

**ABUNDANCE AND BEHAVIOURAL ECOLOGY OF
BOTTLENOSE DOLPHINS (*Tursiops truncatus*) IN THE
MARLBOROUGH SOUNDS, NEW ZEALAND.**

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ABSTRACT

In order to survive, animals require both food and protection from predators. These ecological factors are major determinants in habitat selection and social interactions. Determining the causes of habitat selection and examining the behavioural ecology of marine mammals is often a difficult task. In the ever-changing marine environment, factors such as shifts in prey availability, turbidity, sea surface temperature, and salinity result in a highly dynamic ecosystem that influences distribution. This research's primary focus was to establish baseline information on the behavioural ecology of bottlenose dolphins, *Tursiops truncatus* in and around the Marlborough Sounds, New Zealand. Boat based surveys, photo-identification, and group focal follows were used to assess spatial distribution, abundance, home range, and social interactions. Boat based surveys were conducted from 2003 to 2005. Photo-identification data collected from 1997 to 2005 were used in analysis. Uniquely marked individuals (n = 335) were sighted throughout the Marlborough Sounds and long-term site fidelity was observed among members in this large open population. Aggregations of between 3 to 172 individuals were observed with a median group size of 12. Group size was influenced by the presence of calves, with groups tending to be larger when calves were present. Larger groups were found to rest more than smaller groups and resting occurred less in the spring months. Association patterns revealed long- and short-term preferred associations between individuals throughout the Sounds. Distribution and movement patterns of dolphins showed they used all areas within the Marlborough Sounds. The population of bottlenose dolphins observed in the Marlborough Sounds were found to be semi-resident with 211.5 (C.I. =

195 – 232) individuals utilising the Sounds year round while other individuals were found to migrate in and out of the area on an annual basis. The Marlborough Sounds appear to be only a portion of a much larger home range for this population.

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1.1 General Introduction

Threats to the Marine Environment

Water is the source of all life on earth and is essential to the maintenance and function of all living things (Clapham 1973). Water covers over 70 percent of the earth's surface and provides various ecosystems for approximately 250,000 known marine species (Thurman and Trujillo 2002). Coastal waters support approximately 95 percent of the total mass of marine life in the oceans. What happens on land affects the ocean, marine ecosystems, and ultimately all life that inhabit them. Over the last 50 years land and sea surface temperatures have increased globally as a result of climate change (IPCC 2001). Global and regional impacts from increased temperatures include changes in weather patterns, ocean currents, salinity, pH, sea-ice cover and rises in sea levels (Learmonth *et al.* 2006). Increasing temperatures are predicted to affect marine ecosystems and the ecological communities that they support (Simmonds and Isaac 2007). Climate change has become a high-profile issue worldwide and is considered a potential threat to the marine environment (see Learmonth *et al.* 2006 for a review). As a result, many governments are now establishing plans and taking actions to reduce and monitor the affects of global warming (Skilling 2007).

Both direct and indirect anthropogenic impacts can influence species in the marine environment. However, direct impacts such as boat disturbance, over fishing, by-catch and ship strikes often cause immediate declines among various marine species (Mann *et al.* 2000). High levels of by-catch and overfishing have caused severe declines in many marine vertebrate species. For example, the Maui's dolphin (*Cephalorhynchus hectori maui*) and the vaquita (*Phocoena sinus*) are both listed as critically endangered due to the unsustainable

level of by-catch associated with these species (Mann *et al.* 2000, Slooten *et al.* 2006). Likewise, many *Elasmobranchii* e.g. Ganges shark (*Glyphis gangeticus*), basking shark (*Cetorhinus maximus*), and great white shark (*Carcharodon carcharias*) populations are rapidly declining due to high by-catch rates and overfishing from the shark-fin industry (Verlecar *et al.* 2007). Bascompte *et al.* (2005) suggests that the stability of food webs in the marine environment is largely dependent on the strength of interactions between top-level predators and their prey. Understanding these interactions and the abundance, vitality and behavioural ecology of top predators can act as an indicator on the relative health or state of an ecosystem (Tanabe 2002, Bascompte *et al.* 2005).

Conservation Management Issues

Baseline data on apex predators in an ecosystem can be invaluable to the management and conservation of various species within that system. Knowing the status and stability of a population (increasing, stable or decreasing) prior to natural or anthropogenic influences can provide invaluable information necessary to successfully manage exploited populations. Conservation biologists are frequently asked to provide government officials, courts, and conservation managers with information on the status of threatened or endangered populations or species. Information on the abundance, status, distribution, behaviour and movement patterns of wild populations contributes to establishing appropriate conservation and management initiatives (Wimmer and Whitehead 2004, Lettink and Armstrong 2003).

Habitat Use and Behavioural Ecology of Marine Vertebrates

The relationship between an animal and its environment is often examined in terms of

evolution, habitat use and residency patterns (Hooker *et al.* 2002). To better understand how an organism utilises its environment, researchers often examine its distribution and behaviour patterns (Whitehead 2001). Factors such as reproduction, protection from predators and distribution of food are major determinants in habitat selection and association patterns for many species (Alcock 2001). Through the use of techniques such as, photo-identification, banding, satellite or radio tagging and focal group or individual behavioural sampling, researchers are able to examine populations on a group and individual basis. Group and individual interactions can provide insight on temporal and spatial patterns of habitat use, residency, and association patterns (Hooker *et al.* 2002, Whitehead and Dufalt 1999).

Understanding factors that influence the habitat use of top predators such as marine mammals, sharks, sea birds, sea turtles and large fish, provides knowledge on the impact and influence they have on other species within that system (Heithaus *et al.* 2002). The ocean is a homogeneous environment, but food sources and fish populations within it are not (Roberts and Sargent 2002). The availability and dispersion of prey is an important factor in habitat selection for many top predators. Sea turtles and fish often display ontogenetic migrations where habitat use and selection is influenced by the various developmental stages of each individual (Roberts and Sargent 2002, Luschi *et al.* 2003). For example, loggerhead turtle (*Caretta caretta*) hatchlings in Eastern Florida leave the beach and are carried by the Gulf Stream towards pelagic nursery grounds in the East Atlantic (Carr 1987). They later return to their natal grounds where they will reproduce after reaching sexual maturity (Bowen and Karl 1997). By following the current out to pelagic areas, hatchlings greatly reduce their risk of predation and thus are able to mature into juveniles (Luschi *et al.* 2003). This pattern is also observed in many species of tropical grunts (*Haemulidae*) (Appeldoorn *et al.* 1997). As

young fish mature and their nutritional needs increase while their risk of predation decreases, they move from the shelter of sea grass beds to offshore coral reef habitats (Appeldoorn *et al.* 1997, Roberts and Sargant 2002).

Many species of seabirds and baleen whales migrate over large distances from breeding/nesting grounds to foraging/non-breeding wintering grounds (Spear *et al.* 2003). For example, humpback whales (*Megaptera novaeangliae*), Gray whales (*Eschrichtius robustus*) and minke whales (*Balaenoptera acutorostrata*) migrate over hundreds of miles from tropical breeding grounds in the winter to optimal polar feeding grounds during the summer (Clapham 2002). Likewise, the Chatham Island Albatrosses (*Thalassarche eremita*) nest in New Zealand during the austral spring and summer months and migrate out to non-breeding areas off the coast of South America during the austral winter months (Spear *et al.* 2003). Seasonal movements have been observed in a number of delphinid species. For example, dusky dolphins (*Lagenorhynchus obscurus*) off the coast of Kaikoura, New Zealand, show seasonal movements that correlate with changes in water temperature, moving northward in the winter and south in the warmer months (Markowitz 2004). No matter how large or small, movement and migration patterns evolved because being in a certain place at a certain time increases the fitness of an individual or group (Dodson 1997).

Habitat Use and Behavioural Ecology of Marine Mammals

Determining the cause of habitat selection and examining the behavioural ecology of marine mammals is often a difficult task, especially in the ever-changing marine environment (Mann *et al.* 2000). Factors such as shifts in prey availability, turbidity, sea surface temperature and salinity result in a highly dynamic ecosystem influencing habitat use (Bräger *et. al.* 2003). Sea

surface temperature (SST) has been one factor frequently investigated in relation to habitat use of many marine mammal species. Sea surface temperature is correlated with the seasonal distribution of harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy, Canada (Watts and Gaskin 1985), manatees off the coast of Florida (Reid 1991) and sea otters (*Enhydra lutris*) off the coast of California (Jameson 1989). Other factors, such as salinity, turbidity and depth, in conjunction with SST, influence habitat selection of New Zealand Hector's dolphins (*Cephalorhynchus hectori*), (Bräger *et al.* 2003). Topographic features such as sea floor slope and depth (Ingram and Rogan 2002) and prey abundance have also been found to influence habitat use among marine mammals. Ballance (1992) suggests that the abundance of potential prey in a system influences the habitat use of bottlenose dolphins found off the Atlantic and Pacific coasts. Marine mammals' use of their environment can also be influenced by human activities such as boating (Acevedo 1991, Nowacek *et al.* 2001, Constantine 2004, Lusseau 2003), aquaculture (Markowitz *et al.* 2003, Bearzi *et al.* 2004, Watson-Capps 2005), fishing (Harwood and Croxall 1988, Hucke-Gaete *et al.* 2004) and environmental contamination (Aguilar 1987).

Ecological Influences on Behaviour and Association Patterns

The relationship between habitat use, reproduction and association patterns has been shown for many marine mammals. For example, Australian fur seals (*Arctocephalus pusillus*), California sea lions (*Zalophus californianus*), Northern sea lions (*Eumetopias jubatus*) and New Zealand sea lions (*Phocarctos hookeri*) all display a polygynous mating system where males select and defend haul out sites attractive to females in order to successfully breed (Stewart 2002). Other species, such as the West Indian Manatee (*Trichechus manatus*) have

groups of roaming males that seek out females in oestrus (Powell 2002). Male bottlenose dolphins (*Tursiops truncatus*) in Shark Bay Australia form coalitions or alliances to gain access to females (Connor *et al.* 2001). Likewise, in Sarasota Bay, Florida, males form pair bonds and associate with females before the breeding season to develop affiliative relationships, which may influence female selection during the breeding season (Owens *et al.* 2002). Other species, such as dusky dolphins, common dolphins (*Delphinus delphis*) and spinner dolphins (*Stenella frontalis*) form large aggregations in order to evade predators, rear young and forage cooperatively (Reeves 2002). These reproductive strategies and social patterns have evolved to meet the specific needs of each species in various habitats.

The Bottlenose dolphin

Like many cetacean species, habitat use influences population abundance and social organisation of the bottlenose dolphin. The bottlenose dolphin is a large bodied delphinid, typically 220 to 380cm long, grey in colour with a lighter underbelly (Leatherwood *et al.* 1983, Connor *et al.* 2000, Reeves 2002). Found throughout the world's oceans, the genus *Tursiops* exhibits striking regional variation in body size, with larger body size typically associated with colder sea surface temperatures (Ross and Cockcroft 1990). Phylogenetic variation along with geographic location, body size, tooth count and coloration indicate the presence of two species *T. truncatus* and *T. aduncus* within the genus (Ross 1977, Curry 1997, LeDuc *et al.* 1999). Variation within regions is also common, with two forms “inshore” and “offshore” suggested based on morphology, haematology, parasite faunas, and nuclear and mitochondrial genetic distinctions (Hersh and Duffield 1990, Waerebeek *et al.* 1990, Hoelzel *et al.* 1998).

Regardless of species or form, bottlenose dolphins are long-lived, large-brained social mammals (Ridgway 1986). In Sarasota Bay, Florida, females have been reported to live more than 50 years with males living just over 40 (Wells and Scott 1999). Females reach breeding age between five and thirteen years while males have been estimated from eight to thirteen years (Wells *et al.* 1987). Females give birth to a single calf after a twelve-month gestation period (Schroeder 1990, Schroeder and Keller 1990). Calves are reported to stay with their mothers for several years (Wells *et al.* 1987, Smolker *et al.* 1992). Maternal investment is high, with some calves observed nursing up to five years (Mann and Smuts 1998, Mann *et al.* 1999). Differences in body size and nutritional requirements for lactating females may account for variation observed within and among habitats (Conner *et al.* 1996).

This coastal species is found in various habitats ranging from cold and deep waters to warm and shallow waters (Mann *et al.* 2000). Bottlenose dolphins have been a focus of research for many years (Shane *et al.* 1986). Detailed studies have been conducted worldwide on bottlenose dolphins examining behavioural ecology, residency patterns, abundance, habitat use, associations, and human impacts (Table 1.1) (Ingram and Rogan 2002, Ballance 1992, Bearzi 2005, Mann *et al.* 2000). Long-term studies of bottlenose dolphins in Sarasota Bay, Florida, U.S.A. and Shark Bay, Australia (Connor *et al.* 1992) have demonstrated complex societies, lasting cooperative relationships between individuals, defined ranges and diversity in habitat use (Mann *et al.* 2000).

Table 1.1. Summary of bottlenose dolphin studies discussed in this thesis.

Location	(<i>Tursiops sp.</i>)	Population Size	Habitat	Group size range (mean)(median)	Source
Marlborough Sounds, NZ	(<i>T. truncatus</i>)	211	coastal waters, enclosed bays, sheltered sounds	3-172 (26)(12)	this study
Bay of Islands, NZ	(<i>T. truncatus</i>)	462	coastal waters and semi-enclosed bays	1-40 (9.47)(9)	Constantine 2002, Mourão 2006
Doubtful Sound, NZ	(<i>T. truncatus</i>)	65	sheltered fiords	2-60 (17.2)(14)	Schneider 1999, Lusseau <i>et al.</i> 2003
Sarasota Bay, Florida	(<i>T. truncatus</i>)	120	semi-enclosed bays	1-22 (4.06)(na)	Wells <i>et al.</i> 1987, Irvine <i>et al.</i> 1981
Shark Bay, Australia	(<i>T. aduncus</i>)	600	semi-enclosed bays	1-40 (5)(4)	Smolker <i>et al.</i> 1992, Gero <i>et al.</i> 2005
Moray Firth, Scotland	(<i>T. truncatus</i>)	129	estuarine waters	na (6)(5)	Wilson <i>et al.</i> 1999, Lusseau <i>et al.</i> 2005
Charleston, South Carolina	(<i>T. truncatus</i>)	839	coastal and estuarine waters	1-60 (7.81)(na)	Speakman <i>et al.</i> 2006
Mississippi Sound, Mississippi	(<i>T. truncatus</i>)	515	coastal waters and sheltered sounds	1-50 (4.9)(4)	Hubard <i>et al.</i> 2004
Santa Monica Bay, California	(<i>T. truncatus</i>)	290	exposed coastal waters	1-57 (10.1)(na)	Bearzi 2005
San Diego, California	(<i>T. truncatus</i>)	234-285	exposed coastal waters	2-90 (19.8)(na)	Defran and Weller 1999
Galveston Bay, Texas	(<i>T. truncatus</i>)	200	semi-enclosed bays and coastal waters	1-30 (4.4)(4)	Bräger 1993, Bräger <i>et al.</i> 1994, Irwin and Würsig 2004
Maui and Lanai, Hawaii	(<i>T. truncatus</i>)	134	exposed coastal waters	1-16 (6.3)(6)	Baird <i>et al.</i> 2001
Northern Adriatic Sea	(<i>T. truncatus</i>)	106	exposed and sheltered coastal waters	1-65 (7.4)(5)	Bearzi <i>et al.</i> 1997
Southeastern Cape of South Africa	(<i>T. aduncus</i>)	Na	exposed coastal and offshore waters	3-1000 (140.3)(na)	Saayman and Taylor 1973
Gulf of California, Mexico	(<i>T. truncatus</i>)	206	coastal and estuarine waters	1-125 (15)(na)	Ballance 1992, Balance 1990
Eastern Ionian Sea	(<i>T. truncatus</i>)	48	sheltered coastal waters	1-24 (6.8)(na)	Bearzi <i>et al.</i> 2005
Gulf of San Jose, Argentina	(<i>T. truncatus</i>)	Na	exposed coastal waters	8-22 (14.9)(na)	Würsig 1978

In New Zealand, studies conducted in the Bay of Islands and Doubtful Sound show substantial differences in habitat use and social structure. In the Bay of Islands, an estimated population of 446 (95% C.I. 418 - 487) dolphins were found to be seasonal, changing their habitat use in relation to sea surface temperature and socialising in groups of 2-50 animals (Constantine 1997, Constantine 2002, Constantine *et al.* 2004). In contrast, the population of bottlenose dolphins found in Doubtful Sound is small, consisting of approximately 65 individuals that reside in a deep and cold habitat (Lusseau 2003). They have been documented to be year round residents, part of a closed population, and appear to form a tight social network (Lusseau 2003, Schneider 1999).

Bottlenose dolphins are also found within the Marlborough Sounds, New Zealand. The Marlborough Sounds is located at the top of the South Island and is an intermediate location between the Bay of Islands and Doubtful Sound regions (Figure 2.1). Recreational boaters, tour operators and Ministry of Fisheries researchers have sighted bottlenose dolphins throughout the Marlborough Sounds since the late 1960's (Webb 1973). The presence of bottlenose dolphins has been documented by researchers working in the Marlborough Sounds over the past ten years (Markowitz 2004). Prior to this study, no formal examination of ranging patterns, abundance, residency, habitat use and social affiliations had been conducted for this population.

Justification and Rationale

The work presented here represents a valuable contribution to the knowledge and conservation of bottlenose dolphins inhabiting New Zealand waters. Firstly, no systematic study has previously examined the abundance, behavioural ecology or habitat use of bottlenose dolphins in

the Marlborough Sounds. Second, as bottlenose dolphins are an apex predator, determining the status of this population may prove to be a useful indicator of the health and stability of the Marlborough Sounds. Third, bottlenose dolphins that utilise the Marlborough Sounds are subject to multiple human impacts including heavy vessel traffic, ferries, ecotourism companies and aquaculture. Understanding the behavioural ecology of such a species in this area may provide valuable insight into the possible effects these impacts have on bottlenose dolphins. Finally, bottlenose dolphins in the Marlborough Sounds are genetically and geographically isolated from the two other studied populations of bottlenose dolphins found in New Zealand (de Tezanos Pinto *et al.* 2004). Based on these factors, this population should be of particular interest to researchers and conservation managers.

The work presented here will provide baseline data and insight on the current status of the population of bottlenose dolphins utilising the Marlborough Sounds. This information will aid conservation managers in the management and protection of this population.

1.2 Thesis Aims and Objectives

The primary focus of this thesis is to establish baseline information on the behavioural ecology of bottlenose dolphins in and around the Marlborough Sounds. Specifically, this study examines bottlenose dolphin abundance, spatial distribution, residency patterns and social structure in the Marlborough Sounds region. The primary objectives are to:

1. Examine spatial and temporal distribution.
2. Investigate habitat use within the three different regions: Queen Charlotte Sound (QS), Pelorus Sound/Havelock (PS), and Admiralty Bay/Current Basin (AB), in relation to environmental conditions or factors.

3. Document daily activity budgets and compare these between the three regions.
4. Obtain population abundance and group size estimates for the Marlborough Sounds.
5. Examine residency patterns and establish if they are annual, seasonal, or periodical.
6. Examine association patterns.

1.3 Chapter Overview

Chapter II Distribution, Habitat Use, and Behaviour Patterns

Chapter II examines distribution, habitat use and behaviour patterns within the Marlborough Sounds, New Zealand. Group dynamics are examined and compared by seasons and environmental factors. This chapter assesses activity budget variation in the three different regions (QC, PS, FP) within the Sounds.

Chapter III Abundance, Site Fidelity, and Movement Patterns

Chapter III provides estimates of abundance, site fidelity and movement patterns, using photo-identification data. This chapter examines spatial and temporal variation in the occurrence of dolphins in the three different regions (QC, PS, FP) within the Sounds.

Chapter IV Social Structure and Association Patterns

Chapter IV examines the social structure of the population of bottlenose dolphins within the Marlborough Sounds. Association patterns are examined at the population, community/group and dyad levels. Variability in gregariousness is examined and comparisons between populations are discussed.

Chapter V Conclusions and Recommendations

Chapter V provides an overview of all findings. Similarities and differences between this study and the two other populations of bottlenose dolphins in the Bay of Islands and Doubtful Sound, New Zealand are discussed. A summary of comparisons between other populations of bottlenose dolphins discussed in this thesis is presented. Conservation issues are addressed and recommendations for future work in the Marlborough Sounds area are provided.

Chapter II

Bottlenose dolphin distribution, habitat use and behaviour patterns within the Marlborough Sounds, New Zealand.



Plate 2.1. A juvenile bottlenose dolphin leaping.

2.1 Introduction

Influences on Distribution, Habitat Use and Behaviour of Marine Vertebrates

Determining the factors that influence distribution, habitat use and behaviour patterns can aid in the protection and management of valuable areas and resources individuals need to survive (Meyer *et al.* 2000). Basic knowledge of foraging patterns, predator defences, anthropogenic influences and group organisation, can provide insight on habitat use and the role a species plays within an ecosystem (Hooker *et al.* 2002, Heithaus and Dill 2002b). Distribution and ranging patterns for many species of marine vertebrates have been attributed to many things including shifts in prey

abundance (Heithaus and Dill 2002b, Tricas 1979, Sims and Quayle 1998, Wells 1999, Jaquet *et al.* 2003), changes in sea surface temperature (Reid *et al.* 1991) and seasonal migrations (Spear *et al.* 2003). Predator pressure can also influence the movement, habitat use and grouping patterns of species within a system (Heithaus and Dill 2002a). For example, studies conducted on New Zealand sea lions (*Phocarctos hookeri*) and Cape fur seals (*Arctocephalus pusillus*) have shown how the use of an area and predatory behaviour of one species can influence the vitality of another (Lalas *et al.* 2007, David *et al.* 2003, and Robinson *et al.* 1999).

Conservation Management in the Marine Environment

Documenting and understanding how an animal utilises its environment is a critical step in the conservation and management efforts of that species. Research on habitat use of marine vertebrates, such as green (*Chelonia mydas*), loggerhead (*Caretta caretta*), and olive ridley (*Lepidochelys olivacea*) sea turtles in Brazil (Marcovalidi and Marcovalidi 1999), bottlenose whales (*Hyperoodon ampullatus*) in eastern Canada (Hooker *et al.* 2002), and Hector's dolphins (*Cephalorhynchus hectori*) in New Zealand (Burkhart and Slooten 2003) has improved the management of these species. Resulting initiatives such as marine protected areas have strengthened conservation efforts, allowing in some cases, a population recovery to occur. In these cases, protection of the habitats used by these species has proven to be a key factor in the management and conservation of these populations.

Habitat Variation Among Populations of Bottlenose Dolphins

Intraspecific variation in habitat use is common among populations of marine mammals. A prime example of a single species found in many different habitats

around the world is, the bottlenose dolphin (*Tursiops truncatus*) (Reeves 2002). Considered to be a particularly adaptable species, the bottlenose dolphin is found in a wide variety of habitats including the tropical waters of the Gulf of Mexico (Wells 1987, Wells *et al.* 1990), the temperate waters off the coast of California (Maldini-Feinholz 1996), the shallow bays and estuaries of Florida (Wells 1987) the deep firths in the Moray Firth (Wilson *et al.* 1997) and regions far offshore in South Africa (Saayman *et al.* 1973).

Distribution and Habitat Use of Bottlenose Dolphins

Studies conducted on the distribution and habitat use of bottlenose dolphins show a great deal of diversity. Some populations have been found to display year round residency over many years (Wells *et al.* 1987, Smolker *et al.* 1992, Wilson *et al.* 1997 and Schneider 1999) while others are transient and range over large areas (Bearzi *et al.* 2004, Wilson *et al.* 2004, Stockin *et al.* 2006). Distribution and ranging patterns for this species have been attributed to seasonal migrations (Mead 1975), shifts in prey availability (Würsig 1978) and changes in sea surface temperatures (Hansen 1990, Constantine 2002 and Schneider 1999).

Studies of bottlenose dolphins in New Zealand waters show differences in habitat use between populations. Bottlenose dolphins found in the Bay of Islands, north eastern part of the North Island, were found to change their habitat use in relation to sea surface temperature (range = 10 - 22°C) and inhabit a sub-tropical region with relatively warm temperatures year round (Constantine 2002). In contrast, the population of bottlenose dolphins found in Doubtful Sound, southwestern part of the South Island, reside in a deep and cold habitat (range = 7.0 - 17.7°C) (Schneider 1999). Schneider (1999) reported that bottlenose dolphin in Doubtful Sound, show a

seasonal trend in habitat use, following a sea surface temperature gradient by selecting the warmest water available each season (Schneider 1999). Doubtful Sound is the southernmost location in which bottlenose dolphins have been found and may approach the ecological limit in water temperature that this species can inhabit (Schneider 1999).

Group Size

Many factors such as prey availability, openness of habitat, water depth, reproductive strategies and predation have been reported to influence group size in bottlenose dolphins (Würsig 1986, Wells *et al.* 1987, Smolker *et al.* 1992, Shane *et al.* 1986). Two extreme examples of variation in group size are found in populations off the coast of the eastern cape, South Africa and off the coast of southern Argentina. In South Africa, Saayman and Tayler (1973) reported group sizes ranging from 3 to 1000 individuals with a mean of 140.3 and in Argentina, Würsig (1978) reported group sizes ranging from 8 to 22 with a mean of 14.9. The majority of studies on bottlenose dolphins report group sizes ranging between 2 to 65 individuals with means and medians between 4 and 15, e.g. Galveston Bay, Texas (Bräger *et al.* 1994, Fertl 1994, Irwin and Würsig 2004), Southern coast, Santa Monica Bay, California (Bearzi 2005), Mississippi Sound, Mississippi, (Hubard *et al.* 2004), Charleston, South Carolina (Speakman *et al.* 2006), Northern Adriatic Sea (Bearzi *et al.* 1997), Eastern Ionian Sea (Bearzi *et al.* 2005), Hawaiian Islands (Baird *et al.* 2001), Moray Firth, Scotland (Wilson *et al.* 1993) and Shark Bay, Australia (Mann *et al.* 1999).

Research on New Zealand bottlenose dolphins (*Tursiops truncatus*) has been conducted primarily in two regions, the Bay of Islands, North Island and Doubtful Sound, South Island. The two distinct populations found in these regions differ in

their distribution, group size and behaviour patterns. In the Bay of Islands, dolphins were reported to be seasonal, occurring in groups of 2 - 50 (median = 8 - 15) and range over a 300 km area (Constantine, 2002). In contrast, bottlenose dolphins in Doubtful Sound occur in groups of 2 - 60 individuals (mean = 17.2 median = 14, mode = 8) (Lusseau 2003) and range over a small 40.3 km area (Schneider 1999, Lusseau 2003 and Williams *et al.* 1993).

Despite their presence in the Marlborough Sounds, an intermediate location in the northern part of the South Island, no study to date has investigated the distribution, habitat use and behaviour patterns of bottlenose dolphins in this region. This chapter examines the distribution, habitat use and behaviour patterns of bottlenose dolphins within the Marlborough Sounds, New Zealand. Environmental factors and activity budgets were tested to assess possible influences and differences in habitat use. Findings are discussed in relation to other studies that have been conducted on distinct populations of bottlenose dolphins in the Bay of Islands and Doubtful Sound regions. More specifically the following objectives were addressed:

1. Examine the possible range and distribution of the population.
2. Examine group size and composition and investigate what factors may influence it.
3. Examine possible environmental effects on the entire population of bottlenose dolphins in the Marlborough Sounds.
4. Examine possible environmental effects on the three different group sizes (small, medium and large).
5. Examine focal group behaviour and assess possible influences (i.e. area, group size, and seasons).

