from pilot whale scraps (as suggested for bottlenose dolphins associating with false killer whales, Zaeschmar et al. 2014).

Mixed-species groups may also provide anti-predatory advantages, simultaneously decreasing the likelihood of individual predation and increasing the chances of predator detection (Hamilton, 1971; Krause and Ruxton, 2002). While there were no observed threats of predation for either species during the study period, there have been previous accounts of bottlenose dolphins and false killer whales in New Zealand being predated on by killer whales (Visser et al. 2010), so they could pose a threat to pilot whales. Pilot whales in the Norwegian Sea are attracted to killer whale calls (Curé et al. 2012), although the study could not conclude whether their response constituted a mobbing strategy to chase away conspecifics or a reaction to a potential food source. Regardless, it seems that if there is an anti-predatory advantage to the mixed-species groups observed here, it may benefit bottlenose dolphins.

Social factors have been suggested as another possible function of interspecies associations. Temporally stable associations between singletons of one species and groups of another (e.g. Bearzi, 1996; Baraff and Asmutis-Silvia, 1998) are mostly commonly attributed to social factors, possibly driven by a lack of conspecific social interaction for the singleton species (e.g. Frantzis and Herzing, 2002). In some cases, repeated physical contact between individuals of both species takes place (e.g. Stensland et al. 1998; Zaeschmar et al. 2014), likely indicating strong social bonds. While this behaviour was infrequently observed during the current study, it was limited to surface observations. Hence, future studies could benefit from having underwater footage to accurately confirm how often close physical contact occurs in mixed-species groups. Importantly, it has also been suggested that sociality may be a function of interspecific group formation, rather than a direct cause (Zaeschmar, 2014), based on the observation that many mixed-species groups are short-lived.

4.4.3 Study limitations

Similar to Chapter 3, the opportunistic nature of the data and conservative approach of applying strict quality-control criteria excluded a large majority of encounters. Applying these restrictions resulted in only encounters from offshore Bay of Islands being used in the analysis of interspecies social associations, which means that the any results may not be reflective of all mixed-species groups of bottlenose dolphins and pilot whales that occur in New Zealand waters. These two species were observed

together in Kaikōura (Figure 2.6). Using only well-marked individuals in the analysis further limited the useable subset of data, excluding all immature animals (neonates, calves, juveniles) and all poorly marked individuals. As a result, the conclusions that can be drawn from the analysis presented here are limited. While the inclusion of all individuals of both species in one large social network may be somewhat accurate, the social clusters presented here are not supported by the analysis. The small data set also considerably limited the analysis of temporal stability of the interspecies social associations. Therefore, most of the results presented here cannot be used to make general inferences about particular aspects of the social structure of mixed species groups. Given these limitations, the current study is best considered a preliminary investigation into interspecies associations between pilot whales and bottlenose dolphins in north-eastern New Zealand, providing baseline data and a solid foundation on which to build when undertaking more dedicated data collection in the future.

4.4.4 Summary

While there was no significant evidence supporting the existence of temporally stable interspecific associations, the observed associations between long-finned pilot whales and bottlenose dolphins off the Bay of Islands may not be occurring at random. Some individuals of both species have been shown to associate repeatedly with one another, on variable temporal scales of days to months to years, a pattern which would likely be extended to include other individuals in the population if more robust data were available. In general, the current analysis of mixed-group social structure was unsuccessful due to the limited sampled size, which highlights the importance of, and need for, dedicated, long-term behavioural data collection in the future.

Chapter 5: General discussion

5.1 Main aims

The overarching aims of this thesis were to assess the occurrence of free-ranging long-finned pilot whales off eastern New Zealand, to describe the social structure of individuals encountered off north-eastern New Zealand and to investigate the interspecific associations between long-finned pilot whales and oceanic bottlenose dolphins encountered off the Bay of Islands. This is the first study on living pilot whales in New Zealand waters and one of very few studies on the species in the southern hemisphere; and so, it advances our knowledge of a species best known for its mass-stranding events rather than its place in our oceans.

5.2 Value of opportunistic data sets

This research was founded on a large, opportunistically-collected data set. For the most part, the data, which included a considerable number of photographs, were collected by an experienced researcher. However, a lot of the information was sourced from different tour boat operators, taking advantage of information collected by experienced tour guides from several locations around New Zealand. Thus, the data do not come from a dedicated study with a single research purpose.

Nevertheless, this research has been able to reveal novel insights about long-finned pilot whales in New Zealand waters. This research serves as an important reminder that these large data sets which have been collected in the course of other work should not be left unexplored, as they have the potential to provide valuable information.

Pilot whale strandings occur globally, often with a large number of animals, which is usually attributed to their gregarious nature. Stranding records from New Zealand show that cumulatively, *Globicephala* spp. represent the highest total number of stranded individuals compared to any other cetacean species found in these waters (Department of Conservation, 2019). Everything that we know about pilot whales in New Zealand has come from studies of dead whales involved in stranding events (Brabyn, 1991; Beatson and O'Shea, 2009; Oremus et al. 2009; Oremus et al. 2013; Betty et al. 2019; Betty et al. 2020). However, there remains a paucity of data about these animals when they are alive. Given the opportunity of a large, long-term data

set, the study presented here was warranted to enable a better understanding of pilot whales when they are not stranded on beaches around New Zealand.