2.2 Methods

Study Area

The Marlborough Sounds region (41°S, 174°E) (Figure 2.1) is 890 km² of diverse sounds and estuaries (Potton 1985). The study presented here was conducted in three main areas of the Sounds: Queen Charlotte Sound, Pelorus Sound/Havelock and Admiralty Bay/Current Basin (Figure 2.1). Each of these regions differ in topographic characteristics and recreational boating use. Queen Charlotte Sound has heavy vessel traffic and is the main ferry terminus between the North and South Island. Pelorus Sound/Havelock is the most land locked region and exhibits high levels of fresh water inflow (Potton 1985). Admiralty Bay/Current Basin is the most western part of the Sounds and is separated by French Pass, an oceanographically unique area that acts as a bottleneck between Cook Strait and Tasman Bay (Potton 1985).

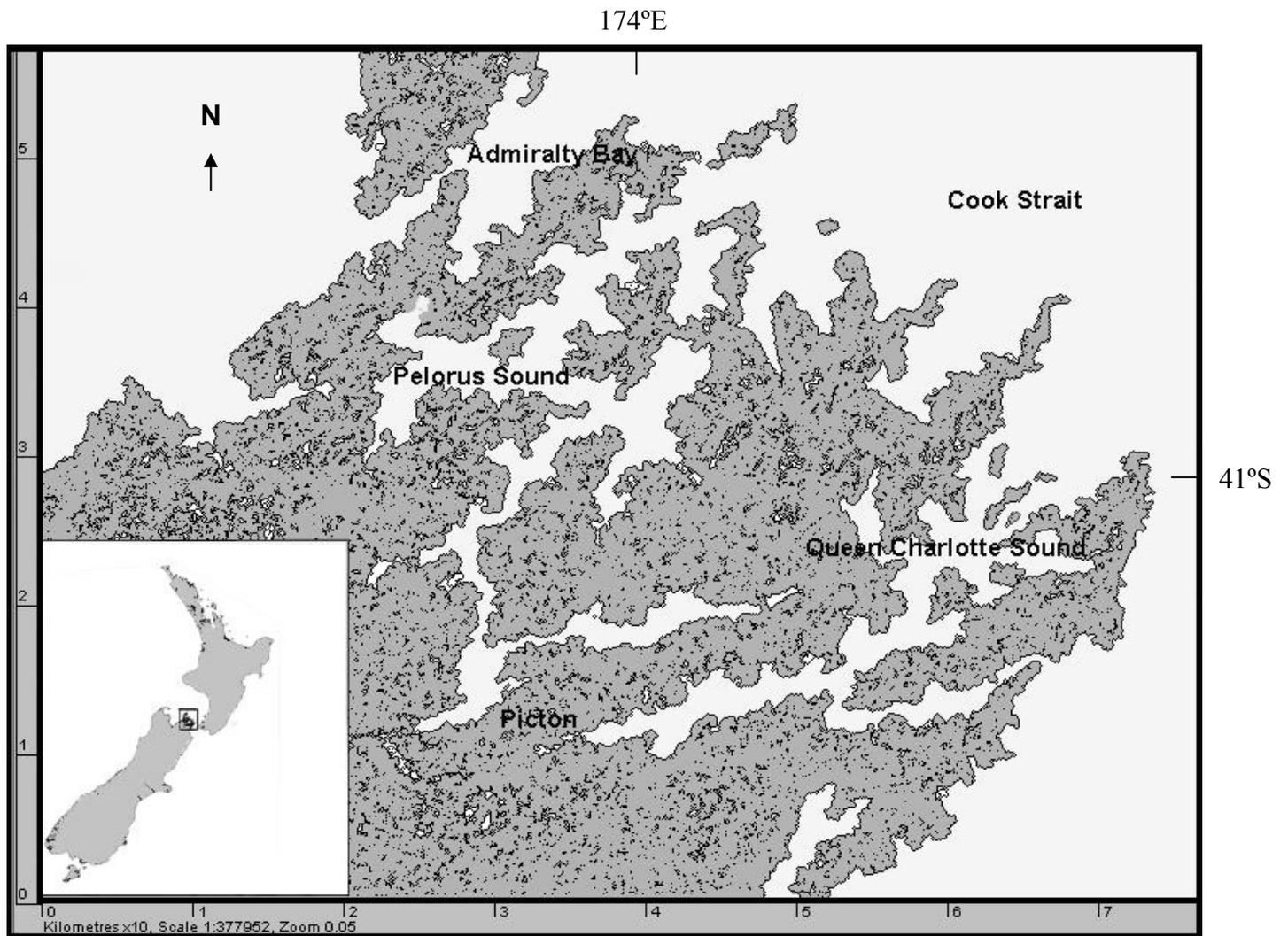


Figure 2.1. The Marlborough Sounds. Northern most area of the South Island, New Zealand.

Data Collection

Boat based surveys were conducted in the Marlborough Sounds region from a 5.6 m stabcraft with a 100hp Yamaha 4-stroke outboard motor. Survey speed averaged 15 km/hr. Surveys were conducted during daylight hours between 0700 – 1800 hours (NZSTD), in sea state conditions of three or less based on the Beaufort scale. Typically, survey effort lasted between four and seven hours. A LCX-15 Sonar/GPS (Lowrance Electronics) was used to determine latitude and longitude, depth, sea surface temperature and speed of travel.

At least one survey was attempted each month in the three different areas of the Marlborough Sounds. Three or more trained observers were present during each survey, assigned a position at the start of every day (port, bow/driver, or starboard) and rotated every two hours.

When a dolphin group was sighted, survey effort was stopped and we travelled to the position where the animals were first observed. Latitude, longitude, time and environmental data (e.g. sea surface temperature, depth, turbidity, wind speed and direction, swell height and direction, tide state and salinity) were all recorded at this time (Appendix A). Environmental data were assessed using a thermometer to measure sea surface temperature, a sonar unit to measure depth, a secchi disc to measure turbidity, an anemometer to measure wind speed, a refractometer to measure salinity and a compass to assess wind and swell direction. Group size was estimated based on a minimum count of animals observed to surface at one time. Group composition was determined by counting the minimum number of adults and documenting the presence of juveniles and calves (Table 2.2). Field count estimates were later adjusted, based on photo-identification data, by increasing the minimum number of individuals present if more marked individuals were photographed than the field estimate obtained. Photo-identification was conducted using a Nikon D-100 digital camera, while maintaining a parallel position to the individuals being photographed (Würsig and Jefferson 1990). For further detail on photo-identification protocols, see Chapter 3 (section 3.2).

Thirty-six independent groups were assessed between 2003 and 2005. Behavioural samples were deemed independent based on the fact that they occurred on different days and/or in different Sounds. Behavioural samples were obtained once photo-identification was completed. At the start of all behavioural samples, data were

collected on group size, location, and inter-spatial proximity between individuals (Appendix C). Dolphin groups were defined by spatial proximity using the “10 meter chain rule” (Smolker *et al.* 1992), with all dolphins within 10 m of their nearest neighbour considered part of the same group. Since, groups were determined by spatial proximity, members within a group could be observed in multiple behavioural states per sample. Therefore, during each interval, all behavioural states present were noted. Focal group follows (Lehner 1996) were conducted using scan sampling (Mann 2000), to assess the predominant behavioural state of the animals (Table 2.1), (Shane *et al.* 1986) and the number of animals present at five-minute intervals for a minimum of one hour. To reduce observer bias, the same observer (M. Merriman) identified all behavioural states throughout the study. All behavioural samples were obtained from the research vessel, thus some influence of the observation platform will undoubtedly have affected the behaviour collected from observed individuals.

Table 2.1. Bottlenose dolphin behavioural states used during this study (Based on Shane *et al.* 1986). For further detail on definitions and behaviours recorded see Appendix B.

Behavioural State	Definition
Foraging/Feeding	Diving for long periods of time, exhibiting behaviours such as fluke out dives, herding and fish in mouth.
Socialising	Different behaviours are observed throughout the group such as social rubbing, aggressiveness, mating and chasing.
Travelling	Moving at a steady pace and in a constant direction. (Faster than idle speed of the research vessel).
Resting	Moving slowly in a constant direction. (Slower than idle speed of the research vessel.)
Milling	No net movement in any particular direction and group members often surface in different directions.

Data Analysis

Distribution and Habitat Use

New Zealand Mapped GPS 2002 software was used to plot bottlenose dolphin sightings based on group size and season. Statistical analysis was conducted using SPSS 10.0 to assess usage of the Sounds by various group sizes in relation to their position within each sound, area, and seasonal occurrence. All data were tested for normality using a Kolmogorov-Smirnov test. In most cases, data were non-normal so I used the non-parametric Kruskal-Wallis test along with a Bonferroni's correction to assess differences in habitat use by season, sea surface temperature, salinity, depth and turbidity.

Group Size and Composition

Group size and age classes were determined from field observations and photo-identification records. Group sizes were defined as small (≤ 25), medium (26 - 60) and large (≥ 61) based on natural separation in the data (Figure 2.5). Group age class definitions are provided in Table 2.2.

Table 2.2. Age classes followed by definitions from Mann and Smuts (1999) and Mann *et al.* (2000).

Age Class	Definition
Neonate	Defined based on the presence of foetal folds (Cockcroft and Ross 1990b). This stage lasts up to 3 months and is denoted by uncoordinated surfacing behaviour (Mann and Smuts 1999).
Calf	One-half the size of an adult dolphin. This stage ranges from 4 months up to 4 years with the animal often observed swimming along side an adult animal in echelon or nursing positions (Mann <i>et al.</i> 2000, Mann and Smuts 1999).
Juvenile	Two-thirds the size of an adult often observed in close association with an adult but never observed in the nursing position (Mann and Smuts 1999).
Adult	Large marked or un-marked individuals that are 3.0m in length. Smaller females were also classified as adults if observed nursing a calf (Mann <i>et al.</i> 2000).

To assess if group size and composition were affected by seasonal variations or other environmental factors, statistical analysis was carried out using SPSS 10.0. All data were tested for normality using a Kolmogorov-Smirnov test. Data were non-normal so I used the non-parametric Kruskal. Influences on group size were tested using a Spearman's rank correlation, Kruskal-Wallis test and Bonferroni's correction to assess if season, salinity, water depth, calf presence, juvenile presence, or sea surface temperature had an affect on group size (Table 2.8). Seasons were based on austral seasons (Winter = June-August, Spring = September-November, Summer = December-February and Autumn = March-May).

Activity Budgets

To better understand how bottlenose dolphins utilise the Marlborough Sounds, activity budgets were examined using focal group follow data from 2003 to 2005. Only behavioural samples exceeding 60 minutes on different groups were used in the present analysis. All samples were standardised to generate proportions of the five different behavioural states. Mean values generated from this were than used in statistical analysis. Data were tested for normality using Kolmogorov-Smirnov in SPSS version 10.0. Non-parametric tests were used in the present analysis, since the data were non-normally distributed. A Kruskal-Wallis test was preformed to test differences in activity states based on group size, location and seasons. Tests were run comparing the three group sizes (small, medium and large) and the population as a whole.

2.3 Results

Survey Effort

Survey effort consisted of 578 hours on 125 days from October 2003 through to the end of August 2005. A total of 132 surveys were conducted in the Marlborough Sounds region, with the highest number ($n = 63$) of surveys conducted in 2004 (Table 2.3). Queen Charlotte Sound had the highest survey effort and the highest number of sightings compared to the other regions (Table 2.4). However, sightings per hour show that Queen Charlotte and Admiralty Bay have the same sighting rates, with Pelorus having a slightly lower sighting rate. Most surveys occurred during the summer months due to weather conditions; hence summer had the highest number of sightings (Table 2.5). Sighting rates are the same for summer and winter, with a slightly lower sighting rate in spring and the lowest sighting rate in autumn.

Table 2.3. Number of surveys conducted, number of sightings recorded and hours of effort for each year from 2003-2005.

Year	No. of surveys	% of surveys	No. of sightings	% of sightings	Hours of effort	% of effort	Sightings per hour
2003	12	9.1	5	11.1	53	9.2	.09
2004	63	47.7	22	48.9	250	43.2	.09
2005	57	43.2	18	40.0	275	47.6	.07
Total	132	100.0	45	100.0	578	100.0	.08

Table 2.4. Number of sightings and survey effort for each of the three areas within the Marlborough Sounds from 2003-2005.

Area	No. of sightings	% of sightings	Hours of effort	% of effort	Sightings per hour
Queen Charlotte Sound	30	66.7	354	61	.08
Pelorus Sound	8	17.8	141	21	.05
Admiralty Bay/Current Basin	7	15.5	83	18	.08

Table 2.5. Number of sightings and survey effort based on Austral seasons for the Marlborough Sounds region from 2003-2005. Note 2004 was the only year in which fieldwork was conducted in all four seasons.

Austral Seasons	No. of sightings	% of sightings	Hours of effort	% of effort	Sightings per hour
Winter	11	24.4	116	14	.09
Spring	11	24.4	146	24	.07
Summer	16	35.6	162	35	.09
Autumn	7	15.6	154	24	.04

Thirty-six independent behavioural samples were collected during these surveys, with 71 total hours of observations documenting the behaviour of focal bottlenose dolphin groups in the Marlborough Sounds.

Distribution

Sightings of bottlenose dolphins occurred throughout the entire 890 km² of the Marlborough Sounds. Individual identifications from photographs taken in each of the three areas showed that 89% (n = 301) of individuals photographed in the sounds (n = 335) were photographed in more than one area; 40.6% (n = 136) in three different areas; 49.3% (n = 165) in two different areas; and 10.1% (n = 34) in only one area. Queen Charlotte Sound had the highest number of individuals photographed (n = 250), although this area also had the greatest amount of effort. Many individuals that were sighted in QC were also observed in the other areas (PS = 44%, AB = 45%) (Table 2.6).

Table 2.6. Number of individuals observed in each area of the Marlborough Sounds. Followed by the number of individuals also observed in other areas.

Area	Number of individuals	Also sited in QC N (%)	Also sited in PS N (%)	Also sited in AB N (%)
QC	250	-----	111 (44)	114 (45)
PS	133	111 (83)	-----	72 (54)
AB	174	114 (65)	72 (41)	-----

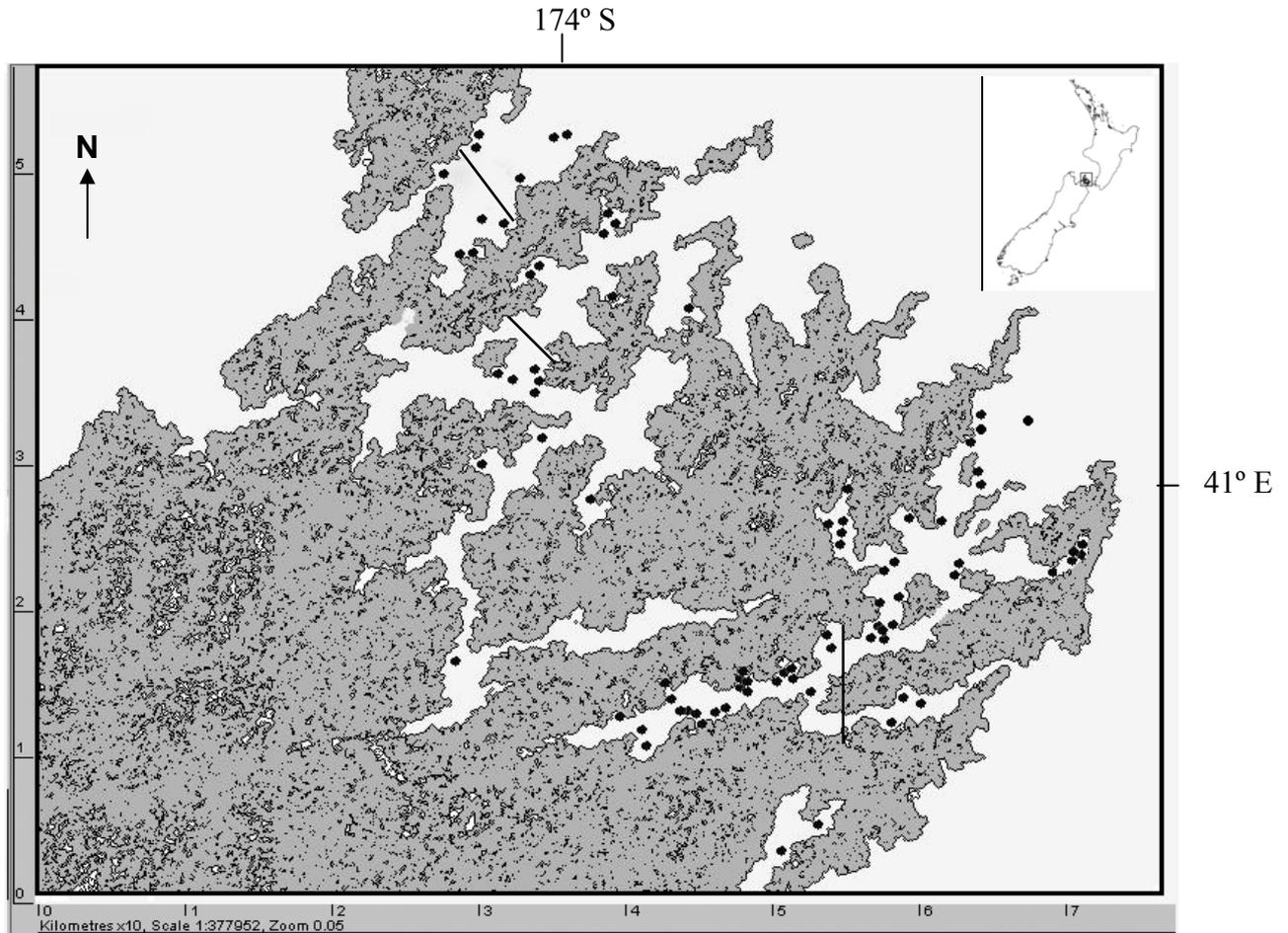


Figure 2.2. Sightings of bottlenose dolphins in the Marlborough Sounds during 2003-2005. Lines denote inner versus outer sound areas.

Habitat Use

Environmental data collected from 2003 to 2005 in the Marlborough Sounds during this study showed sea surface temperatures ranged from 11.0 to 19.5°C (mean = 14.9, \pm SE = 0.39), salinity levels ranged from 34.0 to 37.0 (mean = 35.3, \pm SE = 0.32) and depth ranged from 2.1 to 80.6 m (mean = 29.2 m, \pm SE = 2.8). Sightings during 2003-2005 occurred in all three areas of the Marlborough Sounds (Figure 2.2). Sightings occurred in all seasons during the 2004 field season. The distribution of each group size category throughout the Sounds is shown in Figure 2.4. A Kruskal-Wallis test showed no significant difference in use of the Sounds by different group

sizes with respect to area, location (inner sounds or outer sounds) or season (Table 2.8). No bottlenose dolphin groups were recorded during the summer and autumn seasons in AB and no groups were recorded in PS in the autumn season (Figure 2.3). No medium or large groups were recorded in AB from 2003 to 2005 (Figure 2.4).

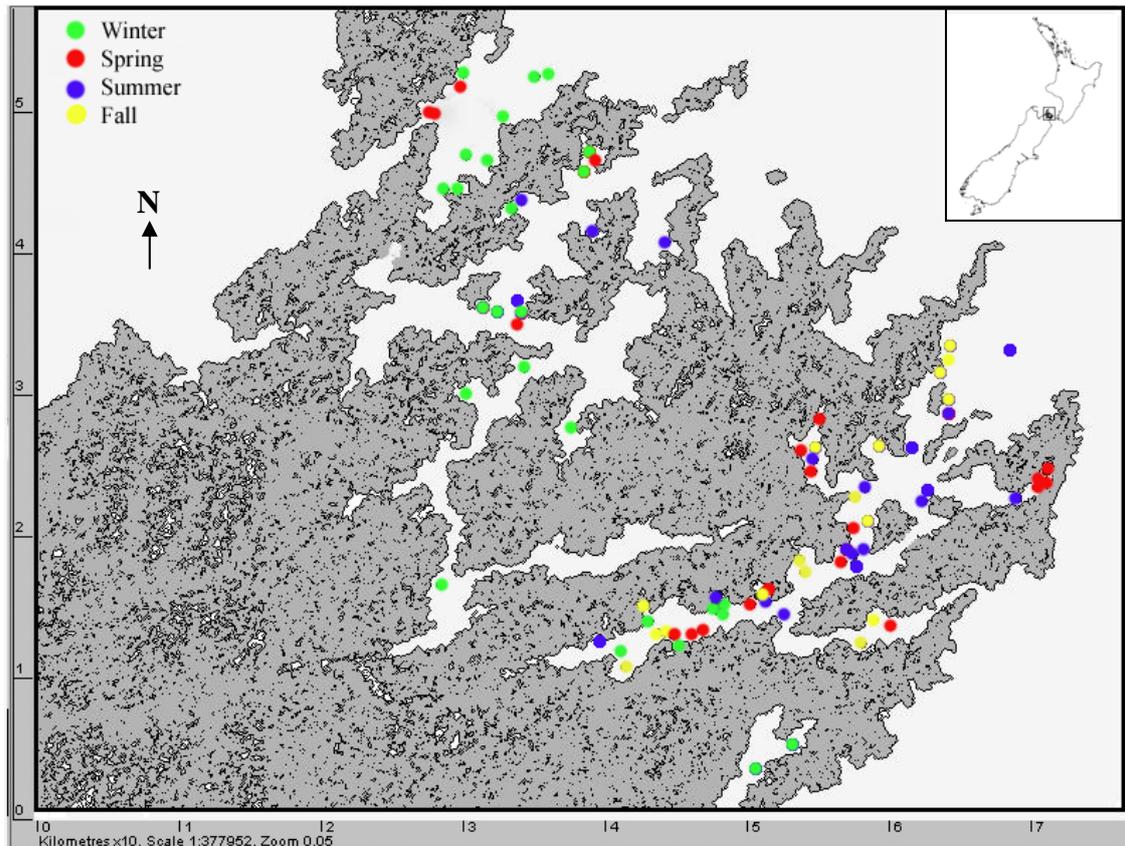


Figure 2.3. Bottlenose dolphin sightings in the Marlborough Sounds from 2003 to 2005 displayed by season (winter = green, spring = red, summer = blue, and autumn = yellow).

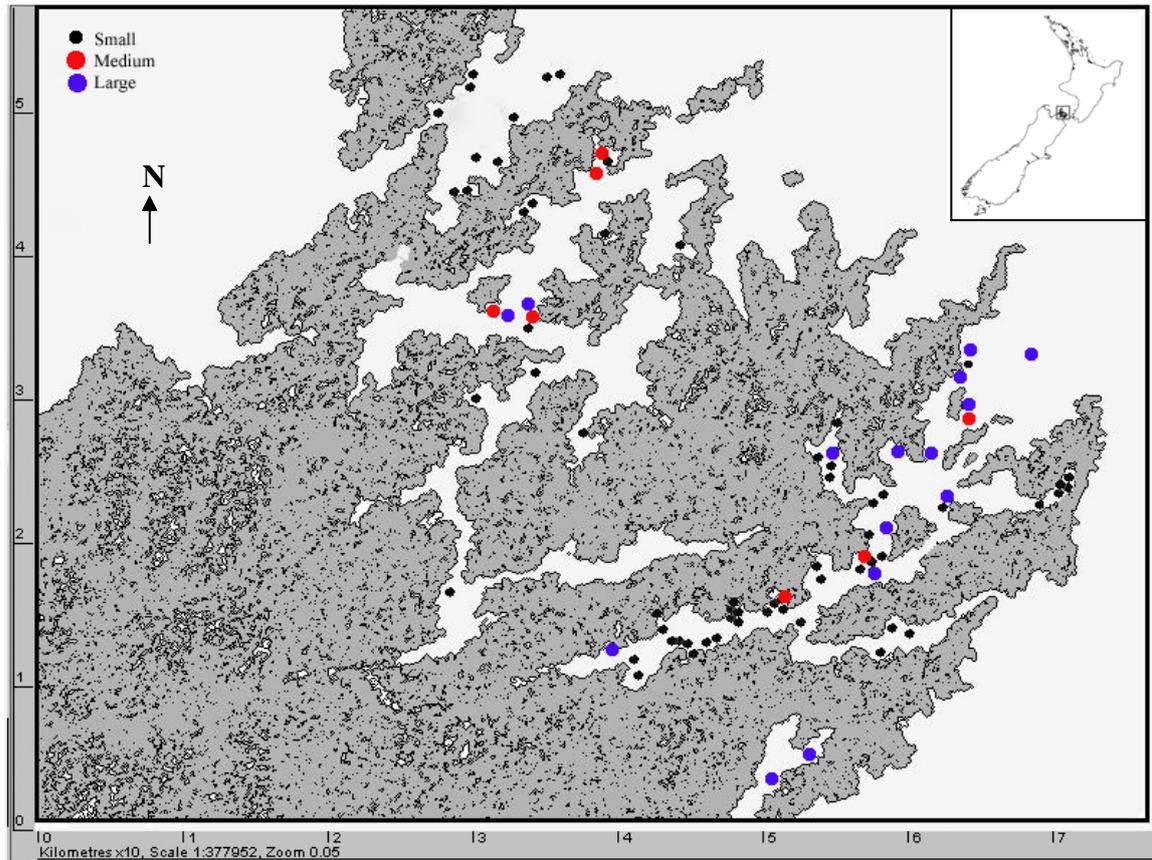


Figure 2.4. Sightings of bottlenose dolphin groups in the Marlborough Sounds from 2003 to 2005. Group sizes are represented by colour; small 0-25 individuals (black), medium 26-60 individuals (red), and large 61+ individuals (blue).

Group Sizes and Composition

Group size and composition were examined for 45 independent groups encountered between 2003 and 2005. Group sizes during 2003-2005 ranged from 3-172 individuals (median = 12, SD = 38, \pm SE = 0.84) with most groups ($n = 19$) encountered containing only 11-15 animals (Figure 2.5). Based on the defined criteria, the percentage of group sizes encountered between 2003 and 2004 was 69% small, 10% medium and 21% large. Calf presence was the only variable that significantly influenced group size (Kruskal-Wallis, $H = 29.42$, $P = 0.000$) (Table 2.8). When calves were present group size was larger ($n = 23$, mean group size = 50.87 , \pm SE = 9.23) than when calves were absent ($n = 22$, mean group size = 10.5 , \pm SE = 0.87) (Table 2.7).

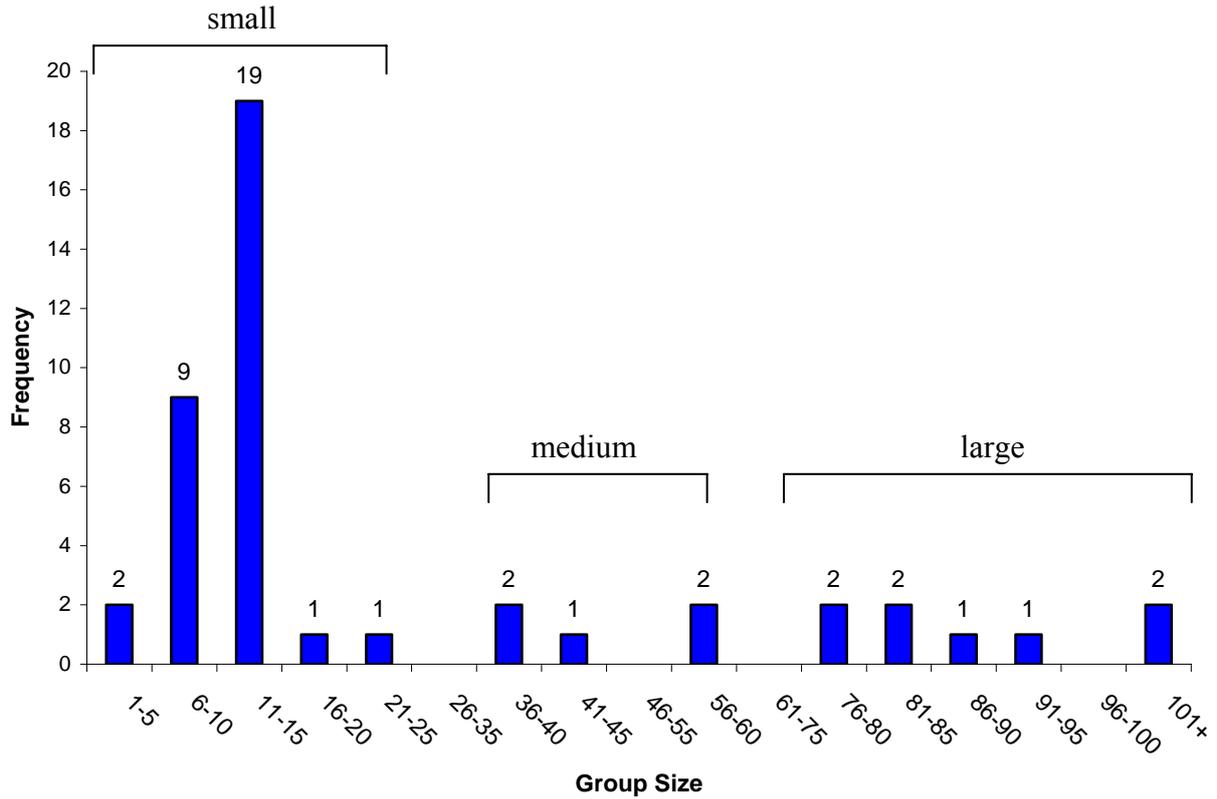


Figure 2.5. Estimated group sizes based on minimum photo-identification and field counts for 2003-2005, ranged from 3 to 172 individuals (median = 12, SD = 38.0), with most groups (n = 19) encountered containing 11-15 dolphins.

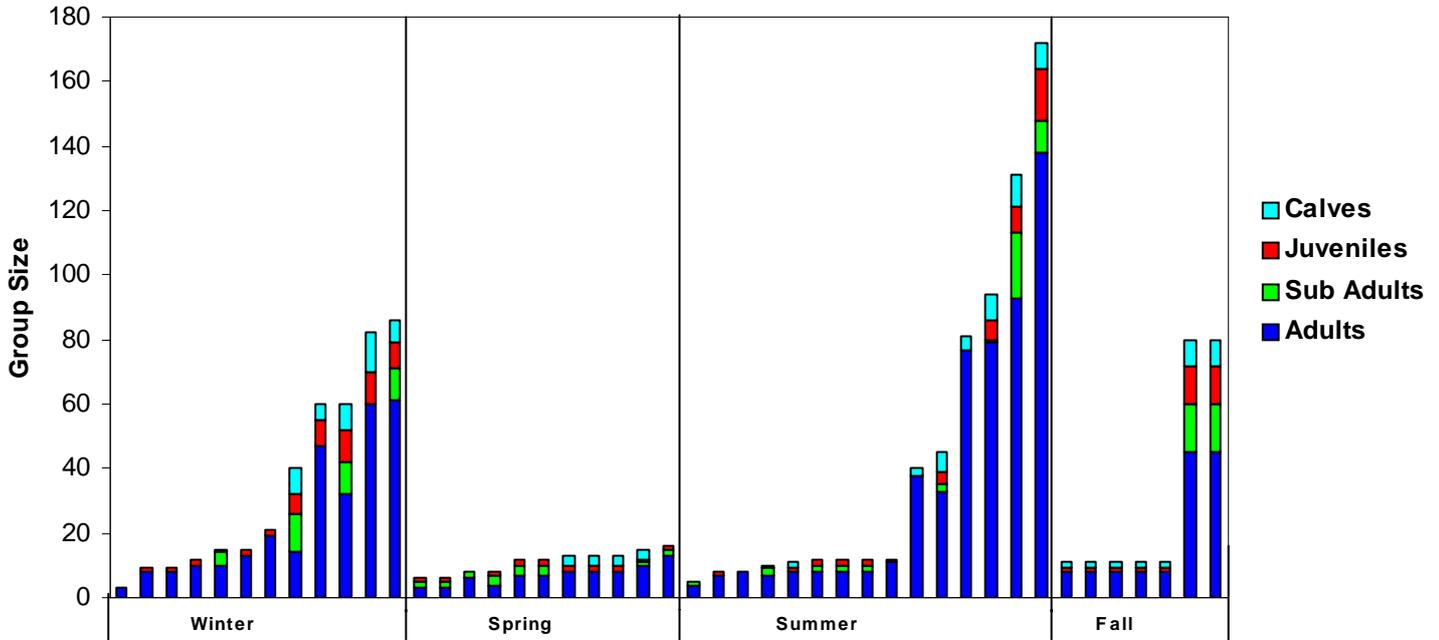


Figure 2.6. Group size and composition for groups (n = 45) encountered on different days or same day different sound from 2003-2005 by season. Each bar = one observation, ordered by group size

Calf Presence

The number of calves present in a group increased with group size (small = 0.72, medium = 5.80 and large = 8.13), with medium and large sized groups having significantly higher numbers than small groups (Kruskal-Wallis, $H = 29.42$, $P = 0.000$, d.f. = 2). The mean percent of calves present per group varied based on group size (small = 5.91, medium = 12.00 and large = 8.57), with medium and large groups showing significantly higher percentages than small groups (Kruskal-Wallis, $H = 6.01$, $P = 0.050$, d.f. = 2) (Table 2.7). Calves were present in small groups during the spring, summer and autumn seasons and were observed in large groups during the winter, summer and autumn. Winter ($n = 40$), summer ($n = 40$) and autumn ($n = 40$) had the highest number of calf observations and spring ($n = 12$) had the lowest number of calf observations. Summer (1.6%) and winter (3.7%) had lower percentages of calves per group compared to spring (9.3%) and autumn (13.8%) seasons (Kruskal-Wallis, $H = 16.41$, $P = 0.001$, d.f. = 3) (Figure 2.6).

Table 2.7. Mean number of calves within various group size classes.

Size Classes	Group size	No. of calves	% of calves per group	No. of groups
Small ≤ 25	10.9	0.7	5.9	32
Medium 26-60	49.0	5.8	12.0	5
Large ≥ 61	100.6	8.1	8.5	8

Group size was tested in relation to water depth, salinity, sea surface temperature (SST) and turbidity using a non-parametric Kruskal-Wallis test. Group size did not vary significantly by position (inner sounds or outer sounds), season, or area (QC, PS, and AB).

Sea surface temperature (Kruskal-Wallis, $H = 7.07$, $P = 0.008$, d.f. = 1) (Table 2.8) was significantly lower in the inner sounds (mean = 13.8, SE = 0.44) than in the

outer sounds (mean = 15.9, SE = 0.54). Salinity (Kruskal-Wallis, H = 11.94, P = 0.008, d.f. = 3) and sea surface temperature (Kruskal-Wallis, H = 31.02, P = 0.000, d.f. = 3) (Table 2.8) varied seasonally with the lowest values for salinity and SST in winter (salinity mean = 34.00, SE = 0.91, SST mean = 11.8, SE = 0.15) and higher values in summer (salinity mean = 36.08, SE = 0.26, SST mean = 17.2, SE = 0.36), autumn (salinity mean = 35.14, SE = 0.14, SST mean = 14.8, SE = 0.00), and spring (salinity mean = 36.11, SE = 0.45, SST mean = 14.8, SE = 0.37).

Turbidity (Kruskal-Wallis, H = 11.42, P = 0.010, d.f. = 3) (Table 2.8) varied significantly between areas with QC having lower water clarity (mean = 6.03, SE = 0.44) than PS (mean = 10.43, SE = 1.10) and AB (mean = 9.40, SE = 1.43).

Table 2.8. Environmental factors influencing group size, position, season and area. Significance based on p-values, * denotes significance.

Test Variables	Kruskal-Wallis		
Group size (small, med, lg) vs.	H	p-value <0.008	d.f.
Salinity	0.008	0.996	2
Sea Surface Temperature	1.154	0.562	2
Location (inner/outer)	1.580	0.454	2
Season	2.477	0.480	3
Depth	1.531	0.465	2
Turbidity	6.810	0.033	2
Area (QC, PS, AB)	5.389	0.068	2
Calf Presence	29.418	0.000 *	2
Juvenile Presence	0.212	0.900	2
Position (inner/outer) vs.	H	p-value <0.01	d.f.
Salinity	6.009	0.014	1
Sea Surface Temperature	7.071	0.008 *	1
Depth	0.019	0.889	1
Turbidity	0.347	0.556	1
Season vs.	H	p-value <0.01	d.f.
Salinity	11.941	0.008 *	3
Sea Surface Temperature	31.020	0.000 *	3
Depth	4.309	0.230	3
Turbidity	6.406	0.093	3
Area (QC, PS, and AB) vs.	H	p-value <0.01	d.f.
Salinity	1.004	0.800	3
Sea Surface Temperature	4.007	0.261	3
Depth	3.677	0.298	3

Activity Budgets

Activity budgets were analysed for 36 independent groups of bottlenose dolphins observed for a minimum of one hour in the Marlborough Sounds from 2003 to 2005. Activity budgets were calculated for the Marlborough Sounds region as a whole and individually for Queen Charlotte Sound, Pelorus Sound and Admiralty Bay areas. Activity budgets were also calculated for all seasons and various group sizes (small, medium, and large). Activity budgets within the Marlborough Sounds showed that bottlenose dolphins spent the majority of their time travelling (48%) and socialising (23%) (Figure 2.7).

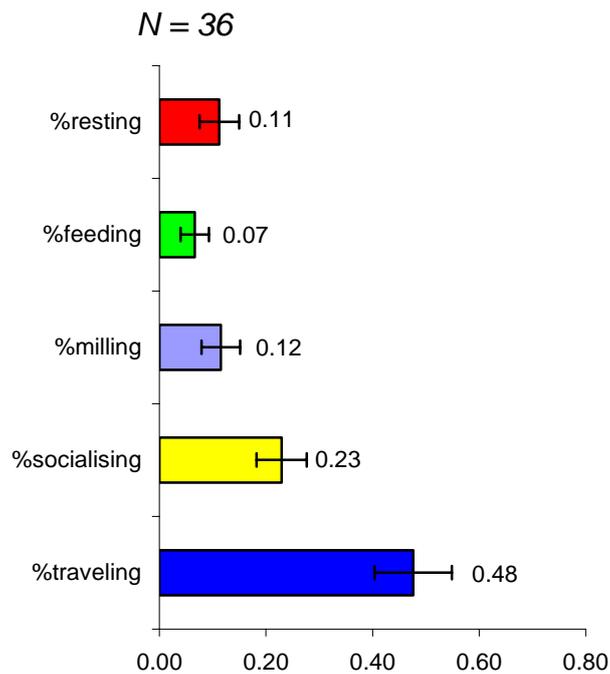


Figure 2.7. Bottlenose dolphin daily activity budgets for the Marlborough Sounds region as a whole. Activity states are represented by percents. All behavioural states observed within groups were noted and standardised per group. Standard error bars are shown.

Area

Dolphins socialised significantly more often in Admiralty Bay ($n = 6$, mean = 0.41) than in Queen Charlotte Sound ($n = 23$, mean = 0.18) and Pelorus Sound ($n = 6$, mean = 0.21) (Kruskal-Wallis = $H = 6.747$, $P = 0.034$, d.f. = 2) (Figure 2.8). No significant difference was detected for the other behavioural states.

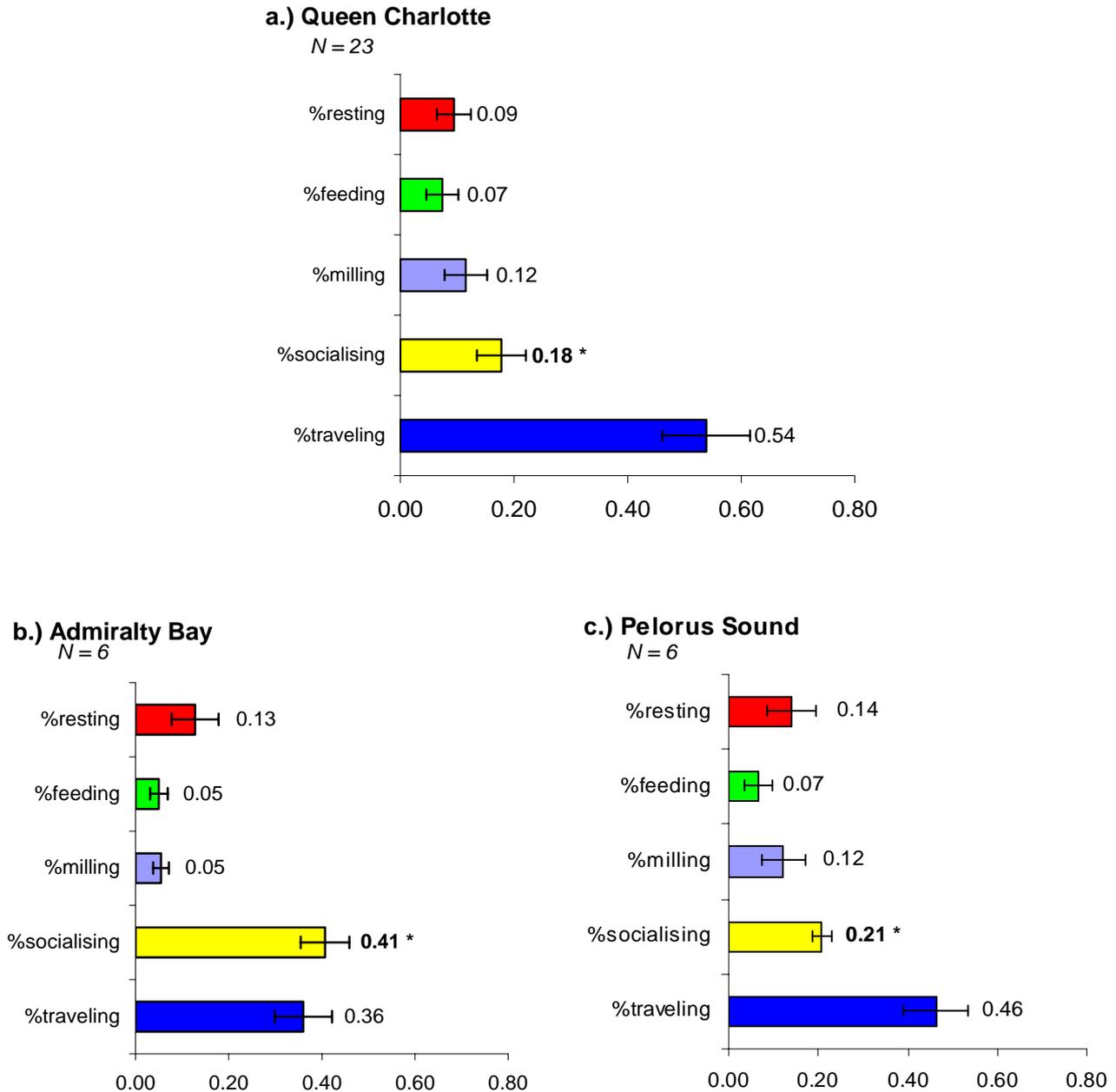


Figure 2.8. Bottlenose dolphin daily activity budgets by area for the Marlborough Sounds region. Activity states are represented by percents. Significant differences (Kruskal-Wallis, $P < 0.05$) are indicated by *. All behavioural states observed within groups were noted and standardised per group. Standard error bars are shown.

Season

Dolphins rested less in spring ($n = 9$, mean = 0.03) than in winter ($n = 9$, mean = 0.11), summer ($n = 12$, mean = 0.15) and autumn ($n = 6$, mean = 0.16) (Kruskal-Wallis = $H = 8.060$, $P = 0.045$, d.f. = 3) (Figure 2.9). No significant difference was detected for the other behavioural states.

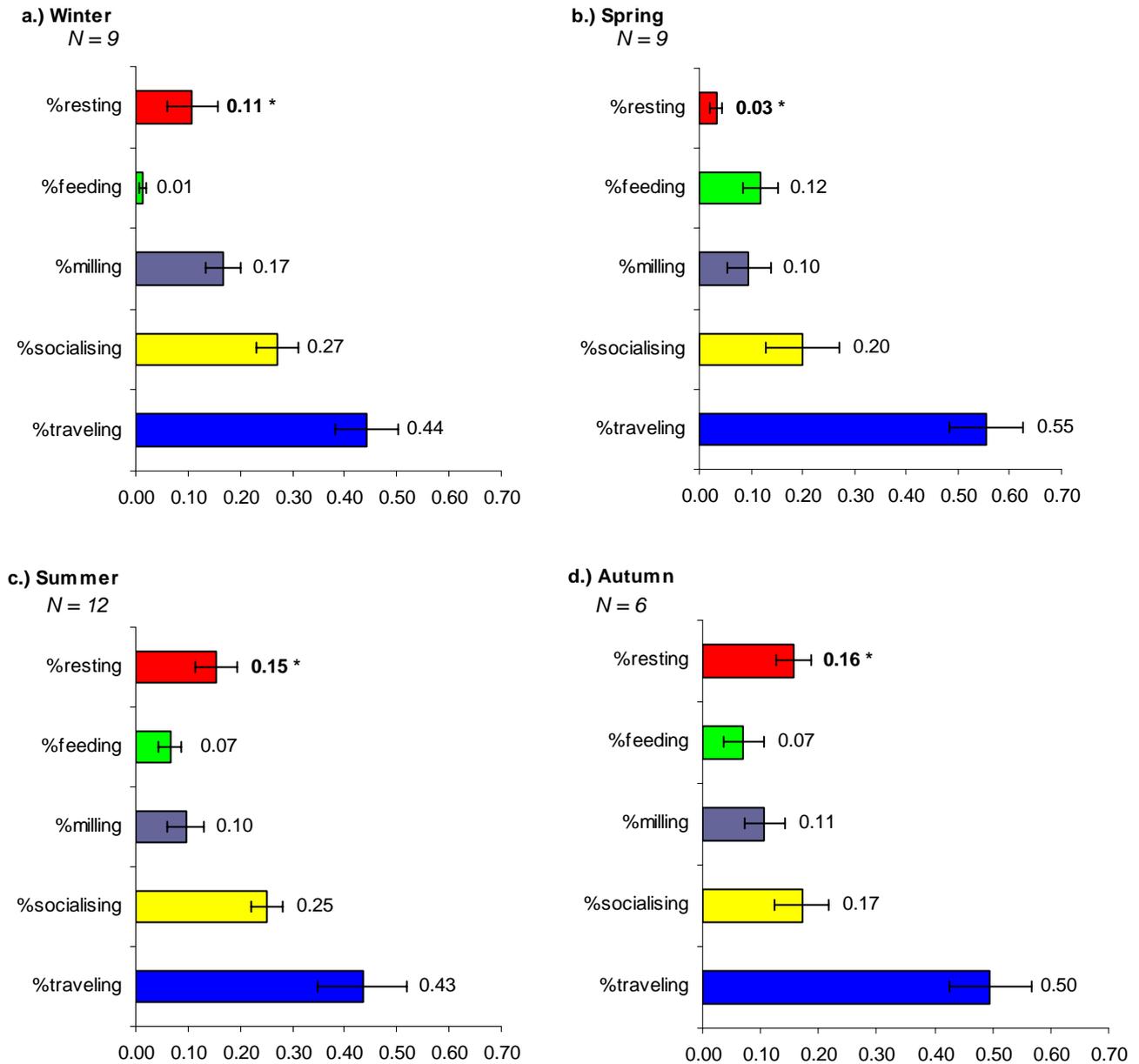


Figure 2.9. Bottlenose dolphin daily activity budgets by season for the Marlborough Sounds region. Activity states are represented by percents. Significant differences (Kruskal-Wallis, $P < 0.05$) are indicated by *. All behavioural states observed within groups were noted and standardised per group. Standard error bars are shown.

Group Size

Analysis of activity budgets for various group sizes showed a significant difference in resting behaviour between the three groups, with smaller ($n = 25$, mean = 0.08) groups resting less (Kruskal-Wallis = $H = 6.515$, $P = 0.038$, d.f. = 2) than medium ($n = 4$, mean = 0.20) and large ($n = 7$, mean = 0.19) groups (Figure 2.10). No significant difference was detected for the other behavioural states.

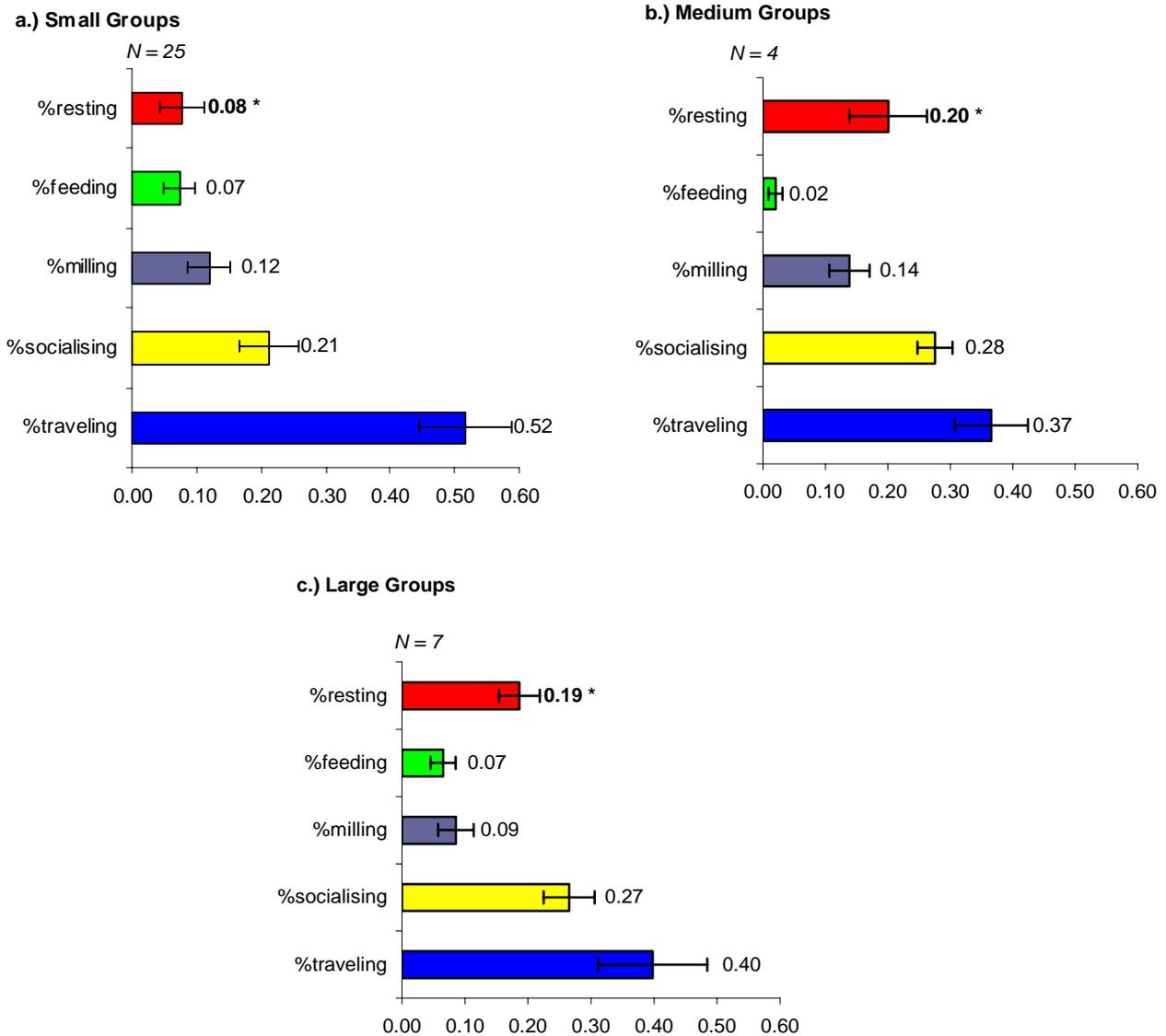


Figure 2.10. Bottlenose dolphin daily activity budgets by group size for the Marlborough Sounds region. Activity states are represented by percents. Significant differences are indicated by *(Kruskal-Wallis, $P < 0.05$). All behavioural states observed within groups were noted and standardised per group. Standard error bars are shown.

Overall, travelling and socialising were the most frequently observed behaviours for all group sizes, over all seasons and in all locations throughout the Marlborough Sounds (Figure 2.7).

2.4 Discussion

Distribution

Bottlenose dolphins were observed in the Marlborough Sounds region year round, ranging over an area greater than 890 km². Variation in range between populations of bottlenose dolphins is great, with individuals in Sarasota Bay, Florida showing movement patterns ranging over a small area of 125 km² (Wells *et al.* 1980, Irvine *et al.* 1981, Scott *et al.* 1990) and in the Northern Adriatic Sea where Bearzi (1997) found individuals occurring year round ranging over an area greater than 800 km². Populations studied in New Zealand show bottlenose dolphins in the Bay of Islands were observed year round with sightings occurring in all seasons ranging over a 300 km area (Constantine 2000). In New Zealand, the southernmost population of bottlenose dolphins in Doubtful Sound inhabit a much smaller home range of only 40.3 km² with individuals showing year round residency (Schneider 1999).

The population in the Marlborough Sounds is similar in the area it covers to the population in the Northern Adriatic Sea that ranges over an area larger than 800 km². Ranging over such a large area may be attributed to patchiness of prey, dolphin density or habitat quality (Shane *et al.* 1986). Decreases in blue cod (*Parapercis colias*) and other fish species in the Marlborough Sounds (local fishermen, personal communication) may be a contributing factor to such large ranging patterns. Further research on spatial and temporal patterns of prey species in the Marlborough Sounds may provide further insight into causal factors in bottlenose dolphin distribution and

habitat use within this region. Additionally, future photo-identification efforts in other adjacent areas could provide valuable insight into the full range of this population.

The distribution of group sightings within the Marlborough Sounds was not consistent for the three group size classes by area or season. The absence of bottlenose dolphins during summer and autumn seasons in Admiralty Bay from 2003 to 2005 is most likely a result of survey effort. Anecdotal evidence and opportunistic photo-identification data document groups in Admiralty Bay during the summer and autumn seasons.

Habitat Use

Population

Bottlenose dolphins in the Marlborough Sounds did not show seasonal variation in their habitat use with regard to depth, turbidity, salinity, sea surface temperatures, and location within the sounds. However, there were significant seasonal differences in salinity and sea surface temperatures. This apparent lack of seasonal changes in habitat use is unlike the two other populations of bottlenose dolphins found in the Bay of Islands (Constantine 2002) and Doubtful Sound, New Zealand (Schneider 1999). Both bottlenose dolphin populations in these areas were found to change their habitat use seasonally in relation to sea surface temperatures (Constantine 2002, Schneider 1999). The three areas differ somewhat in their sea surface temperature ranges with the Bay of Islands ranging from 10 to 22°C (Constantine 2002), Doubtful Sounds from 7 to 17.7°C (Schneider 1999) and the Marlborough Sounds from 11.0 to 19.5°C (Merriman unpublished data). Although seasonal variation in sea surface temperature range in the Marlborough Sounds is smaller than those of the other areas, dolphin habitat use in the area did not vary seasonally. Instead the bottlenose dolphins in the

Marlborough Sounds are more like the bottlenose dolphins found off the southern coast of Argentina (Würsig 1978). Würsig (1978) reported that bottlenose dolphins in the Gulf of San Jose, Argentina were observed year round and occurred in water temperatures ranging from 10.5 to 18°C. Like the bottlenose in the Marlborough Sounds, the bottlenose dolphins in the Gulf of San Jose, showed no seasonal migration patterns and did not appear to follow a sea surface temperature gradient (Würsig 1978).