5.3 Demographics, movement and group living

The global distribution of *Globicephala* spp. (Olson, 2018) indicates that they are a very successful cetacean. Generally considered to be pelagic delphinids, pilot whales are commonly encountered in deep offshore waters, near to or along continental shelves as well as in areas with relatively steep slopes (Abend and Smith, 1999; Lopez et al. 2003; Kiszka et al. 2007; de Stephanis et al. 2008a; Pierce et al. 2010; Silva et al. 2014; Abecassis et al. 2015; Fontaine et al. 2015). These patterns of occurrence were also observed for pilot whales in New Zealand, with the majority of encounters taking place in shallower (~100m) nearshore waters off the northeast coast, as well as in the deeper waters of the Kaikōura Canyon (Chapter 2). However, it must also be noted that the opportunistic nature of the data prevents this from being a comprehensive representation of pilot whale distribution in this region. The spatiotemporal distributions of pilot whales are thought to be influenced by prey availability (e.g. Cañadas and Sagarminaga, 2000; de Stephanis et al. 2008b; Alves et al. 2013; Alves et al. 2019b), since both species occupy the same ecological niche as predators within marine ecosystems, exploiting patchily distributed prey in deep sea habitats (e.g. Aguilar de Soto et al. 2008; Visser et al. 2014; Quick et al. 2017). The waters surrounding New Zealand are oceanographically diverse (Chiswell et al. 2015), with plenty of deep-sea habitat and areas of convergent currents available to serve as feeding areas for pilot whales. Although this study was not able to report on pilot whale feeding behaviour, it is presumed that the repeated occurrence of pilot whales in areas where prey abundance is thought to be high (Chapter 2), serves as an indicator that the animals are using these regions as foraging grounds. However, more research focused on pilot whale feeding and diving behaviour is needed to confirm this.

Long-finned pilot whales in New Zealand share many similarities with populations of pilot whales in the northern hemisphere. They have similar group sizes and similar temperature ranges, being observed in both warmer sub-tropical waters and cooler temperate waters (Cañadas and Sagarminaga, 2000; Ottensmeyer and Whitehead, 2003; de Stephanis et al. 2008a; Visser et al. 2014; Augusto et al. 2017a). Variations in group size and composition have a strong seasonal element for pilot whales, possibly linked to calving and mating processes, with larger groups including young

animals typically observed in the warmer months (de Stephanis et al. 2008c; Alves et al. 2013; Servidio, 2014; Hartny-Mills, 2015). While seasonal trends in group size could not be elucidated here, a high proportion of groups encountered in this study during the austral summer and autumn months included young animals (Chapter 2). In New Zealand, the presence of young calves in groups of long-finned pilot whales is expected to peak in the austral summer months (Betty, 2019), coinciding with a seasonal peak in mass stranding events (Betty et al. 2020). There may be a link between calving, strandings and seasonal inshore movements of pilot whales in New Zealand, as has been suggested for Gray's beaked whales (Thompson et al. 2013).

Betty (2019) hypothesised that groups with calves may not be able to undertake deeper dives to find prey, and may move into nearshore waters where they can still find abundant prey, but are less restricted by the limitations of calves. Pilot whales are highly social delphinids (e.g. Ottensmeyer and Whitehead, 2003; de Stephanis et al. 2008c; Alves et al. 2013; Mahaffy et al. 2015; Augusto et al. 2017a; Alves et al. 2019b), and live in hierarchically-structured, tight-knit groups of mixed age and sex classes (e.g. de Stephanis et al. 2008c; Oremus et al. 2013; Augusto et al. 2017a; Betty et al. 2020). Both male and female adult pilot whales display alloparental care in the form of escorting calves that are not their own (Augusto et al. 2017b). This may explain why entire groups could be moving into shallower waters during the austral summer and autumn months (Betty, 2019; Betty et al. 2020), rather than just females and young calves. At this stage, it is not known whether adult pilot whales babysit (Gordon, 1987) calves at the surface while mothers are foraging, a behaviour which is described in female sperm whales (Whitehead, 1996; Gero et al. 2009). Similar to pilot whales, sperm whales are deep-diving and socially complex cetaceans (Whitehead et al. 1991; Christal and Whitehead, 2001), so it is possible that babysitting behaviour does exist in pilot whales but has not yet been observed or reported.

The lack of obvious geographical barriers in the marine environment could theoretically facilitate interoceanic movement of wide-ranging cetaceans, but other boundaries such as thermal gradients or cultural knowledge may limit movements (e.g. Ramp et al. 2015; Brakes et al. 2019). Both species of pilot whale are generally considered to be nomadic within their particular geographical ranges (Olson, 2018), but there are some examples of resident or island-associated populations (de Stephanis et al. 2008c; Verborgh et al. 2009; Alves et al. 2015; Mahaffy et al. 2015; Alves et al. 2019b). Genetic evidence from mass-stranding events indicates regular

movement, and therefore mixing, of pilot whales throughout all New Zealand waters (Oremus et al. 2009; Oremus et al. 2013). However, there is also evidence to suggest that long-finned pilot whales in New Zealand are somewhat genetically distinct from other populations in the Tasman Sea (Oremus et al. 2009). Seeing as pilot whales in the Northern Hemisphere travel vast distances over relatively short time periods (e.g. Alves et al. 2019a), the possibility that pilot whales in New Zealand have more restricted movement is interesting. Considering the genetic evidence from strandings along with the low re-sight rate of individuals from the current study (Chapter 2), it is possible that some groups of pilot whales remain in these waters year-round, while others travel between ocean basins more regularly. This may be reflective of different “communities” of pilot whales, as outlined by Alves et al. (2013), with some being resident, some seasonally resident and other transient, but with associations occurring between all community types. As pilot whales are reported from other Australian and South Pacific regions, it would be interesting to identify animals from these waters to determine relatedness in the future.

Although this research focused primarily on pilot whales encountered off the east coast of the North Island, with some data from the east coast of the South Island, it is likely that the broad patterns related to group size (Chapter 2), group age composition (Chapter 2) and social structure (Chapter 3) are applicable to all pilot whales found in New Zealand waters. This would reflect the findings from studies of stranded pilot whales in New Zealand, which suggested a high degree of mixing of individuals in this population (Oremus et al. 2009) and concluded that mass-stranded groups are representative of multiple matrilineal units (Oremus et al. 2013), likely consisting of multiple social units or clusters. Additionally, stranding records indicate a year-round presence of pilot whales in New Zealand (Betty et al. 2020), however, patterns of residency and site fidelity are yet to be determined for these animals. Nevertheless, it seems plausible that the population of pilot whales in New Zealand is quite large and that different groups are moving around to exploit various parts of these highly productive waters.

New Zealand lies well-within the preferred temperature range for long-finned pilot whales (Olson, 2018), and so it is unsurprising that there is a regular presence of this species in our waters. However, there is a high likelihood that at least some individuals are also travelling to other temperate, sub-tropical and/or sub-Antarctic regions outside of our jurisdictional waters, although the details of these potential movement patterns remain unknown. Therefore, future studies should focus on

gaining an understanding of the genetic structure of populations in other parts of the southern hemisphere, to determine whether there is evidence of more wide-spread transfer of particular haplotypes (indicating mixing of individuals). Pilot whales can swim great distances over relatively short time scales (Alves et al. 2019a), so it is possible that some pilot whale groups in New Zealand are moving widely between ocean basins (e.g. Tasman Sea and South Pacific), as has been suggested for other pelagic species (e.g. Thompson et al. 2016).

5.4 Photo-identification and pilot whale research

Photo-ID methodology is valuable for gaining information about free-ranging cetaceans, however there are also associated limitations. Pilot whales in New Zealand are not very well-marked animals, which caused some challenges throughout this research. It was necessary to apply reasonably strict quality-control criteria to the raw data set, to ensure that only robust data of a high standard were used to carry out further analyses. However, these criteria were similar to those used in many other studies of social delphinids. While the observed mark rate for this population was certainly low, there are a few instances of similar mark rates in other delphinids, for example, Hector's dolphins (*Cephalorhynchus hectori*; Gormley et al. 2005) and Heaviside's dolphins (*Cephalorhynchus heavisidii*; Elwen et al. 2009), considerably smaller species. Although there is a perception that delphinids should have extremely high mark rates, this is likely based on coastal bottlenose dolphin studies (e.g. Nicholson et al. 2012; Wells, 2014). Instead, it seems more common for delphinids to have intermediate mark rates, roughly between 30 and 70% (e.g. Baird et al. 2008a; McSweeney et al. 2009; Verborgh et al. 2009; Alves et al. 2013; Tyne et al. 2014; Hupman et al. 2018). Overall, applying the necessary restrictions to the data significantly narrowed down the usable data set. Out of 53,857 photographs, there were just 145 identified individuals, sighted a total of 206 times.

Reflecting on this study, it is clear that to address particular research questions comprehensively, large amounts of data and substantial fieldwork are required. To gain a better understanding of social structure, group composition and site fidelity of free-ranging pilot whales in New Zealand, future work should aim to carefully design longitudinal studies and standardise data collection methods. This should hopefully improve the quality data of the data collected and therefore its usefulness to the research process.

5.5 Social structure

Although there were some limitations, it was clear that pilot whales in New Zealand have a complex social structure. We now know that within the large groups observed at sea, there are small, socially cohesive units of individuals (Chapter 3) similar to overseas studies (e.g. Ottensmeyer and Whitehead, 2003; de Stephanis 2008c; Alves et al. 2013; Visser, 2014; Augusto et al. 2017a; Alves et al. 2019b). Additionally, social bonds appear to be strongest within social units, but relatively stable associations are also formed between different social units, representing social clusters. Larger groups of pilot whales display fission-fusion dynamics over short temporal scales, possibly representing breeding aggregations of multiple, unrelated social units (although this has not been confirmed). This appears to be the general pattern of social structure amongst pilot whale populations on a global scale (Chapter 3). Although pilot whales in New Zealand are poorly marked animals, through the use of a longitudinal data set it was still possible to see the potential of some interesting patterns overall. These will almost certainly improve as more data are collected via directed research surveys, which would give us a clearer idea of what the wider social network looks like for these animals.