Other potential factors for use of the Marlborough Sounds year round may be attributed to the availability of prey and protection from predators. Research on bottlenose dolphins off the west coast of Florida showed shifts in habitat use due to prey availability with dolphins following the movements of the striped mullet (*Mugil cephalus*) (Balance 1992). Prey availability in the Marlborough Sounds is unknown but appears to be diverse with the occurrence of bottlenose dolphins and other cetacean species such as dusky dolphins (*Lagenorhynchus obscurus*), common dolphins (*Delphinus delphis*) and Hector's dolphins observed feeding in this region year round (personal observation). Studies of bottlenose dolphins in western Australia reported that Tiger shark (*Galeocerdo cuvier*) predation influenced habitat use (Heithaus and Dill 2002). Seasonal shifts in habitat use were attributed to the increase of shark presence (Heithaus and Dill 2002). It was reported that during the warmer months dolphin groups spent less time in the shallow feeding grounds, where shark densities were high and more time in the deeper waters where shark densities were low (Heithaus and Dill 2002). It is likely that the Marlborough Sounds provides year round prey availability and protection from possible predators for the bottlenose dolphins and other species that utilise this region.

Groups

There was no significant difference in habitat use by the three different group sizes in regards to location (inner/outer) within the sounds, season and area. Group sizes in the Marlborough Sounds were much larger than those reported for other populations. Twenty-one percent of groups encountered in the Marlborough Sounds contained ≥ 81 individuals. One group encountered consisted of at least 172 animals. This number is unusually high for bottlenose dolphins inhabiting a near shore coastal environment (Bräger *et al.* 1994, Rertl 1994, Irwin and Würsig 2004, Bearzi 2005, Hubbard *et al.* 2004, Speakman *et al.* 2006, Bearzi *et al.* 1997, Bearzi *et al.* 2005, Baird *et al.* 2001, Wilson *et al.* 1993, Mann *et al.* 1999). Few studies have reported mean group sizes of bottlenose dolphins higher than 15 (Defran and Weller 1999, Hansen 1990, Scott and Chivers 1990, Saayman and Tayler 1973) and only a few (Scott and Chivers 1990, Saayman and Tayler 1973) have reported group size ranges similar to those encountered in the Marlborough Sounds.

In New Zealand, groups encountered in the Bay of Islands ranged from 2-50 (Constantine 2002). This is smaller than groups encountered in the Marlborough Sounds. However the median group size (8-12) reported in the Bay of Islands (Constantine 2002) is similar to the median group size (12) observed in the Marlborough Sounds. The range in group size reported for the population in Doubtful Sound (Williams 1995) is also different to the Marlborough Sounds population. Group sizes in Doubtful Sound ranged from 2-60 with a mean of 26.7. Differences in group sizes for these three populations may be due to the topography of the habitats in which they are found. Lusseau *et al.* (2003) suggest that basic oceanographic factors such as isolated regions, sea surface temperatures, and depth may influence bottlenose dolphin social organisation in Doubtful Sound. Hence, these factors may also

influence group size. The Marlborough Sounds are larger, warmer and more exposed than Doubtful Sound and cooler, deeper and more protected than the Bay of Islands. These differences in habitats may be a contributing factor in the occurrence of large group sizes in the Marlborough Sounds population.

Group size varied significantly with the presence of calves, with groups containing calves larger than groups without calves. This has been observed for many populations of bottlenose dolphins in various locations including, the northern Adriatic Sea (Bearzi *et al.* 1997, Mississippi Sound, Mississippi (Hubard *et al.* 2004), Galveston, Texas (Fertl 1994), San Diego, California (Weller 1991), and Sarasota Bay, Florida (Wells *et al.* 1987). It has been suggested that populations which form large groups in relation to calf presence may do so for protection from predators, strengthening of social bonds between individuals and access to food through cooperative feeding (Norris and Dohl 1980, Würsig 1986, Weller 1991, Mann *et al.* 1999). However, in the Marlborough Sounds there was no evidence of shark predation and very few cooperative feeding events. Therefore, it seems likely that other sociological benefits associated with large group size influence the structure of this population. Analysis on the social structure of this population is presented in Chapter IV and may provide further insight into these large aggregations.

Calves were observed in the Marlborough Sounds year round with the greatest number of calves per group observed in the spring and autumn seasons. Neonates were only observed in the summer and autumn seasons, suggesting a summer-autumn calving season. This is similar to birthing seasons reported in other bottlenose dolphin populations (Würsig 1978, Irvine *et al.* 1981, Wells *et al.* 1987, Urian *et al.* 1996, Bearzi *et al.* 1997, Mann *et al.* 2000) where births peaked from late spring through to early autumn.

Definitions of seasons used in this study were the same as those used in the Bay of Islands study (Constantine 2002). Seasons were defined differently in the Doubtful Sound study (Schneider 1999), which should be noted when comparing results. Neonates were observed in summer (n = 18), spring (n = 1) and winter (n = 3) in the Bay of Islands and in summer (Jan-March, n = 6), spring (Oct-Dec, n = 1) and autumn (April-June, n = 2) for the Doubtful Sound region. The Bay of Islands appears to have a slightly higher number of births (1997 n = 4, 1998 n = 6, 1999 n = 9) than the Marlborough Sounds (2003 n = 0, 2004 n = 8, 2005 n = 0) and Doubtful Sound (1995 n = 2, 1996 n = 5) regions. This may be due to warmer sea surface temperatures or differences in population size or abundance of available prey. The apparent disparity in the number of neonates observed may also be attributed to lack of data during the spring months in the Marlborough Sounds. Both the Bay of Islands and Doubtful Sound studies show a single peak in births occurring in the summer months. Higher birthing rates during warmer months are a common occurrence among populations of bottlenose dolphins (Würsig 1978, Wells *et al.* 1987, Mann *et al.* 2000) and have been attributed to warmer water temperatures and thermoregulation needs for small calves (Würsig 1978, Wells *et al.* 1987, Mann *et al.* 2000). Other studies have suggested that birthing rates are not influenced directly by water temperature (Urian *et al.* 1996) but instead are linked to prey availability/migration and the nutritional needs of lactating females (Oftedal 1997, Boyd 1991). The availability and migratory patterns of prey species for the bottlenose dolphins in the Marlborough Sounds are unknown and may contribute to the calving season.

Activity Budgets

Activity budgets for the Marlborough Sounds showed that socialising was the only state significantly different between areas, with dolphins socialising more in Admiralty Bay than other regions. This result may be a sampling artefact, due to the fact that only small groups were observed in this region over the course of this study. Activity levels for various group sizes showed that smaller groups rest less than medium and large groups. This result is similar to reports from Shark Bay, Western Australia, where large groups were observed resting more than small groups (Heithaus and Dill 2002). There are many factors, which may explain why a smaller group rests less than a larger group. It is possible that predator detection and foraging opportunities may be reduced for smaller groups compared to larger groups. Reduced numbers of individuals may need to be more attentive to their surroundings, in order to detect predators and take advantage of possible foraging opportunities. Another likely factor is group dynamics. Smaller groups in the Marlborough Sounds primarily consisted of adults of unknown sex. The absence of calves from these groups may mean that the small groups observed in the Sounds are mating or bachelor groups. Further research on sex specific data may provide a better understanding on the small groupings observed in the Sounds.

Seasonal variation in activity budgets for the Marlborough Sounds showed bottlenose dolphins rest significantly less in spring than in winter, summer and autumn. One suggestion is increased feeding during spring for lactating females (Cheal and Gales 1991). Overall activity budgets for the bottlenose dolphins within the Marlborough Sounds show that 48 percent of their time in the sounds is spent travelling. This is similar to the amount of travelling observed in the Bay of Islands (Constantine 2002) and Doubtful Sound (Schneider 1999) populations. Likewise,

populations occurring off the coast of San Diego and in Santa Monica Bay showed high percentages of travelling, with San Diego at 63% (travelling plus travel/dive) (Bearzi 2005) and Santa Monica Bay at 69% (travelling plus travel/dive) (Hanson and Defran 1993). The amount of time spent socialising in the Marlborough Sounds was approximately three times higher than results reported in the Doubtful Sound (5%) (Schneider 1999) and San Diego, California (8.5%) (Bearzi 2005). Feeding occurred at a much lower rate (7%) in the Marlborough Sounds when compared with other areas. Feeding was reported in San Diego at 19% (Hanson and Defran 1993) and 16% in Santa Monica Bay (Bearzi 2005). This result suggests that the Sounds are an area used for activities related to socialising more than feeding. However, behaviour definitions and collection methods could play a roll in the differences observed between various studies (Bearzi 2005).

2.5 Summary

Bottlenose dolphins were observed in the Marlborough Sounds region year round, ranging over an area greater then 890 km². Individual identifications from photographs taken in each region of the Marlborough Sounds showed that the majority of the population were photographed in more then one region. Bottlenose dolphins in the Marlborough Sounds showed no significant variation in their habitat use in relation to the environmental variables measured. Seasonal migration patterns were not present and dolphins do not appear to follow a sea surface temperature gradient.

Group sizes were large, ranging from 3-172 individuals with most groups encountered containing 12 animals. Group sizes were typically smaller in the absence of calves. Calf presence was observed in the Marlborough Sounds year round with the

greatest number of calves per group observed during the spring and autumn seasons. Calving appeared to peak in summer to early autumn based on the presence on neonates.

Socialising was the only activity state that varied significantly with Admiralty Bay groups socialising more than groups in other areas. Resting occurred more in large and medium groups and in the winter, summer and autumn seasons. Overall bottlenose dolphins observed in the Marlborough Sounds spent the majority of their time socialising (23%) and travelling (48%) within this region. Based on the results reported in this study, the Marlborough Sounds appear to be an important part of this population's home range with at least a proportion of all individuals utilising the Sounds year round.

The three studied populations of bottlenose dolphins in New Zealand waters show similarities in their year round occurrence and calving seasons. However, disparity in habitat use, group size and range is evident between the Marlborough Sounds and these previously studied populations. The Marlborough Sounds population differs from other regions in that groups are typically twice the size of those reported for other areas. Moreover, bottlenose dolphins in the Marlborough Sounds appear to range over a much larger area. These inconsistencies could be attributed to differences in prey availability, population size and or the requirement for protection from predators.

Chapter III

Bottlenose dolphin abundance, site fidelity and movement patterns in the Marlborough Sounds, New Zealand.



Plate 3.1. Mother and calf surfacing together in the Marlborough Sounds, New Zealand.

3.1 Introduction

Abundance, site fidelity and movement patterns in nature

Obtaining population estimates and assessing trends is the first step in understanding the ecology of a species (Bowen and Siniff 1999). Abundance, site fidelity and movements patterns have been the focus of researchers for many species across various taxa. Studies on African forest elephants (*Loxodonta cyclotis*) (Eggert *et al.* 2003), long-tailed bats (*Chalinolobus tuberculatus*) (Lettink and Armstrong 2003) and polar bears (*Ursus maritimus*) (Taylor and Lee 1995), have shown that knowing the number of individuals in a population is essential in establishing effective

management and conservation efforts. Likewise, knowing the amount of time an individual spends in an area or how often they frequent it is of great importance to the management of that species. For example research on snapper (*Pagrus auratus*) in the Leigh Marine reserve, New Zealand, showed that individuals of various sizes exhibit long-term site fidelity to a 400m area (Willis *et al.* 2001). The establishment of this protected area has allowed snapper density within the Leigh Marine reserve to increase, becoming 11 times greater than densities in adjacent areas (Willis *et al.* 2001). Therefore, understanding how an animal utilises its environment provides information on the vitality of the population and thus, aids in the construction and implementation of management plans.

Movement and migration patterns are also important factors in the management of threatened or endangered populations, especially for migrating whales and sea birds moving across international waters (i.e., Buller's (*Thalassarche bulleri*), Chatham Island (*T. eremita*) and Salvin's (*T. salvini*) albatrosses and southern right (*Eubalaena australis*), humpback (*Megaptera novaeangliae*) and grey whales (*Eschrichtius robustus*).

Population monitoring in the marine environment

Examining the abundance and residency patterns of animals in the fluid, free-flowing marine environment is often difficult and laborious (Mann *et al.* 2000). Through the use of techniques such as photo-identification, satellite tagging and aerial surveys researchers have been able to assess the abundance and movement patterns of many marine species worldwide. For example, studies using various tagging methods conducted on species such as beluga whales (*Delphinapterus leucas*) (Richard *et al.* 2001), leatherback turtles (*Dermochelys coriacea*) (Wallace *et al.* 2005), black footed

albatross (*Phoebastria nigripes*) (Shaffer *et al.* 2005), California sea lions (*Zalophus californianus*) (Weise *et al.* 2006), yellowfin tuna (*Thunnus albacares*) (Schaefer *et al.* 2007), and white sharks (*Carcharodon carcharias*) (Weng *et al.* 2007), have provided information on diving and movement patterns. While other studies conducted on pacific white-sided dolphins (*Lagenorhynchus obliquidens*), Risso's dolphins (*Grampus griseus*) and blue whales (*Balaenoptera musculus*) have used aerial surveys to assess movement patterns and establish abundance estimates (Forney and Barlow 1998).

One of the most widely used techniques for estimating abundance in cetacean populations is photo-identification. This non-invasive technique uses naturally occurring marks to obtain mark-recapture data (e.g. tail flukes of humpback whales and sperm whales, body scarring of beluga whales, dorsal fins of dusky dolphins, common dolphins, and bottlenose dolphins (Mann *et al.* 2000). Photo-identification has been used on multiple populations of bottlenose dolphins (Würsig 1978, Wells 1987, Connor *et al.* 2001, Bearzi *et al.* 1997, Wilson *et al.* 1999, Lusseau *et al.* 2003) worldwide.

Bottlenose dolphins

Bottlenose dolphins are considered to be the most well studied species of cetacean due to their adaptability and coastal proximity (Reeves *et al.* 2002). Bottlenose dolphins range from temperate to tropical waters and show diversity in abundance, distribution and habitat use between populations. Studies in Sarasota Bay, Florida (Scott *et al.* 1990), Southern coast, Santa Monica Bay, California (Bearzi 2005), Mississippi Sound, Mississippi (Hubard *et al.* 2004), south-eastern cape, South Africa (Saayman and Tayler 1973), Moray Firth, Scotland (Wilson 1999), Bay of Islands, New Zealand

(Constantine 2002) and Doubtful Sound, New Zealand (Lusseau 2003) show great variation among populations in regard to abundance, site fidelity and movement patterns. In Doubtful Sound, New Zealand, abundance estimates reported 65 individuals as year round residents, part of a closed population, showing strong site fidelity to a small area 40.3 km (Lusseau 2003, Williams *et al.* 1993). Likewise, the population in Sarasota Bay, Florida is small consisting of approximately 100 individuals that are resident to a 40 km area (Scott *et al.* 1990).

Larger populations of bottlenose dolphins have also been documented to show strong site fidelity to areas. In the Mississippi Sound (n = 515) and South Carolina (n = 839) studies, populations exceed 500 individuals and show long-term site fidelity to areas larger than 400 km² (Hubard *et al.* 2004, Speakman *et al.* 2006). In contrast, the large population of bottlenose dolphins in Santa Monica, California (n = 290) showed low site fidelity to the 460 km² study area (Bearzi 2005). In the Bay of Islands, dolphins were found to be semi resident displaying long- and short-term site fidelity over a 300 km area, with an estimated population size of 446 individuals (Constantine, 2002).

Despite their presence in the Marlborough Sounds, northern part of the South Island, this study is the first to investigate the occurrence of bottlenose dolphins in this region. This chapter examines the abundance, site fidelity and movement patterns of bottlenose dolphins in the Marlborough Sounds. Findings are compared to two other studies that have been conducted on populations of bottlenose dolphins found in the Bay of Islands and Doubtful Sound regions. More specifically, the following objectives were addressed:

1. Estimate the abundance of bottlenose dolphins that utilise the Marlborough Sounds.

2. Examine resight rates to determine if the population shows signs of long- or short-term site fidelity.
3. Examine movement patterns between the three defined areas of the Marlborough Sounds (Queen Charlotte, Pelorus Sound and Admiralty Bay/Current Basin).

Based on data from other populations of bottlenose dolphins found in semi-enclosed habitats, I hypothesise that this population will consist of approximately 400 individuals, exhibit short- and long-term site fidelity over multiple years, and move randomly throughout the three areas of the Marlborough Sounds.

3.2 Methods

Study Area

The Marlborough Sounds is a sea-drowned valley that is located at the top of the South Island, adjacent to the Cook Strait and the Tasman Sea. For the purpose of assessing differences in movement patterns within the Marlborough Sounds, I divided the area into three main regions (1 = Queen Charlotte Sound, 2 = Pelorus Sound and 3 = Admiralty Bay) (Figure 2.1, Chapter II). Detailed information on the study area is provided in Chapter II (section 2.2).

Data Collection

Surveys were conducted from a 5.6 m boat on 125 days from 2003 to 2005. A full account of survey effort is detailed in Chapter 2 (section 2.2 and 2.3).

Photo-Identification

Abundance was assessed using photo-identification techniques developed in the 1970's by Würsig and Würsig (1977). This non-invasive technique photographically captures naturally occurring marks and has been used in many cetacean studies worldwide (e.g., Würsig and Jefferson 1990, Ottensmeyer and Whitehead 2003, Gero *et al.* 2005, Bearzi 2005, Quintana-Rizzo and Wells 2001, reviewed by Mann 2000). Markings such as; body scars, pigmentation and nicks or notches in the dorsal fin persist over long periods of time (Lockyer and Morris 1990). Photo-identification has been used to measure abundance, distribution, social structure and residency patterns for many cetacean species (Bearzi 2005, Williams 1992, Gero *et al.* 2005, Reid *et al.* 1991, Irwin and Würsig 2004, Wilson *et al.* 1999).

In 1998 bottlenose dolphins were photographically documented by dusky dolphin researchers in the Marlborough Sounds region (Markowitz 2004). The photo-identification obtained from this work and others (I. Visser and G. de Tezanos Pinto), initiated a photo-identification catalogue of bottlenose dolphins in this region. All opportunistic photographic data collected in 1992, 1995 and 1997 - 2003 has been included (with permission) in the population analysis presented in this chapter.

Photo-identification of marked individuals was undertaken using film and digital photography. During 1998 and 1999, photographs were taken on 100 to 400 ISO slide film with a Nikon N90 camera and 80 - 200mm and 100 - 300mm lenses, and later digitised prior to analysis. From 2000 to 2005, photographs were captured digitally with Nikon D1 and D100 cameras using 100 - 300mm, 70 - 300mm and 80 - 400mm lenses (Markowitz 2004). Photo-identification was collected maintaining a parallel position and travelling the same speed as the dolphins being photographed (Würsig and Jefferson 1990). Photo-identification sessions ended when an estimated

two images were obtained of each animal present, when loss of light, deterioration in weather conditions precluded further photography, or when animals were showing avoidance behaviour e.g. moving away from the research vessel (Bejder *et al.* 1999), increases in dive intervals (Lusseau 2002) or change in direction.

Following photographic sorting for suitability based on angle, contrast and focus (Slooten and Dawson 1992), photographs were then catalogued in FINSCAN 1.5.4. (Araabi *et al.* 2000, Hillman *et al.* 2003) and compared manually as per methods recommended in Markowitz *et al.* (2003). After sorting, all duplicate photographs of an individual occurring on the same day were discarded. Thus, ensuring only one photographic record per individual per sighting. A total of 316 photographic records of 182 individuals over 35 days obtained from 1992 to 2002 established the Marlborough Sounds bottlenose dolphin catalogue. From 2003 to 2005, a total of 1127 photographic records were collected over 45 days, adding 153 new individuals to the catalogue. Overall, between 1992 and 2005 a total of 1443 quality photographs from 80 dolphin group encounters were used to develop a computerised photo-identification catalogue of bottlenose dolphins in the Marlborough Sounds, resulting in 335 uniquely marked individuals (Figure 3.1). Typically, only one group of bottlenose dolphins were sighted each day. However, there were seven occasions when more than one group was encountered in a single day. Days in which this occurred were days where more than one Sound was surveyed. Therefore, all group encounters in this study are separated by date and area.

Data Analysis

Population abundance estimates were calculated using SOCPROG 2.3 (written by H. Whitehead; available from <http://is.dal.ca/~whitelab/>). Four population models were

run; *Schnabel*, *mortality*, *mortality+trend*, and *reimmigration+mortality* (Table 3.1). Model selection was based on Akaike's Information Criterion (AIC), which estimates the models' likelihood based on the number of parameters and the probability of obtaining the observed data (Akaike 1973). Models with the lowest AIC value were chosen as the best-fit model (Whitehead 2006).

Table 3.1. Models used to estimate abundance, followed by model definitions from SOCPROG 2.3 (Whitehead 2006).

Model	Definition
Schnabel	Assumes a closed population.
Mortality	Assumes a population of a constant size; where mortality (permanent emigration) is balanced by birth (immigration).
mortality+trend	Calculated per sampling period while assuming population growth or decline occurs at a constant rate.
reimmigration+mortality	Assumes movement emigration and reimmigration within a study area and combines with the mortality model. This assumes maximum likelihood for populations size, emigration rate, reimmigration rate and total estimated population size.

Mark rate (% of permanently marked individuals) was determined from nine independent test days (Table 3.5). On these days concentrated effort was given to maintain that all animals were photographed at random. Total population estimates were calculated using estimates generated from the best model (based on the lowest AIC value) and adjusted based on the mark rate. (Markowitz 2004).

Site Fidelity

Site fidelity was examined using the resight rate, with sampling intervals defined by day, month and year. To test the null hypothesis that individuals were photographed randomly across the study area, a Poisson distribution (Zar 1996) was calculated using

all photo-identification data. Expected values generated from this were then compared to the observed data to assess site fidelity. This test was chosen for comparative purposes, since Constantine (2002) used this method for the Bay of Islands population.

The amount of time individuals spend within the Marlborough Sounds was examined by calculating lagged identification rates (LIR) using the “movement” module in SOCPROG 2.3 (Whitehead 2006). The lagged identification rate is the probability that an individual identified in the study area at time X will be identified again within the study area after a certain time lag (Whitehead 2006).

Lagged identification rates were estimated by an equation described in Wimmer and Whitehead (2004);

$$R(t) = P(t)/N$$

where $R(t)$ is the LIR for time lag t , $P(t)$ is the probability that the individual is still present in the study area after a certain time lag t , and N is the population size in the study area.

Photo-identification data from 1997 to 2005 of individuals sighted four or more times were included in analysis. The cut off point of four or more times was selected since the average number of resights per individual was four (Mourão 2006). This resulted in the removal of 187 individuals, leaving 148 individuals and 1184 records.

Various models were run to assess the amount of time dolphins spend in and around the Marlborough Sounds over the length of the study. Lagged identification rates were calculated using two different methods; whole study area and within/between areas. The whole study area method examines the emigration or

mortality over the entire Marlborough Sounds region. The within/between method calculates lagged identification rates for individuals remaining in the same area (Marlborough Sounds or an outside area) or moving between two areas. Lagged identification rates for the whole study area and within/between areas were then fitted with models to assess residency patterns. Three models were run on the whole study area; *closed*, *emigration/mortality*, and *emigration + re-immigration*. Two models were run for the within/between analysis; *fully mixed* and *migration-full interchange* (Table.3.2). Akaike Information Criterion (AIC) (Akaike 1974) and quasi-AIC (QAIC) values were calculated for all models with the lowest values used to determine the best-fit models (Whitehead 2006). Best-fit models were selected based on their QAIC instead of their AIC, since QAIC accounts for over dispersion of the data (Whitehead 2006).

Table 3.2. Models fitted to lagged identification rates (from Whitehead 2006). Area 1 = Marlborough Sounds, Area 2 = Outside the Sounds.

Equation	Explanation
<u>Models used for one study area: Area 1 only (n=population size in study area)</u>	
$1/a_1$	closed ($a_1=n$) -- no change in the individuals within the study area
$(1/a_1)*\exp(-td/a_2)$	emigration/mortality ($a_1=n$; a_2 =mean residence time) -- individuals leave the study area and never return
$(1/a)*[(1/a_3)+(1/a_2)*\exp(-(1/a_3+1/a_2)*td)]/(1/a_3+1/a_2)$	emigration + reimmigration ($a_1=n$; a_2 =mean time in study area; a_3 =mean time out of study area) -- individuals leave the study area for a time but return again
<u>Models used for two study areas: Area 1 to Area 2 (n= total population size)</u>	
$1/a_1$	fully mixed ($a_1=n$) -- individuals move randomly within the study areas (QC, PS, and AB) at a rapid rate, fully mixing within one time unit (day).
$(1/a_1)*[1-\exp(-td/a_2)]$	migration-full interchange ($a_1=n$; a_2 =mean residence time in area 1) -- individuals move randomly within the study areas (QC, PS, and AB), spending equal amounts of time in each area before moving on to the next.

Movement patterns

Transition probabilities for movements between all areas within the Marlborough Sounds and an external area were calculated using a parameterised Markov model (movements among areas) in SOCPROG 2.3 (Whitehead 2006). The movements among areas model generates estimates so that at each time unit, individuals have a certain probability of moving from one area to another, while accounting for permanent emigration from all study areas in a single day (Whitehead 2006).

3.3 Results

Survey Effort

A total of 132 surveys were conducted in the Marlborough Sounds region between 2003 and 2005. A full account and detailed summaries of survey effort are in Chapter II (section 2.3). Photo-identification was conducted during 40 of these surveys, resulting in 21 hours of focal group photo-identification effort. An additional five surveys from other researchers working in the Marlborough Sounds from 2003 to 2004 added photographic data to the present analysis (T. Markowitz and G. de Tezanos Pinto).

Abundance Estimates

A total of 1443 quality photographs from 80 dolphin group encounters between 1992 and 2005 resulted in 335 uniquely marked individuals (Figure 3.1). The discovery curve shows major increases in the number of identified individuals from 1999 through to 2005. There is no plateau in the discovery curve, which suggests that this population is open.