While it has not been confirmed for free-ranging pilot whales in New Zealand, genetic studies from the northern hemisphere have shown that cohesive, temporally stable social units usually consist of closely related individuals with larger groups representing multiple social units (e.g. de Stephanis et al. 2008c; Alves et al. 2013). This reflects what we see from genetic studies of stranded pilot whales in New Zealand which have shown that some individuals in these larger stranded groups are related, but there are also many unrelated individuals present (Oremus et al. 2013). It is possible then, that these strandings do not represent extraordinary events in terms of the genetic make-up of pilot whale cohorts. Instead, it may be that pilot whales in New Zealand are mixing with groups of unrelated individuals on a relatively frequent basis, unlike what has been suggested for pilot whales in the Faeroe Islands (Amos et al. 1991). As such, future studies of free-ranging pilot whales in New Zealand should focus on gaining information about the levels of individual genetic relatedness both within and between different groups.

The diverse terminology used in the existing literature to describe social cohorts of pilot whales made it challenging to assign names to the different social groups delineated during this study. For example, “clan”, “unit”, “line unit”, “cluster”, “pod”,

“community” and “group” have all been used when referring to pilot whale social cohorts, with the same label sometimes being assigned to two different hierarchical levels of societal grouping (e.g. Ottensmeyer and Whitehead, 2003; de Stephanis 2008c; Alves et al. 2013; Servidio, 2014; Visser, 2014; Hartny-Mills, 2015; Mahaffy et al. 2015; Augusto et al. 2017a; Alves et al. 2019b). Considering that there has been an increase in studies of pilot whale social structure in recent years, it may be timely (and certainly useful) to decide on standardised definitions for these various structural units. A tightening up of terminology and streamlining of associated language may help advance the field of pilot whale research as it has done for populations of bottlenose dolphins (Wells et al. 1987; Connor et al. 2000) and sperm whales (Whitehead and Weilgart, 1990; Whitehead et al. 1991).

As previously outlined, during the course of this study, some data were collected about observations of smaller sub-groups of individuals within larger pilot whale groups (Chapter 2). These data were not comprehensively collected for all encounters, but results have indicated that sub-group membership is likely a key piece of information that would greatly improve our understanding of pilot whale social structure in New Zealand. Although the large definition of group membership used in this study is acceptable (i.e. all animals encountered on a single day are considered to be part of one group), a finer-scale analysis would be very useful. This would help to ascertain sub-group membership and to determine how individuals are moving between different sub-groups. When considering patterns of association in northern hemisphere pilot whale populations, it seems very likely that these smaller sub-groups are more representative of temporally stable social units or clusters of animals (e.g. Ottensmeyer and Whitehead, 2003; de Stephanis 2008c; Alves et al. 2013; Servidio, 2014; Visser, 2014; Hartny-Mills, 2015; Mahaffy et al. 2015; Augusto et al. 2017a; Alves et al. 2019b). Therefore, individuals within these smaller sub-groups would be ideal candidates for genetic analysis, to reveal any patterns of relatedness. Results from genetic studies could then be compared to our existing knowledge from mass stranding events, to see whether free-ranging groups mirror the patterns of relatedness observed in stranded individuals. Additionally, it is highly recommended that future studies endeavour to collect good photographs of all individuals within entire groups, while also focusing on achieving photographic coverage of any sub-groups. Acquiring this information would be a very valuable step forward in developing our understanding of pilot whale social structure in New Zealand.

5.6 Interspecific associations

Another particularly interesting aspect of this study was the high proportion of encounters that involved mixed species groups of pilot whales and oceanic bottlenose dolphins, off both the north-eastern coast of the North Island and the Kaikōura coast. At this stage, it remains unclear whether these associations persist as a result of both species foraging for common prey with large spatiotemporal overlap in their ranges, or whether there are social factors driving group formation and stable bonds between species. The preferred habitat of pilot whales includes temperate and sub-tropical waters such as those found around New Zealand (Olson, 2018). Although little is known about the movements of oceanic bottlenose dolphin populations in New Zealand waters, they appear to be widely distributed throughout the Pacific (e.g. Scott and Chivers, 1990; Sanino and Van Waerebeek, 2008). Therefore, it seems that mixed-species groups may not be following the warm waters specifically, but instead are frequenting areas of high productivity, which may be seasonally driven, however this remains speculative. Overall, it would be very beneficial if future studies focused on collecting robust photographic data of individuals from both species when coming across these mixed-species groups. This would help us to determine whether there are social associations between particular pilot whales and bottlenose dolphins that are temporally stable.

Mixed-species associations of pilot whales and bottlenose dolphins also included groups of other highly social, pelagic delphinid species on occasion. False killer whales were observed during encounters off the north eastern North Island and southern right whale dolphins during encounters off the Kaikōura coast. Such multi-species aggregations are not uncommon in cetaceans, with many of examples in the literature from around the world (e.g. Shane, 1995; Baraff and Asmutis-Silvia, 1998; Psarakos et al. 2003; Frantzi and Herzing, 2002; Elliser and Herzing, 2016) and in New Zealand (e.g. Markowitz, 2005; Stockin et al. 2008; Zaeschmar et al. 2014). While there have been reports of interspecific mating behaviour (e.g. Herzing et al. 2003; Psarakos et al. 2003), only relatively few observations of hybrids have been reported (e.g. Reyes, 1996; Yadzi, 2002; Herzing et al. 2003; Bérubé, 2009). Therefore, it seems that formation of these groups may be largely driven by benefits associated with increased foraging success and protection from predators, with possible social drivers remaining largely unexplored to date.

5.7 Conclusions and future directions

It is promising that this research has been able to reveal relatively detailed insights into the lives of free-ranging pilot whales in New Zealand waters, including information about their demographics, social structure and interspecific associations. This work has also provided a firm foundation on which to build, as we now have a better understanding of what types of data and methodologies are needed to successfully study this species at sea here and in other Southern Hemisphere regions.

Considering that so little is known about the lives of free-ranging pilot whales in New Zealand, it would be extremely valuable for this study to continue. The collection of more photographic, genetic and behavioural data would enable researchers to further investigate trends in pilot whale abundance, group composition, site fidelity, feeding behaviour, social structure and genetic relatedness, all of which are vital for advising management decisions. It is therefore important for tour operators and researchers to continue collecting these data on an opportunistic basis. If more data from the same and different locations around New Zealand become available, it will be possible to assess demographic patterns and social structure on a broader scale. Additionally, acquiring more photo-ID data from different parts of New Zealand would greatly aid in producing a more complete identification catalogue of pilot whale individuals in these waters. In time, there is potential for the NZLFPWIC to be matched to pilot whale identification catalogues from other parts of Australia and the South Pacific, which may help to determine the extent to which these animals move between ocean basins and perhaps reveal whether some groups are more wide-ranging than others.

Based on evidence from mass stranding events and at-sea observations, the waters surrounding New Zealand are an important habitat for long-finned pilot whales. However, it remains unclear whether some of these animals can be considered “New Zealand pilot whales”, displaying patterns of year-round residency, or whether most are visitors, taking advantage of highly productive regions on a seasonal, or possibly random, basis. It is likely that pilot whale movement patterns are closely linked to their complex social organisation, so collecting genetic data from free-ranging groups will be an important step forward in this field of research. If we can improve our understanding of pilot whale social structure, it may also help us to make more sensible and informed decisions during stranding events, which may ultimately increase their chances of survival. It is hoped that this study will encourage further research of long-finned pilot whales in New Zealand, so that we can better appreciate

the important role that they play in marine ecosystems and the intricacies of their social lives.

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Appendices

Appendix 1.

Details of whale-watch operators and dedicated cetacean research platforms used during 81 pilot whale encounters off the north-eastern and south-eastern coasts, New Zealand between 2003 and 2019. Vessels are ordered by the number of encounters they contributed to this study. Also note that “-“ indicates information not available.

Name	Area of operation	Lat. (° S)	Length (m)	Approx. observer eye height (m)	Nature of operation	Operating months	Number of encounters contributed to this study
Manawanui	North Cape, Bay of Islands, Poor Knights, Hauraki Gulf	34-36	22	4	Research	Oct-May	51
Dolphin Encounter	Kaikōura	42	13	4	Tour boat	All year	12
Dolphin Seafaris	Bay of Plenty	37	15	4	Tour boat	Nov-May	4
Orca Research	Bay of Islands, Poor Knights, Hauraki Gulf	35-36	6.3	2	Research	All year	2

Te Epiwhani	Hauraki Gulf	36	5.5	2	Research	All year	2
PeeJay White Is. Tours	Bay of Plenty	37	22	4	Tour boat	All year	2
Orca	Bay of Plenty	37	-	-	Tour boat	Dec-Mar	2
RV Hawere	Poor Knights, Hauraki Gulf	36	15	-	Research	All year	1
Northern New Zealand Seabird Trust vessel	North Cape, Bay of Islands, Poor Knights, Hauraki Gulf	34-36	-	-	Research	All year	1
Amadis	-	-	-	-	Research	-	1
New Zealand Geographic vessel	-	-	-	-	Research	-	1
Medea	-	-	-	-	Tour boat	-	1
Unknown charter vessel	-	-	-	-	Tour boat	-	1

Appendix 2.

Table of unique catalogue identification (ID) numbers of potential pilot whale mothers and the encounter dates on which they were seen with either a neonate (N) or calf (C).

Date	03 Jan 11	01 Apr 14	06 Jan 15	10 Jan 15	12 Jan 15	20 Feb 15	03 May 15	03 Jan 16	04 Jan 16	05 Jan 16	12 Jan 16	13 Mar 16	23 Mar 17	26 Apr 17	13 Jan 18	26 Jan 18	27 Jan 18	26 Mar 18	25 Apr 18	03 May 19	04 May 19	
ID																						
NZGme007	C																					
NZGme009	N																					
NZGme013											C											
NZGme021				C																		
NZGme027																C						
NZGme030		C																				
NZGme058			C																			
NZGme064					N																	
NZGme066						N										N		N				
NZGme069																				N		
NZGme071																				N		
NZGme073							C															
NZGme074													C									
NZGme079								N		N	N	N										
NZGme080									C				C									
NZGme082										C												
NZGme086											N											
NZGme093													C									
NZGme097														C								
NZGme105															C							
NZGme111																C		C				
NZGme117																		C				
NZGme120																					C	
NZGme132																						C
NZGme133																						C
NZGme135																						C
NZGme136																						C
NZGme137																						N
NZGme140																						N

Appendix 3.