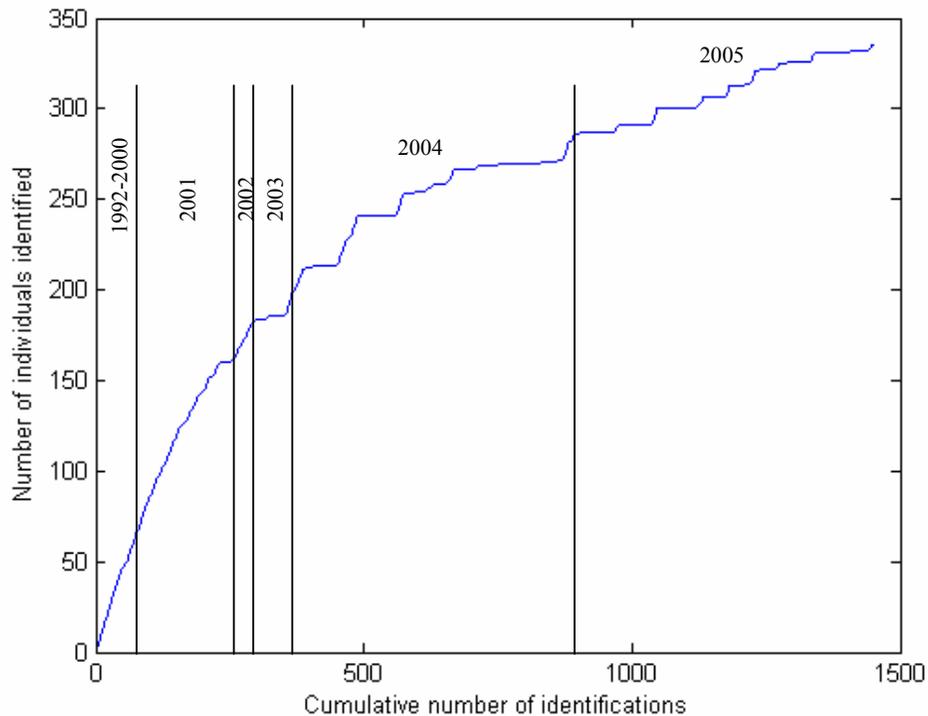


Figure 3.1. Discovery curve showing number of marked individuals identified over time. From 1992,1995,1997-2005. The total number of marked individuals identified from 1992 - 2005 ($n = 335$).

Population estimates were established using SOCPROG 2.3 and adjusted based on mark rate estimates. Photographic data collected from 1992 to 2005 and from 2003 to 2005 were examined independently to compare population estimates for the entire catalogue and for when photographic effort increased (Table 3.3 and Table 3.4). Based on AIC values, the mortality model was selected as the most appropriate model to use for the Marlborough Sounds region. It is an open population model, which estimates the maximum likelihood for the population size while accounting for immigration and emigration. Abundance estimates from 1992 to 2005 and from 2003 to 2005 both produced similar results (Table 3.3 and Table 3.4). Thus, suggesting the total population size (on an annual basis) is 184 (SE = 8.4) individuals, with 25% (SE

= 0.02%) emigrating out and replaced by an additional 25% (SE = 0.02%) not previously encountered.

Table 3.3. SOCPROG model results for 1992-2005 data. Bootstrapped (n = 100), 335 individuals, 11 sampling periods.

Model	Est. Pop. Size	±SE	95% CI	Est. Mortality Rate	±SE	95% CI	Log Likelihood	AIC Value
closed Schnabel	377	9.8	364-404	-----	-----	-----	- 577.8973	1117.7945
mortality	184	8.4	170-202	0.25	0.02	0.20-0.30	- 408.3306	820.6613
mortality +trend	183	77.9	134-335	0.25	0.07	0.10-0.28	- 408.2685	822.5375
reimmi. +mort.	174	11.0	148-194	0.14	0.07	0.00-0.24	- 406.6481	821.2963

Table 3.4. SOCPROG model results for 2003-2005 data. Bootstrapped (n = 100), 234 individuals, 3 samplings periods.

Model	Est. Pop. Size	±SE	95% CI	Est. Mortality Rate	±SE	95% CI	Log Likelihood	AIC Value
closed Schnabel	243	4.8	237-255	-----	-----	-----	- 139.7271	281.4542
mortality	184	7.8	173-205	0.24	0.04	0.13-0.32	- 129.9202	263.8404
mortality +trend	184	9.0	172-206	0.24	0.06	0.08-0.29	- 130.0152	266.0304
reimmi. +mort.	174	20.1	135-201	0.00	0.07	0.00-0.22	- 129.0429	266.0857

Mark Rate

Mark rate test results show that 87 percent (\pm SD = 5.9) of animals are marked (Table 3.5). By adjusting the results from the mortality model by the percent of un-marked individuals, the total estimated population size for dolphins occurring in the Marlborough Sounds on an annual basis is 211.5 (95% CI = 195 - 232).

Table 3.5. Mark rate data from 2005.

Test	Quality Images	Marked	Un-marked	% Marked
1 April 2005	184	157	27	85.3
2 April 2005	200	169	31	84.5
2 July 2005	139	137	2	98.6
15 July 2005	468	390	78	83.3
29 July 2005	54	47	7	87.0
6 August 2005	121	111	10	91.7
15 August 2005	249	195	54	78.3
17 August 2005	350	297	53	84.9
19 August 2005	408	372	36	91.2
Mean		208.3	33.1	87.2
Standard Deviation				5.9

Site Fidelity

A total of 160 catalogued individuals ($n = 335$, 47%) were resighted during more than one year, with the total number of years that individuals were resighted varying from one to seven (Figure 3.2). The average number of resights per individual was four with 13 individuals resighted over ten months within the study. Individual I44 (Aurbie) was first documented in 1995 in Queen Charlotte Sound and was subsequently resighted ($n = 14$ times, in different months) in all three areas (QC, PS and AB) of the Sounds over a ten-year period (Plates 3.2 and 3.3).



Plate 3.2. QC I44 11/03/1995



Plate 3.3. QC I44 01/04/2005

A full account of resights by year for all 335 individuals is provided in Appendix D. Approximately one-third ($n = 106$, 32%) were sighted in more than five months (Figure 3.3).

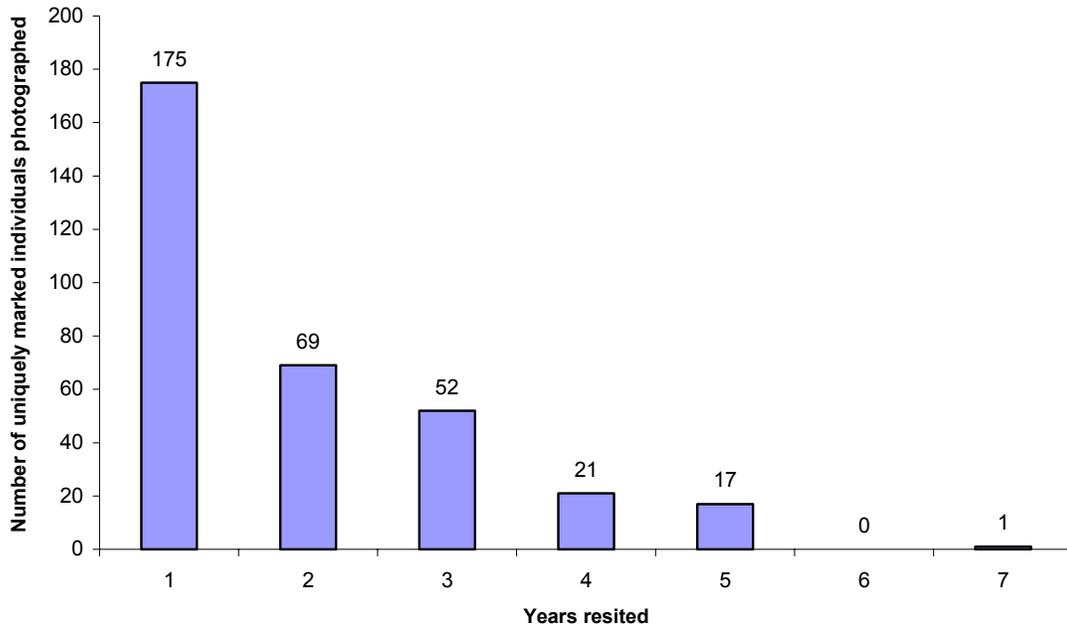


Figure 3.2. Number of uniquely marked individuals versus the number of years photographed from 1992, 1995, and 1997-2005.

Results from the Chi-squared test show a significant difference in the observed versus expected resight rate ($\chi^2 = 306.44$, d.f. = 9, $P < 0.000$) (Figure 3.3). The Poisson generated values showed there were a high number of individuals that were photographed during only one month (observed value, $n = 71$) compared to the expected value (expected value, $n = 14$) and a high number of individuals photographed during more than seven months (observed value, $n = 68$) compared to the expected value (expected value, $n = 36$). Where the observed value of sightings exceeds the expected value (≥ 7) denotes the point where an individuals' use of the Marlborough Sounds region is more frequent than others. Therefore, these individuals can be classified as frequent users. Of the 71 individuals photographed in only one

month, 39 were first photographed in 2005; with 21 of those first photographed in the last month of the study.

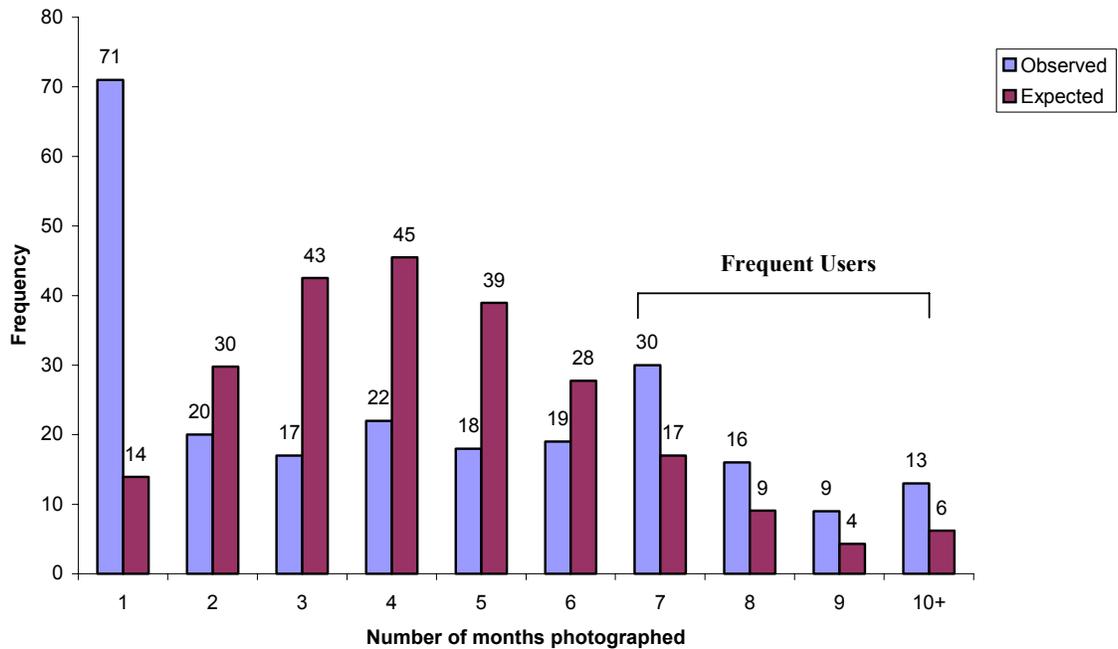


Figure 3.3. Observed versus expected Poisson distribution of the number of months individuals were identified from 2003 to 2005. Frequent users are shown by the horizontal bar.

Lagged Identification Rates

Lagged identification rates showed individuals residing in the Marlborough Sounds over a four-year period (Figure 3.4). The best-fit model for the lagged identification rate within the study area was the emigration + re-immigration model (QAIC = 4074.35) (Table 3.6) (Figure 3.5). Results showed that 67 of the 148 identified individuals used in this analysis spent an average of 12.8 days in the Marlborough Sounds before leaving for 13.9 days, and then returning to the Sounds again. The best-fit model for the lagged identification rate between study areas was the fully mixed (QAIC = 2671.59) (Table 3.6) (Figure 3.6) model. The fully mixed and migration-full

interchange models had similar results, showing that movements are rapid and that individuals spend similar amounts of time in all areas within the Marlborough Sounds (Figure 3.6). The migration–full interchange model shows a mean residence time of only 1.3 days with a total population size of 152 individuals (Table 3.6).

Table 3.6. Models fit to lagged identification rates for bottlenose dolphins found within the Marlborough Sounds. Residence times and movement between the Marlborough Sounds and outside areas for all individuals resighted four or more times between 1997 and 2005, * marks the results fitted to lagged identification rate graphs.

Model	Maximum-likelihood value for parameters	QAIC value	Summed log likelihood
<u>Residence within the Marlborough Sounds (n=estimated population size in study area)</u>			
Closed	n=125	4089.57	-8622.31
emigration/mortality	n=105	4085.72	-8609.98
*emigration + reimmigration	n=68	4074.35	-8581.79
	mean residence time in=12.8 days		
	mean residence time out=13.9 days		
<u>Movements between the different areas of the Marlborough Sounds (n=total population size)</u>			
*fully mixed	n=152	2671.59	-3877.13
*migration-full interchange	n=152	2673.47	-3876.96
	mean residence time=1.4 days		

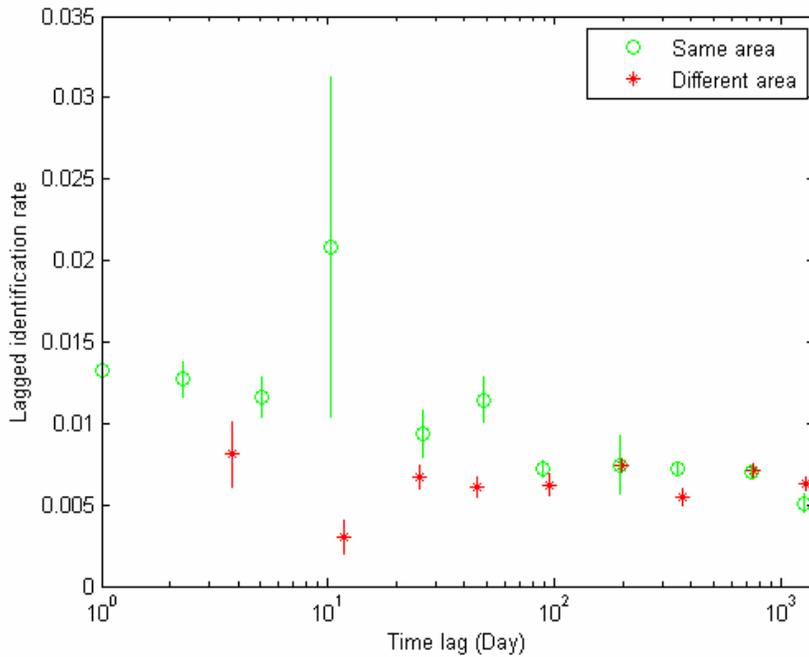


Figure 3.4. Lagged identification rates for all individuals resighted 4 or more times in the Marlborough Sounds from 1997 to 2005. Shows the probability that a dolphin photographed at time “0”, will be identified again at time x within the Marlborough Sounds study area. Data points are represented as circles (same area) and stars (different area). Standard error bars are shown and the maximum time lag used was 1500days.

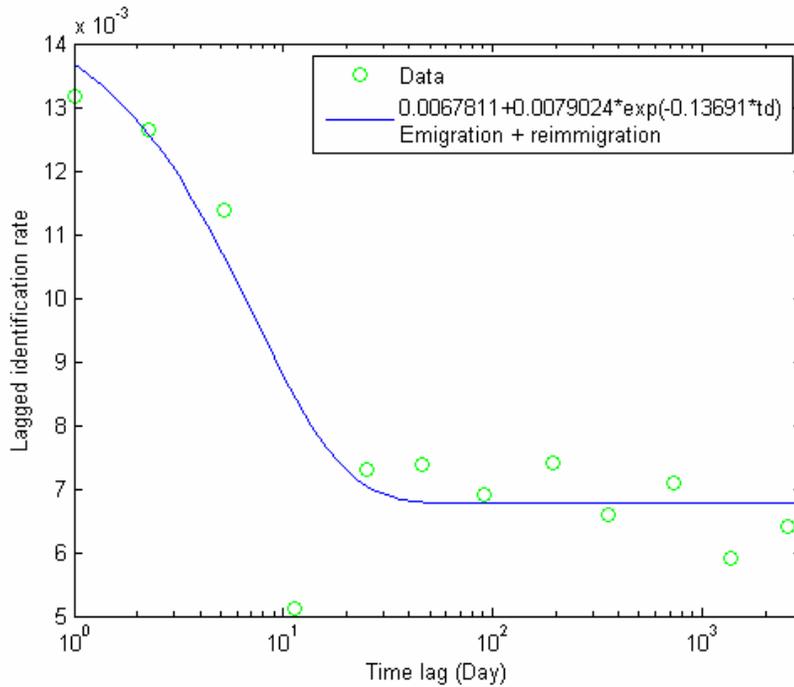


Figure 3.5. Lagged identification rates for all individuals resighted 4 or more times in the Marlborough Sounds. Shows the probability that a dolphin photographed at time “0”, will be identified again at time x within the study area. Data points are represented as circles and the best-fit model (Emigration + reimmigration) is shown.

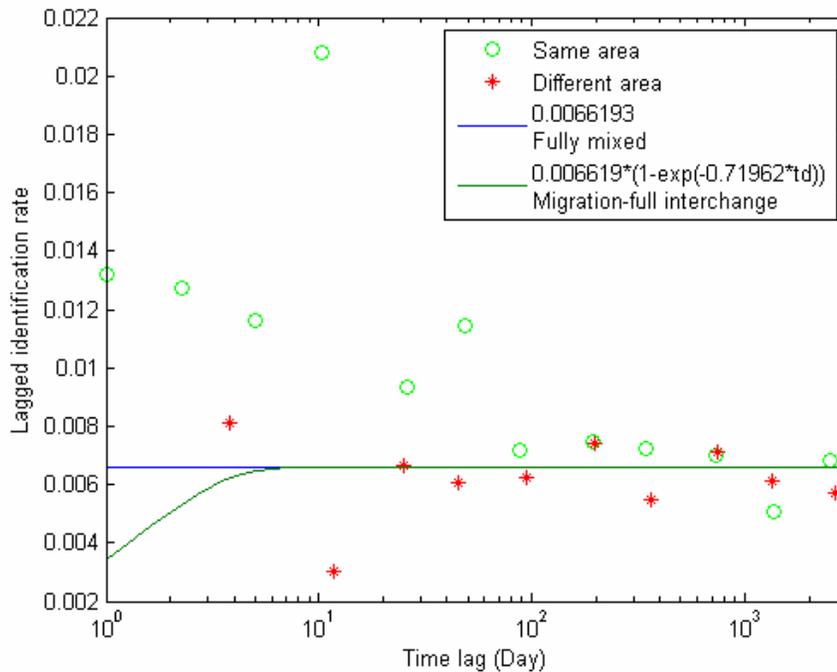


Figure 3.6. Lagged identification rate for all individuals resighted 4 or more times within the Marlborough Sounds from 1997-2005. Same area represents the study area (the Marlborough Sounds) and different area represents all areas outside of the study area. Data points are represented as circles for the Marlborough Sounds and stars for all areas outside of the Marlborough Sounds. The best-fit models are (Migration-full interchange and Fully Mixed) shown.

Movement Patterns

Transition probabilities for movements between all the areas within the Marlborough Sounds and an external area within 1 day were estimated with corresponding standard errors (Table 3.7). The rate of movement from Admiralty Bay to Pelorus and Queen Charlotte Sound follows a linear pattern (animals have a higher probability of moving into the closest adjacent region) (Figure 2.1). Movements from Queen Charlotte Sound to other areas were not linear, with movements to Admiralty Bay being higher than movements to Pelorus Sound. Pelorus Sound, located between Admiralty Bay and Queen Charlotte Sound, showed higher probabilities of movements to Queen Charlotte and outer areas (areas outside the Marlborough Sounds) than movements to

Admiralty Bay. Movements from the outer areas were higher for Admiralty Bay than any of the other regions.

Table 3.7. Probabilities of individuals moving between Queen Charlotte Sound, Pelorus Sound, Admiralty Bay and external areas (Out) within 1 day (\pm SE).

From	To	Queen Charlotte Sound	Pelorus Sound	Admiralty Bay	Out
Queen Charlotte Sound		-----	0.0034 (0.0348)	0.0252 (0.0146)	0.0003 (0.0238)
Pelorus Sound		0.3196 (0.0678)	-----	0.0000 (0.1113)	0.2270 (0.1037)
Admiralty Bay		0.0000 (0.0812)	0.2671 (0.0850)	-----	0.0774 (0.0316)
Out		0.0001 (0.0748)	0.0090 (0.1209)	0.0390 (0.1308)	-----

3.4 Discussion

Population Estimates and Site Fidelity

Photo-identification and mark-rate information indicate that at least 385 individuals used the Marlborough Sounds region between 1992 and 2005. Mark-recapture abundance estimates showed that 211.5 (95% CI = 195 - 232) individuals visit the Sounds annually, with a relatively high interannual immigration/emigration rate of 25%. This suggests that the bottlenose dolphins found in the Sounds are part of a larger population that frequent the northern coast of the South Island. Data also suggest that at least a proportion (32%) of the population shows a high level of site fidelity, while some individuals are observed less frequently. The discovery curve shows no plateau, providing further evidence that the bottlenose dolphins utilising the

Marlborough Sounds form part of a larger open population. Increases seen in the discovery curve were primarily due to varying but increasing photographic effort. From 1992 through 1997 photographic effort was opportunistic and minimal. In 1998 photographic effort increased when dusky dolphin researchers started annual winter surveys of the Marlborough Sounds, photographing any bottlenose dolphins they opportunistically encountered. The final increase from 2003 to 2005 was due to year round effort from the onset of this study, where the primary focus was the population of bottlenose dolphins. At the end of fieldwork in 2005 the discovery curve was still rising with 21 new individuals added to the catalogue in the last month.

Abundance and site fidelity has been found to vary among populations of bottlenose dolphins around the world (Mann *et al.* 2000). It was hypothesised that the Marlborough Sounds population would be similar in size and residency patterns as other populations found in semi-enclosed sheltered habitats e.g. Mississippi Sound, Gulf of Mexico (Hubard *et al.* 2004), Kvarneric, Adriatic Sea (Bearzi *et al.* 1997), and off the coast of Charleston, South Carolina (Speakman *et al.* 2006).

The Marlborough Sounds population was intermediate in size, falling in between the abundance estimates reported for these studies. Long-term site fidelity was observed in the Marlborough Sounds with some individuals showing site fidelity over a ten-year period. This was similar to the site fidelity observed in the Mississippi Sound and South Carolina populations (Hubard *et al.* 2004, Speakman *et al.* 2006).

Of the bottlenose dolphin populations studied in New Zealand, the Marlborough Sounds population is most similar to the bottlenose dolphins found in the Bay of Islands in regards to its proportion of marked individuals (81.5%), estimated abundance ($n = 446$) and year round occurrence (Constantine 2002). However, it differs in that the Bay of Islands population has been classified as a

closed population (Constantine 2002), whereas this analysis shows the Marlborough Sounds population to be an open population.

The population found in Doubtful Sound differs from the Marlborough Sounds population, with the proportion of marked individuals being 20% lower. The Doubtful Sound population is reported to be closed, consisting of only 65 individuals (Lusseau 2003) that show evidence of short- and long-term site fidelity (Schneider 1999).

Lagged identification rates for 67 individual bottlenose dolphins within the Marlborough Sounds show consistency over a four-year period. This corresponds with the 68 individuals noted as having high site fidelity from the Poisson distribution (Figure 3.3).

The migration – full interchange model showed a mean residence time of only 1.3 days which differed from the 12.8 days for the within the Sounds model. The difference between the two models is due to heterogeneity in movements (Wimmer and Whitehead 2004), with some individuals remaining in certain areas for longer periods of time, and others moving more frequently between the different areas of the Marlborough Sounds. The best-fit lines for the residence within and movements between models almost converge at 100 days, representing a fully mixed population with very little heterogeneity in movement patterns at this time scale (Figure 3.6).

Movement patterns

Movement probabilities showed rapid movement between all areas. However, standard errors were high and the analysis does not account for survey effort, which was higher in Queen Charlotte Sound. Movement patterns are therefore likely under represented for other areas. The Marlborough Sounds appears to be an important part of this population's home range, with individuals migrating in and out every 12 days.

It remains to be seen where the dolphins go during the estimated 13 days before returning. Possible locations used by the bottlenose dolphins outside the Marlborough Sounds include Awaroa Bay, Abel Tasman National Park and Palliser Bay. Anecdotal sightings from water taxi operators and local residents have reported bottlenose dolphins in the Abel Tasman National Park waters and off the coast of the Southern region of the North Island. It is realistic to estimate that movement patterns of this population extend into these regions, with Queen Charlotte Sound located only 80 km southwest from Palliser Bay and Admiralty Bay only 80 km east of Awaroa Bay.

Bottlenose dolphins in the Bay of Islands have been reported to move over large areas. Photo-identification records show some individuals moving 82 km north and 388 km south of the Bay of Islands (Constantine 2002). This differs from the bottlenose dolphins in Doubtful Sound where a total of 65 individuals are considered to be locally resident within a small area (40.3 km) (Schneider 1999, Lusseau 2003). Research in Tampa Bay, Florida documented the movement of one dolphin over twenty-five days and reported movements ranging over 581 km, with an average of 23 km per day (Mate *et al.* 1995). Studies conducted on migratory bottlenose dolphins report movements ranging up to 400 km along the mid-Atlantic coast of the United States for the entire population (Mead 1975, Mead and Potter 1990, Blaylock *et al.* 1995). The Marlborough Sounds appears to be only one section of a much larger home range with movements likely to extend at least 80 km out of the sounds. Movements between the sounds show individuals regularly moving across distances of 200 km. Future photo-identification and/or telemetry studies in conjunction with comparisons between regions would provide valuable insight into the full extent of this population's movements and home range.

3.5 Summary

Bottlenose dolphins in the Marlborough Sounds are part of a large open coastal population consisting of approximately 385 individuals, with between 195 to 232 individuals utilising the sounds per annum. Immigration and emigration rates are high, with approximately 25% leaving and entering the 890 km² area annually. Long-term site fidelity was documented, with the majority of individuals re-sighted over multiple years. Lagged identification rates showed consistency over a four-year period, with some individuals remaining in certain areas for longer periods of time, while others moved more frequently between the different areas of the Marlborough Sounds. Movement probabilities showed rapid movement between all areas of the Marlborough Sounds and an outer region. The Marlborough Sounds appears to be only a section of a much larger home range with movements estimated extending out at least 80 km.

Long-term site fidelity is present among all three studied bottlenose dolphin populations (Marlborough Sounds = MS, Bay of Islands = BOI and Doubtful Sound = DS) in New Zealand. The three populations differ in population size, open/closed status and residency patterns. The population of bottlenose dolphins in the MS is similar to the BOI population in that they both are larger, wider ranging and semi-resident compared to the DS population. The main difference between the MS and the other two populations is that the BOI and DS discovery curves plateau, where the MS does not. Due to this, the BOI and DS are considered to be closed populations while the MS is considered to be open. The obvious explanation for this difference is the high annual immigration rate observed in the MS. Future photo-identification effort over a longer time frame may produce a plateau in the discovery curve and

possibly a larger estimate of abundance. However, it may not and this alone makes the MS population unique from the BOI and DS populations.

Bottlenose dolphins in the Marlborough Sounds are different to other populations around the world adding to the evidence that this species shows extreme diversity among populations.

Chapter IV

Social structure of bottlenose dolphins within the Marlborough Sounds, New Zealand.



Plate 4.1. Juvenile bottlenose dolphins colliding in mid-air, a display of social interaction.

4.1 Introduction

Social Structure

Socioecology is the scientific study of how social structure and organisation are influenced by ecological pressures within an organisms' environment (Wittemyer *et al.* 2005). Factors such as foraging, protection from predators, caring for young, mate selection and environmental constraints are all ecological pressures that influence social structure (Whitehead 1997). Social structure has been defined as the “content, quality and patterning of relationships” between individuals within a group (Hinde 1976). These

relationships are described using observations of behavioural interactions among individually identified members within a group (Hinde 1976).