Table of 145 photo-identified long-finned pilot whales with catalogue identification numbers, date of first sighting and total number of sightings per animal.

ID Code	Date	Total sightings	ID Code	Date	Total sightings	ID Code	Date	Total sightings
NZGme001	16-Jan-07	1	NZGme021	30-Mar-14	3	NZGme041	13-May-14	1
NZGme002	03-Jan-11	1	NZGme022	30-Mar-14	1	NZGme042	13-May-14	1
NZGme003	03-Jan-11	1	NZGme023	01-Apr-14	2	NZGme043	13-May-14	2
NZGme004	03-Jan-11	1	NZGme024	01-Apr-14	1	NZGme044	13-May-14	1
NZGme005	03-Jan-11	1	NZGme025	01-Apr-14	1	NZGme045	13-May-14	1
NZGme006	03-Jan-11	2	NZGme026	01-Apr-14	1	NZGme046	05-Jan-15	1
NZGme007	03-Jan-11	1	NZGme027	01-Apr-14	3	NZGme047	05-Jan-15	1
NZGme008	03-Jan-11	2	NZGme028	01-Apr-14	2	NZGme048	05-Jan-15	1
NZGme009	03-Jan-11	1	NZGme029	01-Apr-14	2	NZGme049	05-Jan-15	1
NZGme010	02-Feb-11	1	NZGme030	01-Apr-14	1	NZGme050	05-Jan-15	2
NZGme011	02-Feb-11	1	NZGme031	01-Apr-14	3	NZGme051	05-Jan-15	1
NZGme012	18-Apr-12	1	NZGme032	01-Apr-14	1	NZGme052	05-Jan-15	1
NZGme013	27-Jan-13	2	NZGme033	08-Apr-14	3	NZGme053	05-Jan-15	1
NZGme014	27-Jan-13	2	NZGme034	08-Apr-14	1	NZGme054	05-Jan-15	1
NZGme015	30-Oct-13	1	NZGme035	08-Apr-14	1	NZGme055	06-Jan-15	1
NZGme016	30-Oct-13	1	NZGme036	09-Apr-14	1	NZGme056	06-Jan-15	1
NZGme017	30-Mar-14	3	NZGme037	09-Apr-14	2	NZGme057	06-Jan-15	2
NZGme018	30-Mar-14	3	NZGme038	09-Apr-14	1	NZGme058	06-Jan-15	2
NZGme019	30-Mar-14	2	NZGme039	13-May-14	1	NZGme059	06-Jan-15	1
NZGme020	30-Mar-14	2	NZGme040	13-May-14	1	NZGme060	06-Jan-15	2

ID Code	Date	Total sightings	ID Code	Date	Total sightings	ID Code	Date	Total sightings
NZGme061	06-Jan-15	2	NZGme081	04-Jan-16	2	NZGme101	22-May-17	1
NZGme062	10-Jan-15	1	NZGme082	04-Jan-16	3	NZGme102	22-May-17	1
NZGme063	12-Jan-15	1	NZGme083	04-Jan-16	2	NZGme103	22-May-17	1
NZGme064	12-Jan-15	1	NZGme084	04-Jan-16	2	NZGme104	13-Jan-18	1
NZGme065	12-Jan-15	1	NZGme085	04-Jan-16	3	NZGme105	13-Jan-18	1
NZGme066	20-Feb-15	3	NZGme086	12-Jan-16	1	NZGme106	21-Jan-18	1
NZGme067	03-May-15	1	NZGme087	12-Jan-16	2	NZGme107	21-Jan-18	1
NZGme068	03-May-15	1	NZGme088	12-Jan-16	2	NZGme108	21-Jan-18	1
NZGme069	03-May-15	2	NZGme089	16-Jan-16	1	NZGme109	26-Jan-18	2
NZGme070	03-May-15	1	NZGme090	16-Jan-16	1	NZGme110	26-Jan-18	4
NZGme071	03-May-15	2	NZGme091	16-Jan-16	1	NZGme111	26-Jan-18	2
NZGme072	03-May-15	1	NZGme092	13-Mar-16	1	NZGme112	26-Jan-18	1
NZGme073	03-May-15	3	NZGme093	13-Mar-16	1	NZGme113	26-Jan-18	1
NZGme074	03-May-15	3	NZGme094	23-Mar-17	2	NZGme114	26-Jan-18	1
NZGme075	23-Dec-15	1	NZGme095	26-Apr-17	2	NZGme115	05-Feb-18	4
NZGme076	23-Dec-15	1	NZGme096	26-Apr-17	1	NZGme116	05-Feb-18	2
NZGme077	23-Dec-15	1	NZGme097	26-Apr-17	1	NZGme117	05-Feb-18	2
NZGme078	23-Dec-15	1	NZGme098	26-Apr-17	1	NZGme118	05-Feb-18	2
NZGme079	03-Jan-16	3	NZGme099	08-May-17	1	NZGme119	25-Apr-18	1
NZGme080	04-Jan-16	2	NZGme100	08-May-17	1	NZGme120	25-Apr-18	1

ID Code	Date	Total sightings	ID Code	Date	Total sightings
NZGme121	25-Apr-18	1	NZGme141	04-May-19	1
NZGme122	25-Apr-18	1	NZGme142	04-May-19	1
NZGme123	25-Apr-18	1	NZGme143	04-May-19	1
NZGme124	25-Apr-18	1	NZGme144	04-May-19	1
NZGme125	25-Apr-18	1	NZGme145	04-May-19	1
NZGme126	26-Apr-18	1			
NZGme127	26-Apr-18	1			
NZGme128	16-Feb-19	1			
NZGme129	03-May-19	1			
NZGme130	03-May-19	1			
NZGme131	03-May-19	1			
NZGme132	03-May-19	1			
NZGme133	03-May-19	1			
NZGme134	03-May-19	1			
NZGme135	03-May-19	1			
NZGme136	03-May-19	1			
NZGme137	03-May-19	1			
NZGme138	04-May-19	1			
NZGme139	04-May-19	1			
NZGme140	04-May-19	1			

Appendix 4.

Social clustering of individual long-finned pilot whales delineated using Newman's (2008) eigenvector method ($n = 27$, modularity-G = 0.390).

Individual ID	Eigenvector value	Cluster
33	-0.5731	1
37	-0.4777	1
111	-0.2956	1
27	-0.3866	2
28	-0.3372	2
29	-0.3372	2
31	-0.3866	2
66	0.0421	3
109	0.0421	3
110	0.1519	3
115	0.1519	3
116	0.3195	3
117	0.3195	3
118	0.3195	3
69	0.314	4
71	0.314	4
73	0.3893	4
74	0.3893	4
94	0.3203	4
6	-0.0795	5
8	0.2693	5
17	0.0761	5
18	0.0761	5
19	0.3511	5
20	0.0387	5
21	0.39	5
58	0.3259	5

Appendix 5.

Long-finned pilot whale dyads that had high association indices of more than twice the population mean half-weight index (HWI) ($AI = 0.2$), but were not significantly stronger than expected by chance ($n = 86$).

HWI: 1.00		HWI: 0.80		HWI: 0.67		HWI: 0.50	
Individual catalogue IDs of dyad							
17	18	27	28	6	20	6	8
27	31	27	29	8	20	6	17
28	29	27	33	17	20	6	18
33	37	28	31	18	20	6	28
66	109	29	31	19	20	6	29
69	71	31	33	20	28	8	17
73	74	66	110	20	29	8	18
110	115	66	115	28	111	8	19
116	117	73	94	29	111	17	19
116	118	74	94	33	111	17	28
117	118	109	110	37	111	17	29
		109	115	66	111	17	33
		110	116	109	111	17	37
		110	117			18	19
		110	118			18	28
		115	116			18	29
		115	117			18	33
		115	118			18	37
						20	21
						20	27
						20	31
						21	58
						27	111
						28	33
						28	37
						28	66
						28	109
						29	33
						29	37
						29	66
						29	109
						31	111
						33	66
						33	109
						37	66
						37	109
						66	116
						66	117
						66	118
						109	116
						109	117