Many population and behavioural biologists have emphasised the importance of understanding the relationship between social structure and ecological variables (Wittemyer *et al.* 2005, Kappeler and Van Schaik 2002, Whitehead and Dufalt 1999). Hinde (1976) developed a framework used to study social structure based on interactions between individuals. Stating that the content, quality and temporal patterning of interactions between a pair of individuals over time describes their relationship, which then gives rise to the content, quality and temporal patterning of relationships between members of a population over time and defines the social structure of that population (See Figure 1, Hinde 1976). This analytical framework has since been used to examine the social structure of complex fission-fusion societies for a number of taxa including primates (Goodall 1986, Moreland 1991, Byrne *et al.* 1989), elephants (Wittemyer *et al.* 2004, Moss and Poole 1983) and cetaceans (Cheney *et al.* 1987, Dunbar 1988, Whitehead and Dufalt 1999, Slooten *et al.* 1993, Smolker *et al.* 1992, Norris *et al.* 1994, Lusseau *et al.* 2003, Lusseau *et al.* 2005).

Fission-fusion societies are defined by Whitehead and Dufalt (1999) as ‘societies in which most animals associate with a number of other animals at different times, but associations form and are broken over a range of time scales’. Associations within fission fusion societies are often measured by assuming that clusters or groups of individuals that occur spatially or temporally are interacting with one another and are often referred to as the “gambit of the group” (Whitehead and Dufalt 1999). The gambit of the group principal has been applied in many cetacean studies (Whitehead and Dufalt 1999) primarily due to the difficulty of recording social interactions between individuals (Mann 2000).

Cetaceans

Studies conducted on cetaceans show prime examples of highly dynamic fission-fusion societies (e.g. Hector's dolphin, *Cephalorhynchus hectori* (Slooten *et al.* 1993), Hawaiian spinner dolphin, *Stenella longirostris* (Norris *et al.* 1994) and bottlenose dolphins, *Tursiops truncatus* (Lusseau *et al.* 2005, Bräger *et al.* 1994, Balance 1990, Smolker *et al.* 1992, Wells *et al.* 1987, Würsig 1978). Understanding the social interactions between individuals within a population is often difficult when groupings can range from a few individuals as observed with New Zealand's Hector's dolphin to large aggregations of several thousands as with the Hawaiian spinner dolphin. Differences in social structure between species and populations are common among cetaceans. This is especially true for bottlenose dolphins, which have been observed ranging from small groups of just a few to large groups of 100 or more individuals (Irvine *et al.* 1981, Smolker *et al.* 1992, Saayman and Taylor 1973).

Bottlenose dolphins

Bottlenose dolphins are one of the most well studied cetaceans due to their coastal proximity and various locations around the world. These highly adaptable mammals range from tropical to temperate climates and show great variation in social structure amongst populations (Mann 2000). The longest running study of free ranging bottlenose dolphins was initiated in Sarasota Bay, Florida in 1970 by Irvine and Wells (1972). This ongoing work has provided insight into the life history, population dynamics, social structure, and association patterns of this population (Irvine and Wells 1972, Wells *et al.* 1987, Wells and Scott 1990). Studies on bottlenose dolphins in Shark Bay, Australia; Sarasota Bay, Florida; Moray Firth, Scotland; Bay of Islands, New Zealand and Doubtful Sound, New Zealand show the diversity and social plasticity of this species. Resident

populations of bottlenose dolphins in Florida and Australia were found in sex specific groups described as fission-fusion societies. In both Florida and Australia, females formed bands with other females, displaying high levels of associations lasting over multiple years (Wells *et al.* 1987, Smolker *et al.* 1992). Males were found to form pair bonds in both Florida and Australia, however in Shark Bay male pair bonds formed larger alliances with other males to gain reproductive access to females. In the Moray Firth, dolphins were found in mixed sex groups of relatively low levels of associations. Long-term associates based on ranging patterns were present, dividing the population into two groups (Lusseau *et al.* 2005). Studies on bottlenose dolphins in Bay of Islands and Doubtful Sound, New Zealand, have provided insights into the intra- and inter-specific relationships formed within these two populations (Mourão 2006 and Lusseau *et al.* 2003). In the Bay of Islands, the large semi-resident population of bottlenose dolphins was found to be a fission-fusion system, with individuals ranging over a wide area of coastal habitat and forming long lasting inter- and intra-sexual associations (Mourão 2006). In Doubtful Sound, the small resident population of bottlenose dolphins was described as a fission-fusion system with long-lasting associations consistent over multiple years across sexes (Lusseau *et al.* 2003).

Bottlenose dolphins have long been known to reside in the Marlborough Sounds (Webb 1973), where they have been the basis of dolphin watching tours for over 20 years (personal communication Danny Bolten and Les and Zoey Battersby). However, these dolphins have not been systematically studied until relatively recently. Some limited photo-identification sampling of bottlenose dolphins in the Marlborough Sounds began in 1998, by researchers studying dusky dolphins in the area (Markowitz *et al.* 2004). Photo-identification data obtained from 2003 to 2005, combined with earlier work and others (I.

Visser 1997 and G. de Tezanos Pinto 2005) have been included in the analysis presented in this chapter.

This chapter examines the stability and longevity of associations between individuals and compares association rates in small, medium and large groups. More specifically, the following questions will be addressed.

- 1: Do bottlenose dolphins in the Marlborough Sounds exhibit short- and or long-term preferred associations?
- 2: If preferred associations exist, do they remain stable over time and for how long?
- 3: Are some individuals observed consistently in larger groups than others?
- 4: Does group size affect the strength of associations between individuals?

Based on previously studied populations of bottlenose dolphins, I hypothesise that the population of bottlenose dolphins in the Marlborough Sounds will display both short- and long-term preferred associations that remain stable over multiple years. I further hypothesise that comparisons between group associations based on size will show that smaller groups have stronger more stable associations than larger groups.

4.2 Methods

Data Collection

A total of 132 surveys were conducted in the Marlborough Sounds region between 2003 and 2005. A full account and detailed summaries are provided in Chapter II (section 2.3) and will not be presented in this chapter. Photo-identification was conducted during 40

of these surveys, resulting in 21 hours of focal group photo-identification effort. Five additional surveys from other researchers working in the Marlborough Sounds from 2003 to 2004 added photographic data to the present analysis (T. Markowitz and G. de Tezanos Pinto). The photo-identification obtained from this work and others (e.g. I. Visser and A. Harlin), initiated a photo-identification catalogue of bottlenose dolphins in this region. All opportunistic photographic data from 1997 to 2004 has been included (with permission) in the population analysis presented in this chapter.

Further detail on photo-identification methods are presented in Chapter III (section 3.2) and will not be repeated in this chapter. Following photographic sorting for suitability based on angle, contrast and focus (Slooten and Dawson 1992), photographs were catalogued in FINSCAN 1.5.4. and compared manually as per methods recommended in Markowitz *et al.* (2003). Photographic data obtained from 1997 to 2005 along with date and ID number were entered into EXCEL 2000 sheets and uploaded into SOCPROG 2.3 (Whitehead 2006).

Data Analysis

Only photo-identification data from individuals resighted four or more times between 1997 and 2005 were used in the present analysis. The cut off point of four or more times was chosen based on the average number of resights per individual (Mourão 2006). All analyses were conducted using SOCPROG 2.3 (Whitehead 2006). Models within the program were fitted to data, with the corresponding statistical tests providing insight into the association patterns of the bottlenose dolphin population in the Marlborough Sounds (written by H. Whitehead; available from <http://is.dal.ca/~whitelab/>).

Social Structure

Associations were defined as a number for each pair of individuals in each sampling period 1:0 (1=associated, 0=not associated). Individuals were considered associated in a sampling period if they were photographed in the same group during the sampling period, and not associated if they were never photographed in the same group within the sampling period (Whitehead 2006). Coefficients of association were classified into five categories based on strength of associations using divisions from Quintana-Rizzo and Wells (2001); very low= 0.01-0.20, low=0.21-0.40, moderate=0.41-0.60, high=0.61-0.80 and very high=0.81-1.0.

Association Indices

All models were run using the simple ratio (SRI) and half-weight index (HWI). The SRI estimates the co-occurrence of individuals by their presence in the same group, using the formula,

$$SRI=X/[X+Ya+Yb]$$

where X is the number of groups in which a and b were both present. Ya is number of groups in which a was present and b was not. Yb is the number of groups in which b was present and a was not (Ginsberg and Young 1992).

The HWI estimates the likelihood of seeing two individuals together compared to seeing either of the two in any group, using the formula,

$$HWI= X/[X + 0.5 (Ya +Yb)]$$

where X is the number of groups in which a and b were both present. Ya is number of groups in which a was present and b was not. Yb is the number of groups in which b was present and a was not (Cairns and Schwager 1987).

Results for both indices are reported but the HWI was the chosen index for association plots, preferred/avoided tests, lagged association rates, cluster analysis, and sociograms. The HWI is used in most behavioural studies on bottlenose dolphins (e.g. Lusseau 2003, Lusseau *et al.* 2005, Quintana-Rizzo and Wells 2001, Gero *et al.* 2005). Since it minimises biases by accounting for pairs of individuals that may have been present but were not photographed during the sampling period (Cairns and Schwager 1987, Lusseau *et al.* 2005) and allows for comparisons between multiple studies (Wells *et al.* 1987, Smolker *et al.* 1992, Lusseau *et al.* 2005). The SRI was not chosen based on the likelihood of underestimating true associations between individuals in photo-identification studies (Smolker *et al.* 1992, Whitehead 2006). Results for all tests run using the simple ratio index are reported in Appendix E and F for future comparisons with other studies.

Social Structure (Population Level)

Association Plots

Histograms were plotted for association matrices of non-diagonal elements (all associations) and maximum association indices (by individual, ignoring diagonal elements). Results were plotted for all individuals, small, medium and large groups sighted four or more times within the Marlborough Sounds between 1997 and 2005.

Preferred/Avoided Associations

Tests for preferred/avoided associations were conducted in SOCPROG 2.3. This examines the probability that individuals associate with all other individuals at the same rate based on their availability (Whitehead 2006). To reject the null hypothesis, the distribution of the association indices of the real data should be different from the

distributions of the random data (generated from multiple permuted data sets). SOCPROG 2.3 generally permutes the data starting at 1000, as is typical for Monte Carlo methods. However, too few permutations may result in inaccurate p-values (Manly 1995). To amend this, it is recommended that permutations be increased until the p-values stabilise (Bejder *et al.* 1998, Whitehead 2006). Two permutation methods available in SOCPROG 2.3 were used to test the null hypotheses of no preferred/avoided associations, with each method testing the data in different ways. To test for long- (between sampling period) and short-term (within sampling period) preferred associations, the permute groups within samples method was used. This test accounts for scenarios where not all individuals are present in the sampling period due to birth, death and migration. A significantly higher standard deviation of the real association indices compared to the random association indices, indicates long-term preferred companions (Whitehead 2006). A significantly lower mean of the real association indices compared to the random association indices, indicates short-term preferred companions (Whitehead 2006). To test for long-term (between sampling period) preferred/avoided associations, the permute associations within samples test was used. This test only works by permuting associations based on 1:0 associations. A significantly higher standard deviation or coefficient of variation of the real association indices compared to the random association indices indicates long-term preferred/avoided associations (Whitehead 2006).

Test for Variation in Gregariousness

To test for differences in sociality among individuals (are some individuals observed in larger groups and others found in much smaller groups repeatedly over time) associations were defined as ‘permute groups within samples’ using SOCPROG 2.3. If some

individuals are observed more frequently in larger or smaller groups the test statistic for the standard deviation of typical group size will be significantly higher for the observed data than the standard deviation of the randomly generated data (Whitehead 2006).

Temporal Analysis

Standardised Lagged Association Rates

Since it was not possible to photograph all individuals in all sampling periods, the standardised lagged association rate was used. The standardised lagged association rate (SLAR) defined by Whitehead (2006) states ‘the SLAR is an estimate of the probability that if two individuals are associated at any time, the second is a randomly chosen associate of the first after the specified lag’. SLAR were generated using daily sampling periods (e.g. individuals photographed on the same day were considered to be associated). Standard errors were generated using the jack-knife approach (Efron and Gong 1983) to assess the precision of the SLAR (Sokal and Rohlf 1981, Whitehead 1999, Gowans *et al.* 2001). Mathematical models were fitted to the SLAR, the best-fit models were chosen to assess association indices for the population as a whole over time. Mathematical model definitions are provided in Table 4.1. Various combinations of these models were fitted using maximum likelihood estimates. Best-fit models were selected based on the lowest QAIC value (Whitehead 2006) results from this are provided in Appendix G.

Table 4.1. Mathematical models that can be fitted to standardised lagged association rates in SOCPROG 2.3 with their definitions.

Model	Definition
Constant companions	Individuals who associate together permanently over time.
Casual acquaintances	Individuals who associate for a period of time, than disassociate and may re-associate at some time later.
Rapid disassociation	Some individuals disassociate very quickly, within one time period.

Social Structure (Community and Dyad Level)

Group/ Individual Association Plots

Hierarchical cluster analysis and sociograms were generated for 148 individuals resighted four or more times in the Marlborough Sound from 1997 to 2005. Results are presented for the population as a whole, and for the various group sizes, in order to examine social groupings and individual association patterns.

Hierarchical Clusters (Community Level)

Dendograms of the association data represent various groupings of individuals based on the selected linkage method. The average-linkage method was used in this study as per recommendations from Miligan and Cooper (1987) and Whitehead (2006). Cophenetic correlation coefficients indicate how well dendograms match the association matrix. A cophenetic correlation coefficient above 0.80 indicates a good match (Whitehead 2006).

Sociograms (Dyad Level)

Sociograms of the association matrix are plotted with individuals distributed evenly around a circle with lines of various widths linking individuals. The thickness of the line indicates the strength of the relationship between individuals. Large numbers of individuals can make sociograms cluttered, so minimum values of associations were set at 0.61 to clearly show high (0.61-0.80) and very high (0.81-1.0) association levels.

Table 4.2. Associations examined using SOCPROG 2.3 followed by the test method used, dataset selected, association index used (location of results), sampling period tested, group association defined and the cut off point for individuals used in this analysis. Table modified from Mourão 2006.

Association Types	Method Used	Dataset Used	HWI (Results)	SRI (Appendix E)	Sampling Periods Tested	Group Asso.	Re-sights
Overall associations	Histogram of non-diagonal elements	Population	Yes	Yes	Weekly, Day, Month, Year	Day	≥4
		Small groups	Yes	Yes		Day	
		Medium groups	Yes	Yes		Day	
		Large groups	Yes	Yes		Day	
Closest companion associations	Histogram of maximum coefficients of associations	Population	Yes	Yes	Weekly, Day, Month, Year	Day	≥4
		Small groups	Yes	Yes		Day	
		Medium groups	Yes	Yes		Day	
		Large groups	Yes	Yes		Day	
Preferred/ avoided Associations	Test “permute groups within samples”	Population	Yes	Yes	Weekly, Day, Month, Year	Day	≥4
		Small groups	App. E	Yes		Day	
		Medium groups	No	No		No	
		Large groups	App. E	Yes		Day	
Variation in Gregariousness	Test “permute groups within samples”	Population	Yes	Yes	Weekly	Day	≥4
Associations between individuals	Lagged association rates	Population Small groups Medium groups Large groups	Yes	Yes	Weekly	Day	≥4
Associations between clusters of individuals	Hierarchical average linkage analysis	Population	Yes	Yes	Weekly, Day, Month, Year	Day	≥4
		Small groups	Yes	Yes		Day	
		Medium groups	Yes	Yes		Day	
		Large groups	Yes	Yes		Day	
Associations between Individuals	Sociograms	Population	Yes	Yes	Weekly	Day	≥4
		Small groups	Yes	Yes		Day	
		Medium groups	Yes	Yes		Day	
		Large groups	Yes	Yes		Day	

4.3 Results

Social Structure

Association Plots

The observed distribution of coefficients of association (COA) for the population as a whole and for all groups (small, medium and large) from 1997 to 2005 are shown in Figures 4.1.-4.4. To show differences in the association patterns, non-diagonal (all non-diagonal elements) and maximum (individuals closest companion) coefficients of association are presented.

Population

The population as a whole shows very stable associations with a large number of COA values being higher than 0.40 (low) (Figure 4.1 a.). The maximum coefficient of association plot shows even higher levels of associations between individuals and their closest companions with most COA values above 0.61 (high) (Figure 4.1 b.).

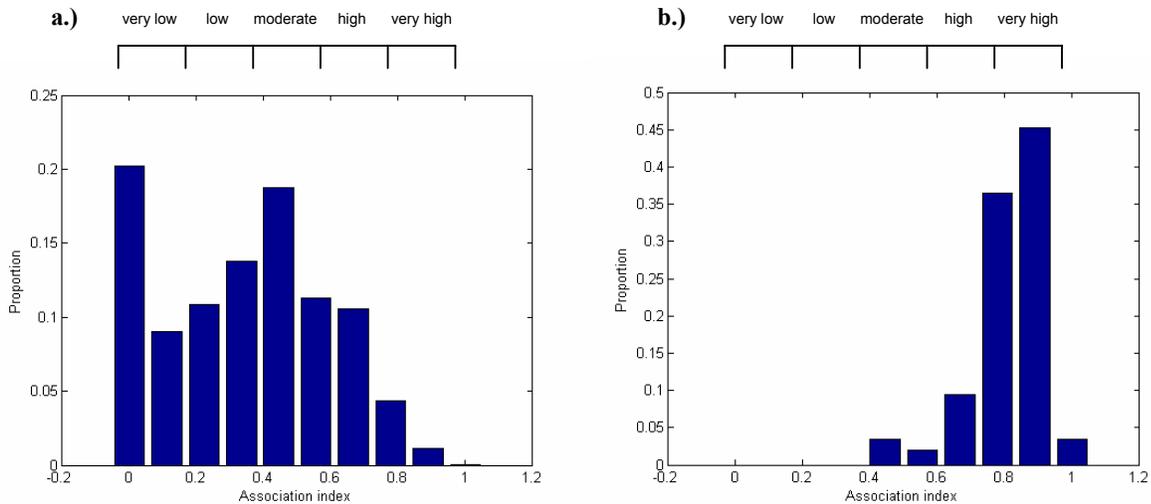


Figure 4.1. a.) Non-diagonal association plot, b.) Maximum coefficient of association plot, both based on a weekly sampling period, (half weight index) for all individuals photographed four or more times in the Marlborough Sounds from 1997-2005. Proportion = the proportion of the number of coefficients of association between individuals.

Groups

Coefficients of association values for all non-diagonal elements were different between group sizes, with small groups having the lowest COA values (Figure 4.2 a.), medium having slightly higher COA values (Figure 4.3 a) and large groups with the highest COA values (Figure 4.4 a.). All group sizes had high COA values for maximum coefficients (individuals and their closest companions), with most associating at moderate (0.41) or higher levels (Figure 4.2 b. and 4.3 b.). The strongest COA values between individuals and their closest companions were observed in large groups with all associating at 0.75 (high) or higher (Figure 4.4 b.).

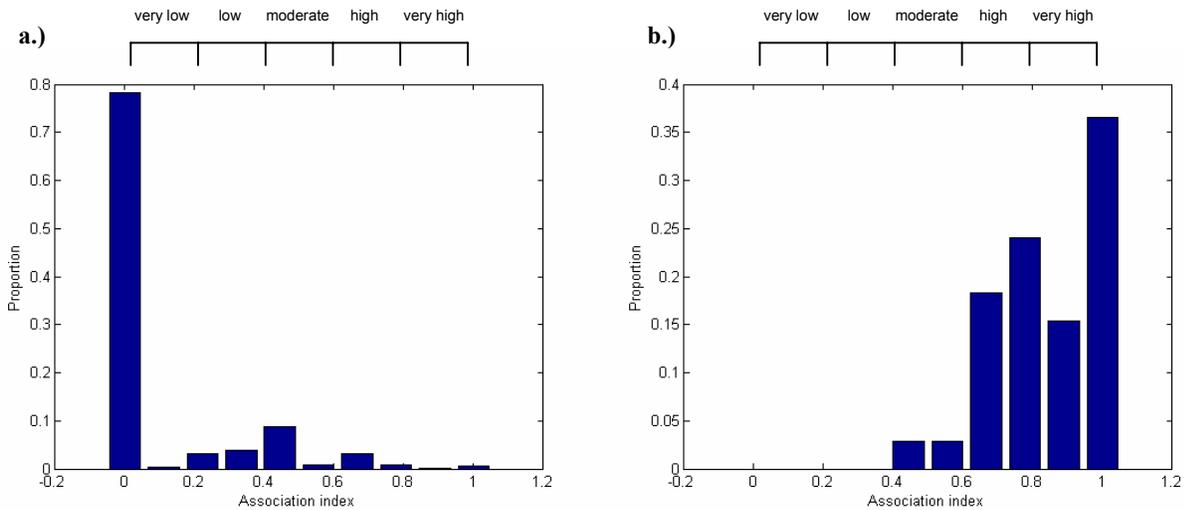


Figure 4.2. a.) Non-diagonal association plot, b.) Maximum coefficient of association plot, both based on a weekly sampling period, (half weight index) for all individuals photographed four or more times occurring in small groups (less than 25) in the Marlborough Sounds from 1997-2005. Proportion = the proportion of the number of coefficients of association between individuals.

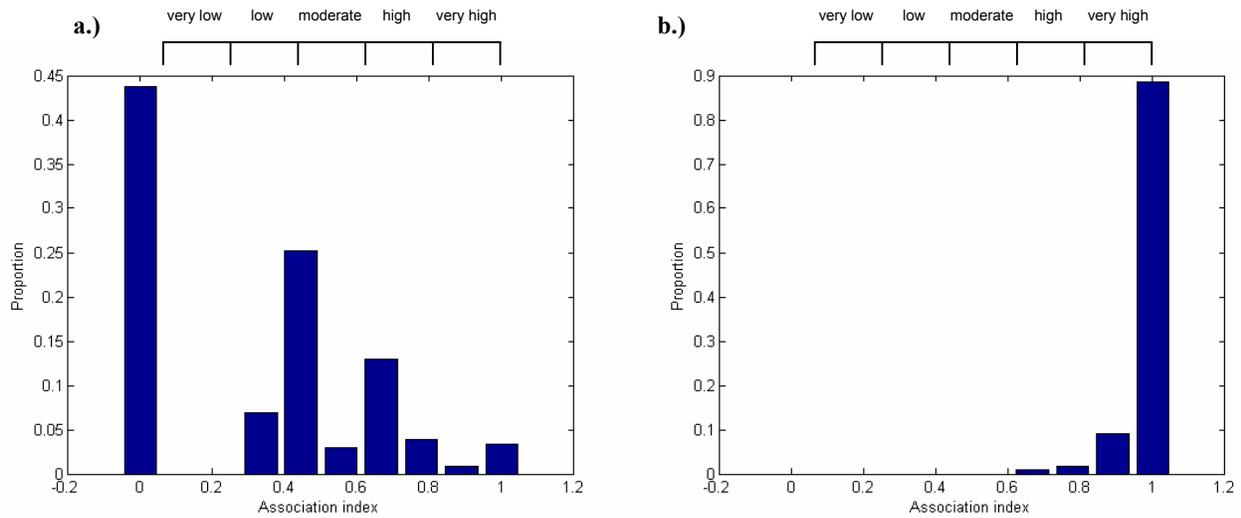


Figure 4.3. a.) Non-diagonal association plot, b.) Maximum coefficient of association plot, both based on a weekly sampling period, (half weight index) for all individuals photographed four or more times occurring in medium groups (26-60) in the Marlborough Sounds from 1997-2005. Proportion = the proportion of the number of coefficients of association between individuals.

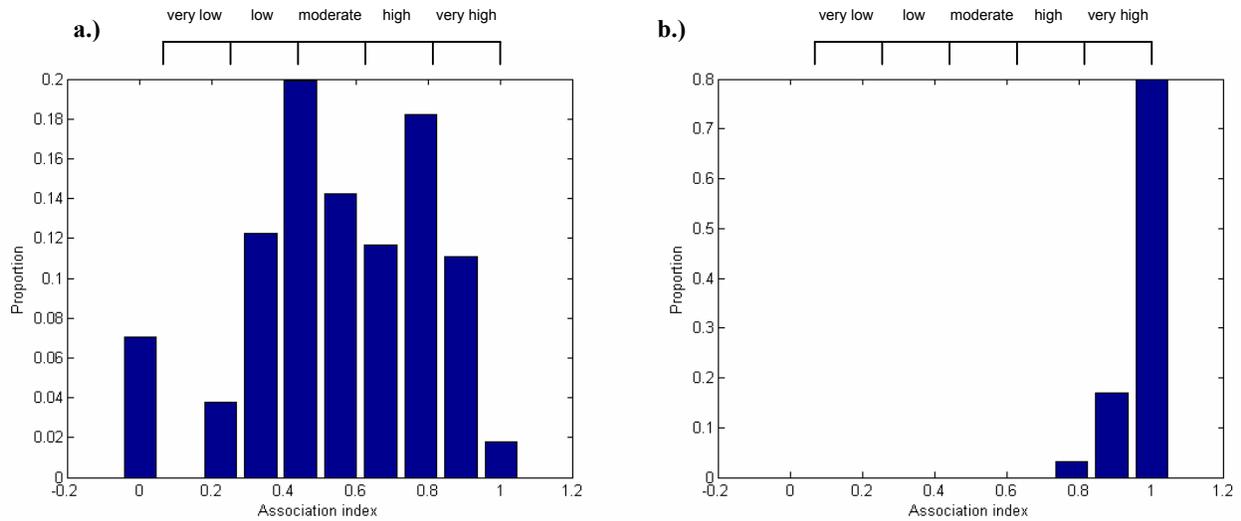


Figure 4.4. a.) Non-diagonal association plot, b.) Maximum coefficient of association plot, both based on a weekly sampling period, (half weight index) for all individuals photographed four or more times occurring in large groups (greater than 61) in the Marlborough Sounds from 1997-2005. Proportion = the proportion of the number of coefficients of association between individuals.

Preferred/Avoided Tests

Preferred/Avoided tests for “permute groups within samples” show that there are long- and short-term companionships present within the population of bottlenose dolphins in the Marlborough Sounds (Table 4.3). Among the various group sizes, long-term preferred companions were only observed in large groups (p-value= 0.87080) and short-term companions were only observed in small groups (p-value= 0.03870) (Table 4.3). Results for “permute associations within samples” show that the population as a whole, large and small groups, all have preferred/avoided associations between sampling periods (Table 4.4).

Table 4.3. Results for permutation tests for “permute groups within samples” of individuals resighted four or more times in the Marlborough Sounds from 1997 to 2005. Real values represent observed data and random values represent the generated values from 10,000 permutations. SOCPROG 2.3 settings are as follows; sampling period: 7days, association: group association; day; grouped in sampling period, association index: half weight. * denotes there is evidence to reject the null hypothesis.

Permute groups within samples						
Group size	Standard Deviation			Mean		
	Real	Random	p-value	Real	Random	p-value
All	0.24244	0.23378	* 1.0000	0.34351	0.34435	* 0.05820
Small	0.20905	0.21078	0.05090	0.10007	0.10114	* 0.03870
Medium	0.30672	-----	-----	0.31240	-----	-----
Large	0.24343	0.24278	* 0.87080	0.55394	0.55404	0.35380

Table 4.4. Results for permutation tests for “permute associations within samples” of individuals resighted four or more times in the Marlborough Sounds from 1997 to 2005. Real values represent observed data and random values represent the generated values from 10,000 permutations. SOCPROG 2.3 settings are as follows; sampling period: 7days, association: group association; day; grouped in sampling period, association index: half weight. * denotes there is evidence to reject the null hypothesis.

Permute associations within samples						
Group size	Standard Deviation			Coefficient of Variation		
	Real	Random	p-value	Real	Random	p-value
All	0.24244	0.24205	* 0.97920	0.70577	0.70462	* 0.98190
Small	0.20905	0.20881	* 0.77570	2.08904	2.08765	* 0.72430
Medium	0.30672	-----	-----	0.98182	-----	-----
Large	0.24343	0.24304	* 0.91890	0.43946	0.43874	* 0.92630

Variation in Gregariousness

Gregariousness is the tendency to be around others, the desire to be in a group. Group size defined by Jarman (1974) is the group size most commonly experienced by an individual. Results for the half-weight and simple ratio indices were both applied to all individuals resighted 4 or more times within the Marlborough Sounds. The standard deviation of typical group size for the observed data was significantly higher than the standard deviation of the generated data for both indices (Table 4.5). This suggests that some individuals are found consistently in larger groups and some are found consistently in smaller groups.

Table 4.5. Standard deviation of typical group size for “permute groups within samples” for 148 individuals resighted 4 or more times. Real values are observed values and random values are generated values from 1000 permutations with a sampling period of one week. * denotes there is evidence to reject the null hypothesis.

Association Index	Real Value	Random Value	p-value
Half-weight	18.71433	17.82633	*1.00000
Simple ratio	18.71433	17.82846	*0.99900

Longevity of Associations

Population

Standardised lagged association rates were generated for 148 individuals resighted 4 or more times in the Marlborough Sounds region. Figure 4.5. indicates that bottlenose dolphins associate non-randomly for approximately 600 days. The model curve drops at 40 days and again at 250 days, suggesting that associations among most individuals are high within a 40 day period. Some associations lessen between 40 to 250 days and after 250 days only some individuals maintain long-term associations, lasting up to 600 days.

The best-fit model selected based on the log likelihood ratio and lowest QAIC value was constant companions + casual acquaintances (Appendix G).

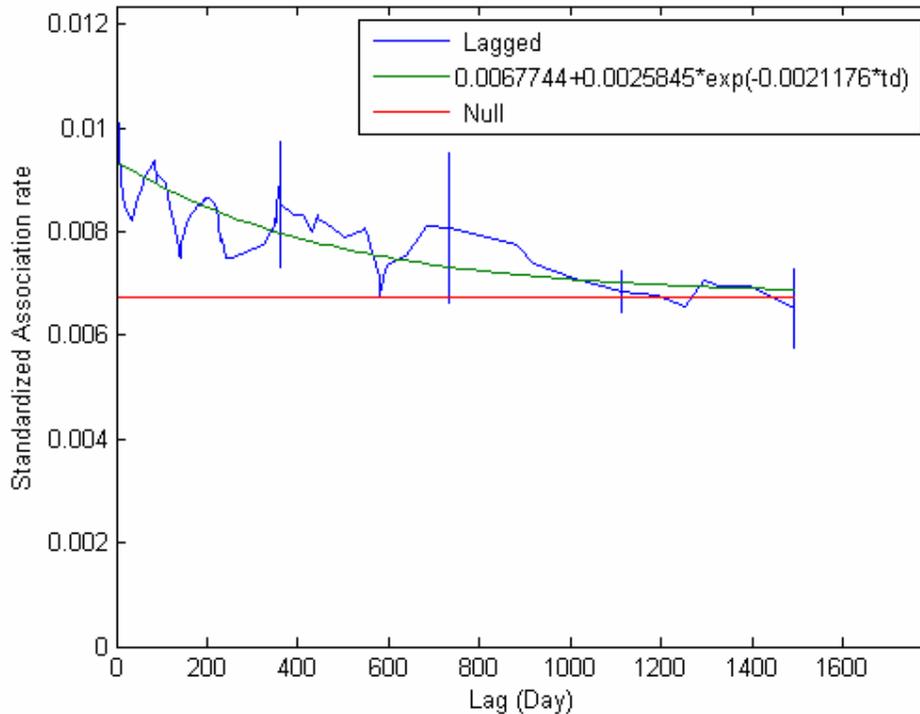


Figure 4.5. Lagged association rates of bottlenose dolphins observed 4 or more times from 1997-2005 indicate the probability that dolphins photographed together at time 0 will be photographed together again at time x. Bars represent 1 standard error (jack-knife). The red line at the bottom represents the null associations rate. All associations above the red line are non-random. The green curve represents the best-fit model (Constant companions + Casual acquaintances) based on the log-likelihood ratio for this dataset.

Groups

Standardised lagged association rates were generated for individuals observed 4 or more times from 1997 to 2003, occurring in three different group sizes. Best-fit models were selected for each data set based on the log-likelihood ratio and the lowest QAIC value.

SLAR for small groups indicate that dolphins associate non-randomly for 1200 days (Figure 4.6). The model curve drops at 40 days and again at 250 days, further suggesting that associations among most individuals are high within a 40 day period. Some associations lessen from 40 to 250 days and after 250 days only some individuals

maintain long-term associations, lasting up to 1200 days. Constant companions + Casual acquaintances was the best-fit model for this data set.

SLAR for individuals occurring in medium groups indicate that associations remain stable up to 300 days before falling below the null association rate (Figure 4.7). The model curve falls at 100 days suggesting that individuals within these groups maintain some level of long-term associations lasting up to 100 days. The constant companion model was the best-fit model for this data set. SLAR for individuals occurring in large groups show individuals associate non-randomly up to 600 days (Figure 4.8). The casual acquaintances model proved the best-fit model for this data set.

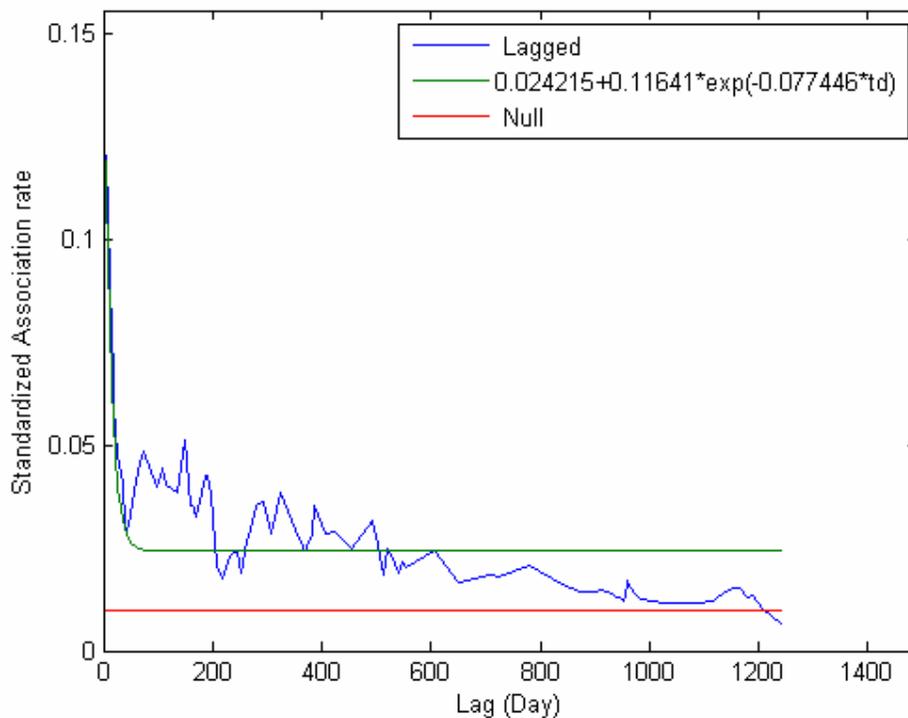


Figure 4.6. Lagged association rates of bottlenose dolphins observed 4 or more times in small groups from 1997-2005 indicate the probability that dolphins photographed together at time 0 will be photographed together again at time x. The red line at the bottom represents the null associations rate. All associations above the red line are non-random. The green curve represents the best-fit model (Constant companions + Casual acquaintances) based on the log-likelihood ratio for this dataset.

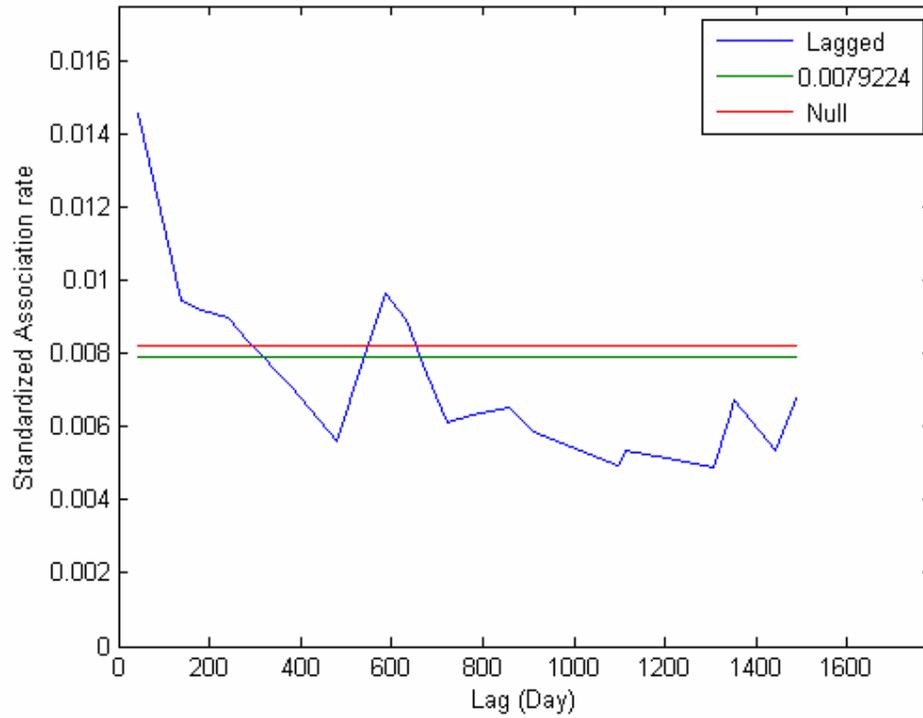


Figure 4.7. Lagged association rates of bottlenose dolphins observed 4 or more times occurring in medium groups from 1997-2005 indicate the probability that dolphins photographed together at time 0 will be photographed together again at time x. The red line at the bottom represents the null associations rate. All associations above the red line are non-random. The green curve represents the best-fit model (Constant companions) based on the log-likelihood ratio for this dataset.

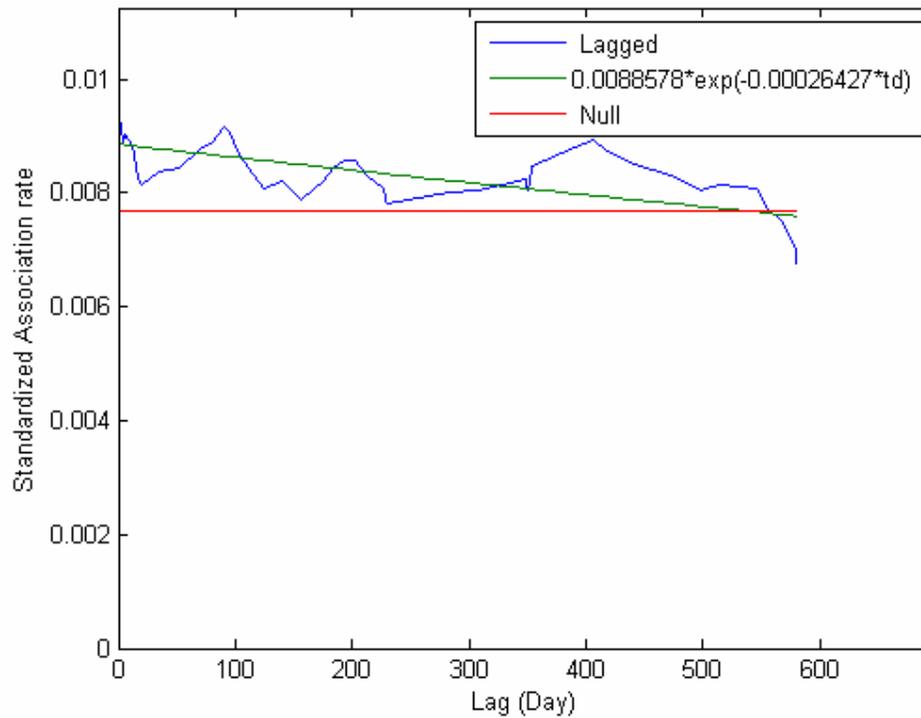


Figure 4.8. Lagged association rates of bottlenose dolphins observed 4 or more times occurring in large groups from 1997-2005 indicate the probability that dolphins photographed together at time 0 will be photographed together again at time x. The red line at the bottom represents the null associations rate. All associations above the red line are non-random. The green curve represents the best-fit model (Casual acquaintances) based on the log-likelihood ratio for this dataset.

Hierarchical Cluster Analysis

Dendrograms of 148 individuals observed 4 or more times in the Marlborough Sounds from 1997 to 2005 were plotted using the half-weight index. Nine clusters of individuals were found to associate at higher levels than the overall mean (0.34) (Figure 4.9). These clusters of individuals appear to associate closely with each other and avoid the other clusters of individuals. The hierarchical clusters produced for small, medium and large groups show clusters of individuals that associate at levels higher than the overall averages, with small groups forming six clusters (Figure 4.10), medium groups forming four clusters (Figure 4.11) and large groups forming seven clusters (Figure 4.12).

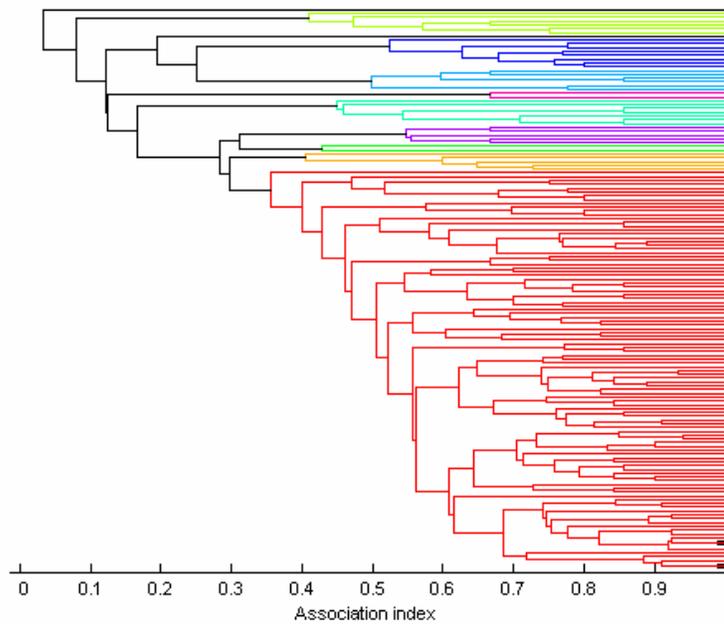


Figure 4.9. Association index displayed in cluster form, based on half-weight indices for all individuals (n=148) photographed four or more times from 1997-2005, using average linkage; cophenetic correlation coefficient=0.812. Nine clusters of individuals were found to associate at levels higher than the mean (0.34). All colorized clusters are above the mean.

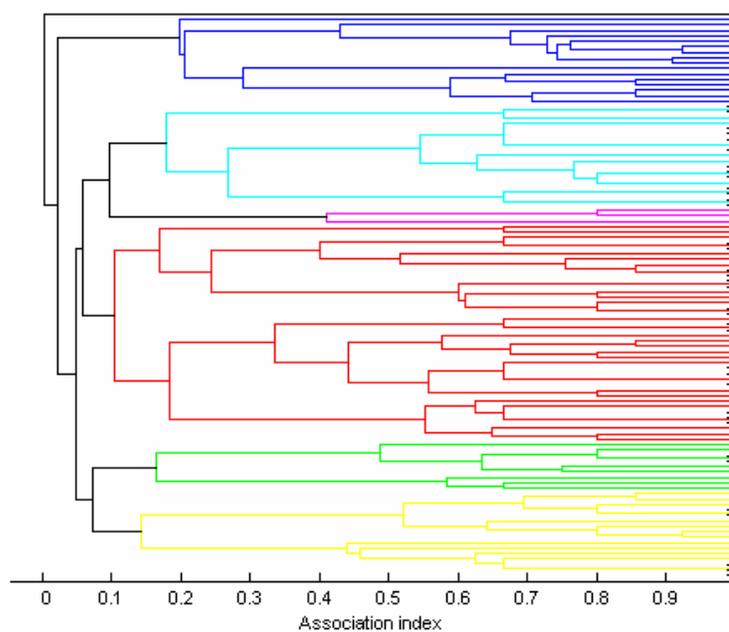


Figure 4.10. Association index displayed in cluster form, based on half-weight indices for all individuals (n=104) photographed four or more times occurring in small groups (less than 25) from 1997-2005, using average linkage; cophenetic correlation coefficient=0.737. Six clusters of individuals were found to associate at higher levels than the mean (0.10). All colorized clusters are above the mean.

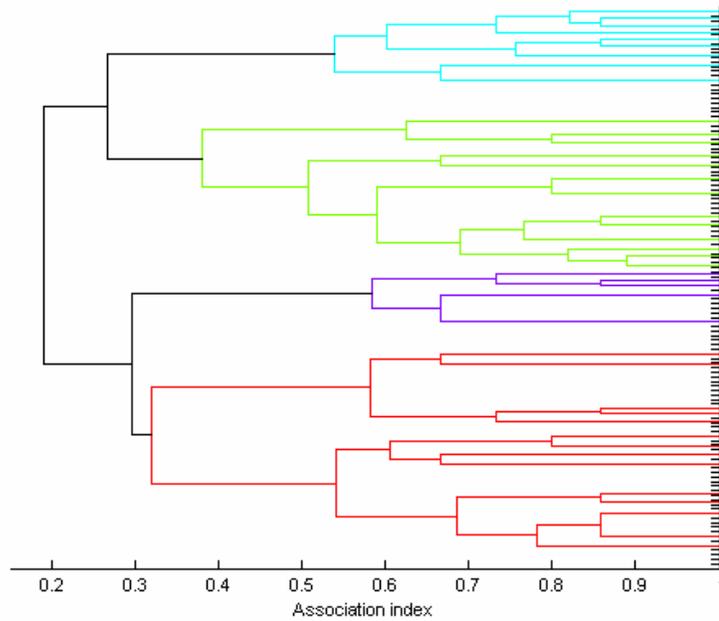


Figure 4.11. Association index displayed in cluster form, based on half-weight indices for all individuals (n=122) photographed four or more times occurring in medium groups (26-60) from 1997-2005, using average linkage; cophenetic correlation coefficient=0.628. Four clusters of individuals were found to associate at levels higher than the mean (0.23). All colored clusters are above the mean.

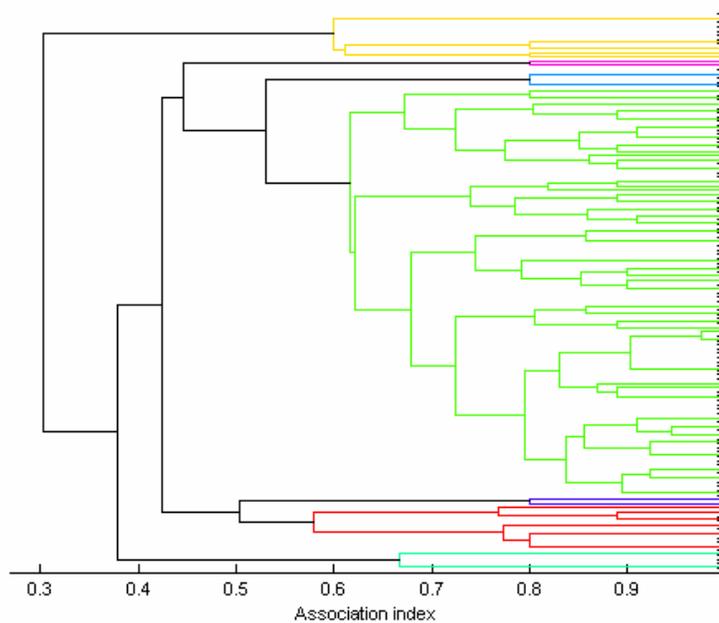


Figure 4.12. Association index displayed in cluster form, based on half-weight indices for all individuals (n=130) photographed four or more times occurring in large groups (greater than 61) from 1997-2005, using average linkage; cophenetic correlation coefficient=0.708. Seven clusters of individuals associate at higher levels than the mean (0.55). All colored clusters are above the mean.

Sociograms

Sociograms were generated for 148 individuals observed 4 or more times in the Marlborough Sounds from 1997 to 2005. Results based on the half-weight index reveal strong association between individuals. To limit the number of casual associates represented, only associations higher than 0.61 are shown (Figure 4.13). Despite the removal of moderate to low associations (noise) these sociograms still make it problematic to differentiate between the levels of high associations. However, their inclusion here still depicts the general degree of overall associations between the population and between the various group sizes.

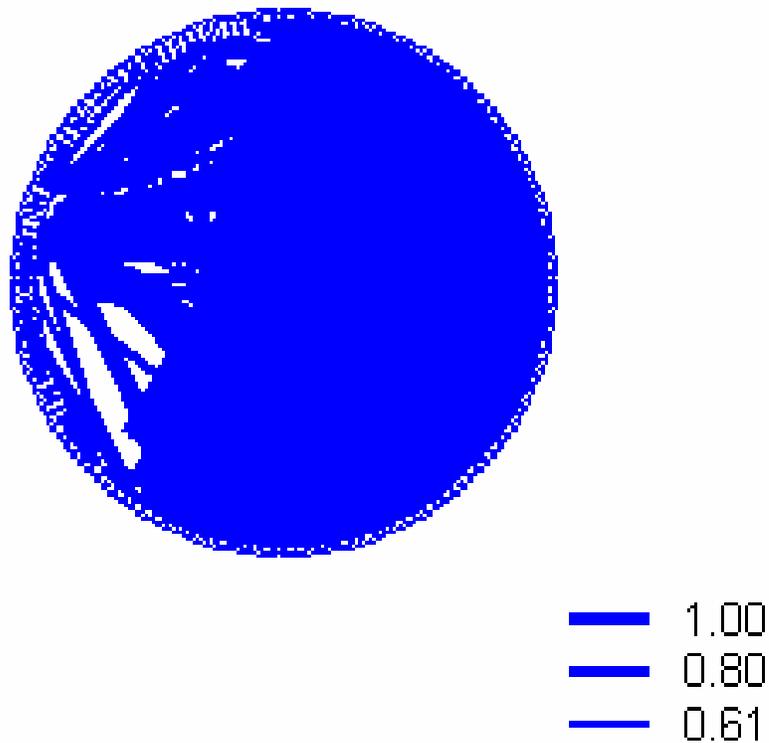


Figure 4.13. Sociogram of all individuals observed 4 or more times from 1997-2005, based on the half weight index.

Sociograms generated for small (Figure 4.14a), medium (Figure 4.14b) and large (Figure 4.14c) groups based on the half-weight index, revealed that associations between individuals are strong for all group sizes. There was some variation between the groups, with large and medium groups having higher associations between individuals than small groups.

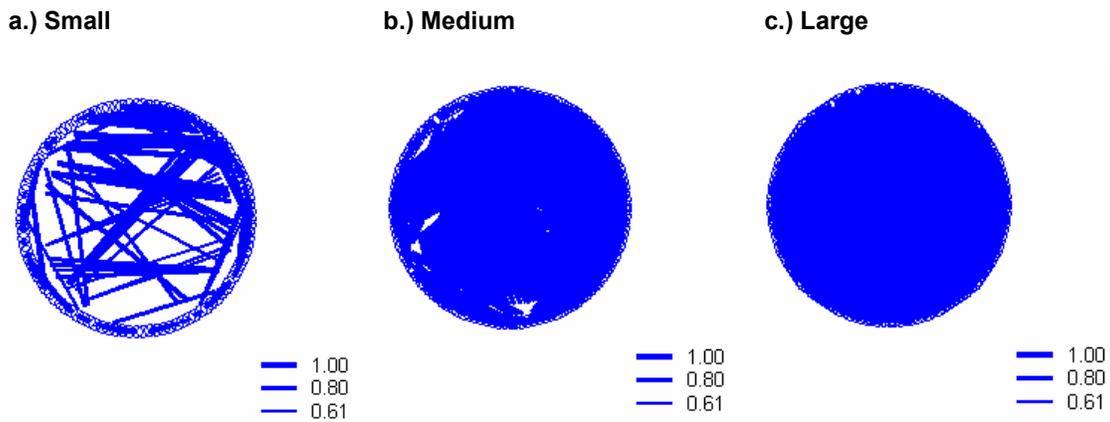


Figure 4.14. Sociograms of all individuals observed 4 or more times occurring in various sized groups from 1997 to 2005, based on the half weight index.

4.4 Discussion

Social Structure

Coefficients of Association

The semi-resident population of bottlenose dolphins found in the Marlborough Sounds showed coefficients of associations (COA) ranging from moderate to very high for some individuals, while others appear to avoid each other. COA for various group sizes showed small groups having lower levels of association than larger groups. This result is

consistent throughout the various tests (preferred/avoided, cluster analysis and sociograms) presented in this study. COA levels (between sexes) reported in other studies are lower than the levels found in the Marlborough Sounds (Wells *et al.* 1987, Smolker *et al.* 1992, Bräger *et al.* 1994, Connor *et al.* 2000, Mourão 2006, Quintana-Rizzo and Wells 2001). In the Bay of Islands, New Zealand the majority of COA ranged from low (0.01-0.40) to moderate (0.41-0.60) (Mourão 2006), suggesting that this population is highly fluid in nature. In contrast, research from Doubtful Sound, New Zealand reported all individuals associate at levels higher than 0.40 (Lusseau 2003) displaying consistent stable associations. The bottlenose dolphins in the Marlborough Sounds are more stable in their associations than the population in the Bay of Islands and more fluid in their associations compared to the population found in Doubtful Sound. This suggests that there is a high level of stability in the associations of Marlborough Sounds dolphins but that they still maintain the fluidity of a fission-fusion society. This level of association could, at least in part, be due to the topographic features evident in the Marlborough Sounds area. It was suggested that topographic isolation and prey availability are contributing factors to the high levels of stable associations observed among the Doubtful Sound population (Lusseau 2003). Populations in the Marlborough Sounds and Bay of Islands (Mourão 2006) are not likely to be subjected to such ecological constraints (i.e. thermal stress) and therefore may be able to maintain higher levels of fluidity in their associations.

Preferred/Avoided Associations

The preferred/avoided association tests show that long- and short-term preferred associations were present in the population of bottlenose dolphins in the Marlborough Sounds. However, tests conducted on various group sizes showed long-term preferred

associations were only significant in the large groups and that short-term preferred associations were only significant among the small sub-groups. This was apparent in field observations and photo-identifications, where large groups of bottlenose dolphins (100+ individuals) come into the sounds, then exit for a period of time. When the large group exits a number of small sub-groups (between 7-15 individuals) break off and remain in various parts of the Marlborough Sounds. When the large group returns the smaller sub-groups re-join the large group and the cycle repeats itself (Merriman *et al.* unpublished data). Long- and short-term preferred associations are present in many populations of bottlenose dolphins (e.g. long-term; Shark Bay, Australia (Connor *et al.* 1992, Smolker *et al.* 1992, Gero *et al.* 2005), Sarasota, Florida (Wells *et al.* 1987), and short-term; Moray Firth, Scotland (Lusseau *et al.* 2005)) one of the longest running studies reported long-term associations lasting up to 14 years (Conner *et al.* 2000). Long-term and short-term preferred association were detected in the Bay of Islands (Mourão 2006) and in Doubtful Sound (Lusseau *et al.* 2003). This appears to be a consistent pattern in the social structure for all studied populations of bottlenose dolphins in New Zealand.