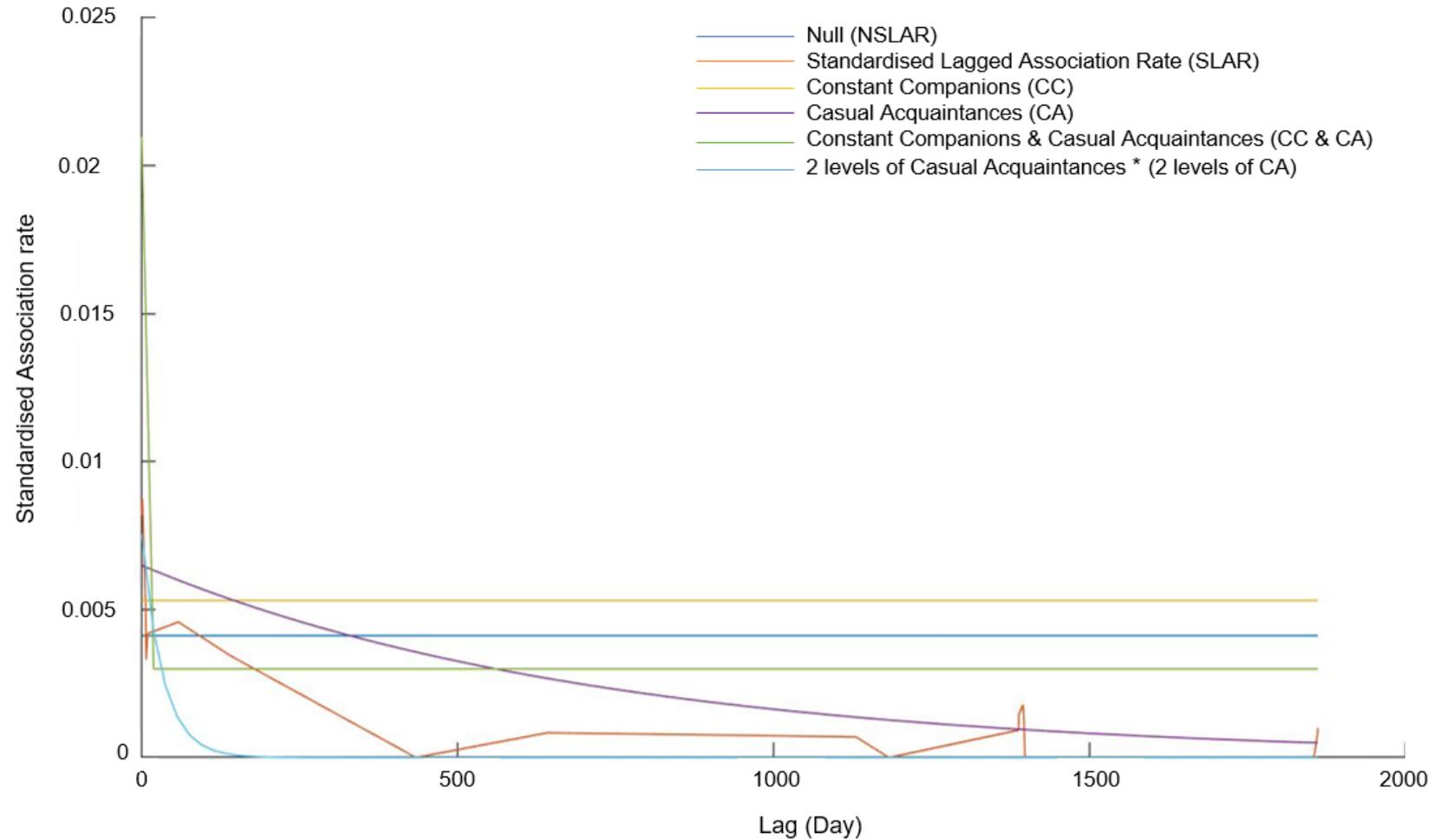
109	118
110	111
111	115

Appendix 6.

Encounter history of 21 long-finned pilot whale dyads which have been sighted together on more than one occasion in north-east New Zealand waters.

Dyad individual IDs	Encounter date 1	Encounter date 2	Encounter date 3
017 - 018	30 Mar 2014	01 Apr 2014	09 Apr 2014
019 - 021	30 Mar 2014	04 May 2019	
027 - 028	01 Apr 2014	26 Jan 2018	
027 - 029	01 Apr 2014	26 Jan 2018	
028 - 029	01 Apr 2014	26 Jan 2018	
031 - 033	08 Apr 2014	26 Jan 2018	
033 - 037	09 Apr 2014	26 Jan 2018	
069 - 071	03 May 2015	25 Apr 2018	
073 - 074	03 May 2015	23 Mar 2017	21 Jan 2018
109 - 110	26 Jan 2018	26 Mar 2018	
109 - 115	26 Jan 2018	26 Mar 2018	
110 - 115	26 Jan 2018	05 Feb 2018	26 Mar 2018
110 - 116	05 Feb 2018	26 Mar 2018	
110 - 117	05 Feb 2018	26 Mar 2018	
110 - 118	05 Feb 2018	26 Mar 2018	
115 - 116	05 Feb 2018	26 Mar 2018	
115 - 117	05 Feb 2018	26 Mar 2018	
115 - 118	05 Feb 2018	26 Mar 2018	
116 - 117	05 Feb 2018	26 Mar 2018	
116 - 118	05 Feb 2018	26 Mar 2018	
117 - 118	05 Feb 2018	26 Mar 2018	

Appendix 7. Standardised lagged association rate (SLAR) for all distinctive long-finned pilot whale and oceanic bottlenose dolphin individuals captured off the Bay of Islands between 2011 and 2019, using a moving average of 1500 associations. All models are shown with the SLAR represented by an orange line and the best-fit model 'casual acquaintances' represented by a purple line. The NSLAR is included (dark-blue line) for reference.



Appendix 8.

Fit of, and relative support for, exponential social-system models to the standardised lagged-association rate (SLAR) for long-finned pilot whales and oceanic bottlenose dolphins encountered off the Bay of Islands. Associations were defined as individuals grouped within an encounter; the lowest Δ QAIC value indicates the best-fit model.

Description of model	Model formula	Maximum likelihood values for parameters (SE)	QAICc	Δ QAICc	Model support
Constant Companions	$g' = a1$	$a = 0.005 (0.05)$	508.07	8.02	Little support
Casual Acquaintances	$g' = (a2 \cdot e)^{-a1\tau}$	$a2 = 0.007 (0.006)$ $a1 = 0.001 (0.119)$	500.05	0	Best
Constant Companions & Casual Acquaintances	$g' = a2 + a3 \cdot e^{-a1\tau}$	$a2 = 0.003 (0.261)$ $a1 = 1.311 (2.901)$ $a3 = 0.067 (0.83)$	501.89	1.84	Some support
Two levels of Casual Acquaintances	$g' = a3 \cdot e^{-a1\tau} + a4 \cdot e^{-a2\tau}$	$a4 = -0.752 (0.895)$ $a2 = 0.030 (1.047)$ $a3 = 0.760 (0.843)$ $a1 = 0.030 (1.007)$	533.48	33.43	No support