Variation in Gregariousness

Tests on gregariousness showed that certain individuals were consistently observed in larger groups while others were consistently observed in smaller groups. This result was also reported for the population of bottlenose dolphins in the Bay of Islands (Mourão 2006). In contrast, the population in Doubtful sound were reported to occur in one to two larger sized groups that moved synchronously throughout their home range (Schneider 1999). While Australia, Florida and the Moray Firth studies showed that individuals typically associate in smaller groups (Smolker *et al.* 1992, Wells 1991 and Lusseau *et al.* 2005).

Why an individual prefers a larger group to a smaller one or vice versa for the population of bottlenose dolphins in the Marlborough Sounds is unknown. One hypothesis is that ecological pressures such as predation and food availability may influence the social structure of this population. In Shark Bay, Australia, Heithaus and Dill (2002) reported that the presence of tiger sharks (*Galeocerdo cuvier*), a known predator of bottlenose dolphins, was linked to the occurrence of larger group sizes. Norris and Dohl (1980) suggested that predation risk is the main determinant in the formation of groups among cetaceans.

Group formation for protection against predators has been observed in a number of other species such as squirrel monkeys (*Saimiri oerstedii*) (Mitchell *et al.* 1991), Thomson's gazelles (*Gazella thomsoni*) (FitzGibbon 1994), mule deer (*Odocoileus hemionus*) (Lingle 2001) and spinner dolphins (Lammers 2004). Group formation has also been linked to prey abundance and foraging techniques (Würsig 1986). Many cetacean species have been observed hunting and feeding cooperatively. For example, killer whales (*Orcinus orca*) off the coast of British Columbia have been observed hunting in groups, attacking large baleen whales (Ford *et al.* 1998). Delphinids that feed on small schooling fish such as, common dolphins (*Delphinus delphis*), spotted dolphins (*Stenella frontalis*), dusky dolphins (*Lagenorhynchus obscurus*), and spinner dolphins are often found working cooperatively to herd fish (Norris and Dohl 1980, Würsig and Würsig 1980). Bottlenose dolphins in Cedar Key, Florida have been observed feeding cooperatively by herding fish and flushing them out of the water to other non-herding group members (Gazda *et al.* 2005).

Bottlenose dolphins in the Marlborough Sounds are rarely found feeding on small schooling fish or feeding cooperatively. Instead, they feed independently, pushing their prey up against the rocky shoreline (personal observation M. Merriman). Mann (2000)

suggests that some individuals or small groups often leave larger non-foraging groups to locate food for the betterment of the group or alternatively separate to hunt alone. Each of these suggestions may account for the reason why some individuals in the Marlborough Sounds are found more often in smaller groups than others. The most likely reason is that non-breeding individuals benefit from forming groups with other individuals in a similar state or condition. Future research on foraging patterns, social structure and prey availability may provide further insight into this complex society.

Standardised Lagged Association Rates

Standardised lagged association rates show that the population of bottlenose dolphins in the Marlborough Sounds form a social structure with two levels of associations; constant companions and casual acquaintances, that associate non-randomly over periods up to 600 days. This is consistent with the populations found in the Bay of Islands, New Zealand (Mourão 2006) and the Moray Firth, Scotland (Lusseau *et al.* 2005). In the Bay of Islands, Mourão (2006) reports members of the population showed two levels of associations; constant companions and casual acquaintances that maintained long lasting associations over three years. Two levels of associations were also found in the Moray Firth population, constant companions and casual acquaintances. Long-term associates were reported with some lasting between 7-9 years, the majority of the population displayed short-term associations between all members (Lusseau *et al.* 2005). Lagged association rates for the population in Doubtful Sound were described as constant companions with some individuals maintaining long-term associations over three years (Schneider 1999, Lusseau 2003). All the populations show some level of long-term associations but the population in Doubtful Sound show stronger, more stable associations among all members compared to the Marlborough Sounds, Bay of Islands

and Moray Firth populations which seem to be more fluid in their associations. Close associations may be an important factor in the functionality of a group. Strong social bonds among members of a population may provide individuals with the knowledge they need to function successfully in their environment (Lusseau 2003). In many gregarious, long-lived species (e.g. elephants (*Loxodonta africanus*), gorillas (*Gorilla gorilla*), killer whales, humpback whales (*Megaptera novaeangliae*), and bottlenose dolphins) the passing on of knowledge and the development of social skills is vital to the fitness of each member (Rendell and Whitehead 2001).

Hierarchical cluster analysis

Nine clusters of individuals were found to associate at higher levels than the overall mean for the population of bottlenose dolphins in the Marlborough Sounds. These nine clusters appear to associate closely with each other and avoid other clusters. This is consistent with the preferred/avoided test results in section 4.2. The hierarchical clusters produced for small, medium and large groups show clusters of individuals that associate at levels higher than the overall averages, but their cophenetic correlation coefficients are not as high as the cophenetic correlation coefficient for the population as a whole (0.81). Whitehead (2006) suggests that a cophenetic correlation coefficient below 0.80 is not a good representation and probably should not be reported. Hierarchical cluster analysis (cophenetic correlation coefficient=0.73) for the population of bottlenose dolphins in the Bay of Islands, showed three clusters of individuals where association indices were greater than average and the three clusters appear to avoid each other (Mourão 2006). In Doubtful Sound cluster analysis revealed three clusters that associated more frequently than all individuals within the population, but clusters did not avoid each other. Other studies have reported the clustering of individuals based on sex and reproductive qualities

such as the formation of nursery groups for the protection of calves (Wells *et al.* 1987) or the formation of alliances between males to gain access to females (Conner *et al.* 1992a). In contrast, the populations of bottlenose dolphins in the Bay of Islands and Doubtful Sound show clusters formed between mixed sex groups. For the bottlenose dolphins in the Marlborough Sounds, it is assumed that the various clusters are mixed sexed groups, although there was not enough sex specific data for this to be statistically determined.

Sociograms

Sociograms revealed stronger associations exist within the larger groups compared to the smaller groups. This is consistent with the results from the COA, preferred/avoided tests and the SLAR, indicating stronger co-occurrences of individuals within large groups. In other studies sociograms were generated for inter-sexual associations (Quintana-Rizzo and Wells 2001, Mourão 2006, Smolker *et al.* 1992). Most of the studied populations of bottlenose dolphins form a loose network of associations with females and males typically displaying strong, long-term associations among sex specific groups (Wells 1991, Wells 2003, Smolker *et al.* 1992, Connor *et al.* 1999). Few studies on bottlenose dolphins show strong, long-term associations between members of the opposite sex (Lusseau *et al.* 2003, Lusseau *et al.* 2005, Mourão 2006). Based on the large group sizes observed in the Marlborough Sounds population, I believe these groups to be comprised of both males and females. Unfortunately, due to the lack of sex specific data on individuals within the population I was unable to conduct this analysis.

4.5 Summary

This chapter examined the social structure of bottlenose dolphins in the Marlborough Sounds, New Zealand. I found that this population has short- and long-term preferred

associations, with long-term associates lasting over three years. The bottlenose dolphins in the Marlborough Sounds are part of a highly flexible fission-fusion society that are characterised by constant companions and casual acquaintances. Bottlenose dolphins in the Marlborough Sounds (MS) show similarities and differences in their association patterns with populations found in the Bay of Islands (BOI) and Doubtful Sound (DS).

All three studied populations of bottlenose dolphins in New Zealand show long-term associations that last over multiple years. The clustering of individuals that associate more frequently than others was reported for all three populations. However, in the DS population the clustered groups showed no evidence of avoiding each other (Lusseau 2003), unlike the MS and BOI populations where clustered groups appear to avoid each other (Mourão 2006). Studies on populations of bottlenose dolphins in DS and the BOI report strong associations between individuals within mixed sex groups (Lusseau 2003, Mourão 2006). It is suspected that this is also the case for bottlenose dolphins in the Marlborough Sounds. However, further sex specific data is required to test this hypothesis.

The majority of associations for the population of bottlenose dolphins in the Marlborough Sounds have a COA that is lower than that for the DS population and higher than the BOI population (Lusseau 2003, Mourão 2006). The Marlborough Sounds population is not only a geographically intermediate population, it also displays intermediate levels of social structure and association patterns compared to the other studied populations of bottlenose dolphins in New Zealand.

Social structure and ecological pressures are important elements in the daily lives of individuals (Whitehead 1997). Understanding the social interactions between individuals can provide basic knowledge on the functions and dynamics of a population (Hinde 1976). This knowledge can provide conservation managers with the base line

data needed to make informed decisions relevant to the social organisation of a specific population (Lusseau 2005).

The population of bottlenose dolphins in the Marlborough Sounds is unique in that it exhibits high levels of associations within large groups. Results from this study add to the overwhelming evidence of diversity and social dynamics for this species. Future studies on genetics and sex specific data may provide further insight into the social interactions, occurrence of mixed sex groups and the relatedness of this population.

Chapter V

Conclusions and Recommendations



Plate 5.1. An inquisitive calf, the future of the Marlborough Sounds.

5.1 Introduction

This thesis is the first systematic study to be conducted on the population of bottlenose dolphins that range across the northern region of the South Island, New Zealand. This final chapter highlights findings from each of the previous chapters and discusses how they link together. Similarities and differences between the Marlborough Sounds and the two other studied populations of bottlenose dolphins in New Zealand are provided. This is followed by a summary comparing the findings of this study with other international studies on populations of bottlenose dolphins discussed in this thesis. Findings are then related to possible conservation and

management issues for bottlenose dolphins utilising the Marlborough Sounds. Finally, recommendations and future research objectives are presented.

Summary of Findings

Chapter II:

- Bottlenose dolphins were observed in the Marlborough Sounds region year round and ranged over an area greater than 890 km².
- Twenty-one percent of groups encountered in the Marlborough Sounds contained ≥ 81 individuals.
- Groups containing calves were significantly larger than groups without calves.
- Calves were observed in the Marlborough Sounds year round.
- Neonates were only observed in the summer and autumn seasons, suggesting a summer-autumn calving season.
- Activity budgets showed the proportion of time socialising differed significantly between areas.
- Activity levels for various group sizes showed smaller groups rest less than larger groups.
- Seasonal variation in activity budgets showed bottlenose dolphins rest less in spring.

Chapter III:

- 335 individuals were photographically documented in the Marlborough Sounds region between 1992 and 2005.
- Abundance estimates showed that 195-232 individuals visit the Sounds annually, with an interannual immigration/emigration rate of 25%.

- The discovery curve showed no plateau, providing evidence of an open population.
- Long-term site fidelity was documented over multiple years.
- Lagged identification rates showed consistency over a four-year period.
- Movement probabilities showed rapid movement between all areas of the Sounds.

Chapter IV:

- Coefficients of associations (COA) ranged from moderate to very high for some individuals, while others appear to avoid each other.
- COA for groups showed smaller groups display lower levels of association than larger groups.
- Hierarchical cluster analysis showed that nine clusters of individuals were found to associate at higher levels than the overall mean.
- Long- and short-term preferred associations are present in the population of bottlenose dolphins in the Marlborough Sounds.
- Long-term preferred associations were only significant among large groups.
- Short-term preferred associations were only significant among small groups.
- Associations were non-random over 600 days, with two levels of associations evident; constant companions and casual acquaintances.
- Certain individuals were consistently observed in larger groups while others were consistently observed in smaller groups.
- Sociograms revealed stronger associations exist within larger groups compared to smaller groups.

Base line data, behavioural patterns and basic ecology are required to successfully manage and protect populations. Findings from the outlined chapters show that the population of bottlenose dolphins in the Marlborough Sounds is unique and should be managed accordingly.

Chapters II, III, and IV provide base line data on the population of bottlenose dolphins in the Marlborough Sounds. Chapter II detailed data on the distribution and habitat use of this population, while in Chapter III abundance estimates and data on long-term site fidelity were provided. Lastly, Chapter IV detailed information on the social structure and organisation of the bottlenose dolphins in the Marlborough Sounds. Chapters II and IV showed that group size and calf presence appear to be important factors to the overall structure of this population. When compared to small groups, larger groups of bottlenose dolphins contained a higher percentage of calves, rested more and displayed a higher level of long-term preferred associations. All groups were found to rest less in spring before calving season begins. Chapters II and III showed that bottlenose dolphins utilise the Marlborough Sounds year round with a relatively high interannual migration rate. These two chapters also showed that long-term site fidelity is present among this large, wide ranging, open population.

*Similarities and differences between Populations of *T. truncatus* in New Zealand*

The three studied populations of bottlenose dolphins in New Zealand (Marlborough Sounds (MS), Doubtful Sound (DS) and Bay of Islands (BOI) populations) show similarities in their year round occurrence, calving seasons, long-term site fidelity, long-term associations and clustering of individuals. However, differences in habitat use, group sizes, range, abundance estimates and residency patterns between these populations are apparent.

The MS population differs from the other two in that it forms groups twice the size of those reported in the other areas, ranges over a larger area, is considered open and does not follow seasonal trends in habitat use.

The population of bottlenose dolphins in the MS is similar to the BOI population in that they both show avoidance between clustered groups (Mourão 2006), are larger, wider ranging and semi-resident compared to the DS population.

The majority of associations for the population of bottlenose dolphins in the MS have a coefficient of association (COA) that falls between those reported for DS and BOI populations, with the DS population having the highest COA values and the BOI population having the lowest COA values (Lusseau 2003, Mourão 2006). The Marlborough Sounds population is not only a geographically intermediate population, it also displays intermediate patterns of association when compared to the other studied populations of bottlenose dolphins in New Zealand.

*Comparisons between Populations of *T. truncatus* Worldwide*

Abundance Estimates and Residency Patterns

Earlier in this thesis it was hypothesised that the Marlborough Sounds population would be similar in size and residency patterns as other populations found in coastal and semi-enclosed habitats such as, the Mississippi Sound, Gulf of Mexico (Hubard *et al.* 2004), Kvarneric, Adriatic Sea (Bearzi *et al.* 1997), Bay of Islands, New Zealand (Constantine 2002), Shark Bay, Australia (Smolker *et al.* 1992), Gulf of California, Mexico (Ballance 1992) and off the coast of Charleston, South Carolina (Speakman *et al.* 2006). The Marlborough Sounds population was intermediate in size falling in between the abundance estimates reported for most of these studies. The Marlborough Sounds population was most similar in size to populations found off the coast of Santa

Monica Bay, California (Bearzi 2005), San Diego, California (Defran and Weller 1999), and Gulf of California, Mexico (Ballance 1992).

Long-term site fidelity was observed in the Marlborough Sounds with one individual showing site fidelity over a ten-year period. This was similar to the site fidelity observed in the Mississippi Sound, South Carolina and Bay of Islands populations (Hubard *et al.* 2004, Speakman *et al.* 2006, Constantine 2002).

Group Size and Behaviour

Most studies on bottlenose dolphins report maximum group sizes less than 60 individuals (Table 1.1, Constantine 2002, Lusseau 2003, Wells *et al.* 1987, Smolker *et al.* 1992, Speakman *et al.* 2006, Hubard *et al.* 2004, Bearzi 2005, Bräger 1993, Barid *et al.* 2004, Bearzi *et al.* 2005 and Würsig 1978). However, a few studies (Ballance 1992, Defran and Weller 1999, Saayman and Tayler 1973) have reported group size ranges similar to those encountered in the Marlborough Sounds. Potential reasons for forming larger groups may be needed for detecting prey and protection from predators.

In the Marlborough Sounds, groups containing calves were significantly larger than groups without calves. This has been observed among many populations of bottlenose dolphins in various locations such as the Northern Adriatic Sea (Bearzi *et al.* 1997, Mississippi Sound, Mississippi (Hubard *et al.* 2004), Galveston, Texas (Fertl 1994), San Diego, California (Weller 1991), and Sarasota Bay, Florida (Wells *et al.* 1987). Birthing seasons for the Marlborough Sounds population are similar to those reported in other studies (Würsig 1978, Irvine *et al.* 1981, Wells *et al.* 1987, Urian *et al.* 1996, Bearzi *et al.* 1997, Mann *et al.* 2000) where births peaked from late spring through to early autumn. Activity levels for various group sizes showed that smaller

groups rest less than medium and large groups. This result is similar to reports from Shark Bay, Western Australia, where large groups were observed resting more than small groups (Heithaus and Dill 2002). Seasonal variation in activity budgets for the Marlborough Sounds showed bottlenose dolphins rest significantly less in spring than in winter, summer and autumn.

Association Patterns

Long- and short-term preferred associations are present in many populations of bottlenose dolphins (e.g. long-term; Shark Bay, Australia (Connor *et al.* 1992, Smolker *et al.* 1992, Gero *et al.* 2005), Sarasota, Florida (Wells *et al.* 1987), and short-term; Moray Firth, Scotland (Lusseau *et al.* 2005)) one of the longest running studies reported long-term associations lasting up to 14 years (Conner *et al.* 2000). Long- and short-term preferred association were detected in the Bay of Islands (Mourão 2006) and in Doubtful Sound (Lusseau *et al.* 2003). This appears to be a consistent pattern in the social structure for all studied populations of bottlenose dolphins in New Zealand.

The Marlborough Sounds population forms a social structure with two levels of associations; constant companions and casual acquaintances that associate non-randomly over 600 days. This is consistent with the populations found in the Bay of Islands, New Zealand (Constantine 2002) and the Moray Firth, Scotland (Lusseau *et al.* 2005).

There are many similarities and differences among the studied populations of bottlenose dolphins around the world. The diversity and adaptability of this species allows these populations to exploit the various habitats in which they occur. One element that remains consistent among all populations of bottlenose dolphins is the

complexities of their social systems. As future studies commence and more literature is published, the intricate daily lives of these individuals unfold.

How it Relates to Possible Management Issues

Abundance estimates showed that 195-232 individuals visit the sounds annually, with a high interannual immigration/emigration rate of 25%. Data also suggest that at least a proportion of the population show, a high level of site fidelity, while some individuals are observed less frequently.

Seasonal variation in activity budgets for the Marlborough Sounds showed bottlenose dolphins rest significantly less in spring than in winter, summer and autumn. This may be a result of increased feeding during spring for lactating females (Cheal and Gales 1991).

Neonates were only observed in the summer and autumn seasons, suggesting a summer-autumn calving season. Calves were observed in the Marlborough Sounds year-round with the greatest number of calves per group observed in the spring and autumn seasons. Groups containing calves were significantly larger than groups without calves. These are important factors in the management of this population since the amount of recreational vessel traffic increases substantially over this time. Increased group size can lead to easier detection by ecotourism and recreational vessels. This may disrupt group dynamics and cause increased energetic needs, particularly for lactating females and calves. Close monitoring of dolphin/ vessel interactions and increasing public awareness of the rules and regulations set by the Marine Mammal Protection Act (1992) would be valuable during this time.

Overall, bottlenose dolphins observed in the Marlborough Sounds spent the majority of their time socialising and travelling. Based on the results reported in this

study, the Marlborough Sounds appear to be an important part of this population's home range with at least a proportion of individuals utilising all of the sounds year round.

Sociograms, COA, preferred/avoided tests and the SLAR all revealed stronger associations exist within larger groups compared to smaller groups. This again is consistent with the fact that calves were observed more frequently in larger groups. Understanding the social interactions between individuals can provide basic knowledge on the functions and dynamics of a population (Hinde 1976). This knowledge can provide conservation managers with the base line data needed to make informed decisions relevant to the social organisation of a specific population (Lusseau 2005).

Bottlenose dolphins in the Marlborough Sounds are subjected to many anthropogenic impacts (Markowitz *et al.* 2004) including commercial and recreational vessel traffic, ecotourism, aquaculture and agriculture and forestry run off. The potential effects of these human impacts on this population remain unknown. However, results presented here provide base line data on this population and show how they utilise the Marlborough Sounds. This data is important for conservation managers who are responsible for monitoring and protecting this population.

Directions for Future Work

Further photo-identification effort is required to assess the overall status of this population and determine if it is truly open or closed. Additionally, photo-identification effort in adjacent areas and comparisons between catalogues could provide insight into the full extent of the movements and home range for this population. Research on spatial and temporal patterns of prey species in the

Marlborough Sounds may provide further insight into causal factors in bottlenose dolphin distribution and habitat use within this region. Future studies on genetics and sex specific data may provide additional insight into the social interactions, occurrence of mixed sex groups and the relatedness of this population. Finally, future studies focused on ecotourism, vessel traffic and aquaculture may provide a better understanding of the impact human activities have on this unique population.

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APPENDIX A: Initial sighting sheet for data collection.

DATE:		MARLBOROUGH SOUNDS DOLPHIN PROJECT				LOCATION:	
CREW:		TIME OUT:				TIME IN:	
ENVIRONMENTALS							
1	TIME:	SPEED/DIRECTION		HEIGHT/DIRECTION		WATER/AIR TEMP.	
BEAUFORT:	VISIBILITY:	WIND:	KN/	SWELL:	M/		
WEATHER:	DEPTH:	M	SALINITY:	TURBIDITY:	M	TIDE:	
2	TIME:	SPEED/DIRECTION		HEIGHT/DIRECTION		WATER/AIR TEMP.	
BEAUFORT:	VISIBILITY:	WIND:	KN/	SWELL:	M/		
WEATHER:	DEPTH:	M	SALINITY:	TURBIDITY:	M	TIDE:	
3	TIME:	SPEED/DIRECTION		HEIGHT/DIRECTION		WATER/AIR TEMP.	
BEAUFORT:	VISIBILITY:	WIND:	KN/	SWELL:	M/		
WEATHER:	DEPTH:	M	SALINITY:	TURBIDITY:	M	TIDE:	
4	TIME:	SPEED/DIRECTION		HEIGHT/DIRECTION		WATER/AIR TEMP.	
BEAUFORT:	VISIBILITY:	WIND:	KN/	SWELL:	M/		
WEATHER:	DEPTH:	M	SALINITY:	TURBIDITY:	M	TIDE:	
5	TIME:	SPEED/DIRECTION		HEIGHT/DIRECTION		WATER/AIR TEMP.	
BEAUFORT:	VISIBILITY:	WIND:	KN/	SWELL:	M/		
WEATHER:	DEPTH:	M	SALINITY:	TURBIDITY:	M	TIDE:	
SIGHTING #:	LAT:41.	LONG:174.		START:			
SPECIES:	LAT:41.	LONG:174.		END:			
BEAUFORT:	VISIBILITY:	SPEED/DIRECTION		HEIGHT/DIRECTION		WATER/AIR TEMP.	
WEATHER:	DEPTH:	M	WIND:	KN/	SWELL:	M/	TIDE:
WEATHER:	DEPTH:	M	SALINITY:	TURBIDITY:	M	TIDE:	
ASSO. SP.:							
GROUP#:	ADULTS	SUB	JUV.	CALVES	# SUB GROUPS:		
BEHAVIOR: T	F	S	R	M	HEADING: INT.	GEN.	FIN.
#VESSELS:	TYPE:				DIS. FROM:		
CHUFF	FLUKE OUT		TAIL SLAP		SIDE SLAP	PORPOISING	
LEAP	SPY HOP		SYN. DIVE		SOCIAL RUB	BOW RIDING	
FISH WHACKING	VOCALIZING		SYN . LEAPING				
NOTES:							
CARD:	FRAMES:				BLANK:		

APPENDIX B: Ethogram

Behaviour States

Feeding-	Group is diving for long periods of time and exhibiting behaviours such as fluke out dives, herding and fish in mouth.
Socializing-	Different behaviours are observed throughout the group such as social rub, aggressiveness, mating and chasing.
Travel-	Group is moving at a steady pace and in a constant direction. (Faster than idle speed of the research vessel.)
Resting-	Group is moving slowly in a constant direction. (Slower than idle speed of the research vessel.)
Milling-	No net movement in any particular direction and group members often surface in different directions.

Behaviours

Leaping-	Animal comes out of the water completely
Belly slap-	Animal comes partly out of the water and slaps down on its belly
Chin slap-	Animals head comes out of the water and slaps down
Side slap-	Animal comes partly out of the water and slaps down on its side
Spy hop-	Animal is vertical in the water and pops its head out.
Tail slap-	Animal slaps its tail against the surface of the water.
Chuff-	Animal takes a forceful breath, sounds like a cough
Fluke out dive-	Animal lifts its fluke out of the water before it dives down
Social rub-	Animal rubs against another in any way.
Bow riding-	Animal is riding the pressure wave on the front of the boat
Belly up-	Animal is swimming upside down
Porpoising-	Animal is swimming fast and coming out of the water
Logging-	Animal is resting or travelling at a very slow rate. Looks like the animal is just floating on the surface
Fish in mouth-	Animal is observed with a fish in its mouth
Chasing-	One animal is following another very quickly

Herding- A group of animals is working a school of fish into a ball

Vocalizing- High pitched whistles

Synchronous surfacing- Members of the group are surfacing to breathe at the same time

Surfing- Animals are surfing in the waves.

Dispersion

Tight- Less than one body length apart.

Average- 1 to 3 body lengths apart.

Loose- More than 3 body lengths apart.

Environmentals

Weather- 1 sunny- sun is out less than 20 percent cloud cover
 2 cloudy- sun is out or covered and cloud cover is greater than 21 percent
 3 rain- cloudy with showers or cloudy with massive down pour
 4 fog- thick marine layer either lifting off the water or rolling in

Sightability- 1 Excellent- Sunny, no clouds, no glare, SAC
 2 Very Good- Sunny, few clouds, little glare, beaufort 1-2
 3 Good- Cloudy, some clouds, some glare, beaufort 2-3
 4 Fair- Cloudy, much clouds, much glare, beaufort 3-4
 5 Poor- Cloudy, Foggy, Rainy, much glare, beaufort 4 and up.

Beaufort Sea State- 0 (SAC) Slick and Clam- mirror like surface
 1 Small ripples
 2 Small wavelets making crests but not breaking
 3 Few scattered white caps
 4 Many white caps
 5 Many white caps and breaking waves
 6 Many white caps, breaking waves, and spray coming off the waves

APPENDIX D: Number of sightings per individual per year in 1992, 1995 and from 1997 to 2005.

ID	1992	1995	1997	1998	1999	2000	2001	2002	2003	2004	2005	Total
I80	1									3	4	8
I124		1	1									2
I44		1	1				3	1	1	4	3	14
I114		1										1
I115		1										1
I116		1										1
I117		1										1
I118		1										1
I119		1										1
I120		1										1
I121		1										1
I122		1										1
I123		1										1
I125		1										1
I126		1										1
I127		1										1
I128		1										1
I175		1										1
I180		1										1
I130			1									1
I131			1									1
I132			1									1
I133			1									1
I134			1									1
I136			1									1
I137			1									1
I170			1									1
I173			1			1						2
I183			1									1
I188			1									1
I189			1									1
I190			1									1
I192			1									1
I33			1				2			2	1	6
I43			1				3			3	5	12
I95			1									1
I135				1								1
I193				1								1
I198				1								1
I52				1			3			2	3	9
I199					1							1
I10						1	4		1	2	3	11
I11						1	1	1		4	1	8
I141						1	1		1	3	4	10
I151						1						1

APPENDIX D: Cont.

ID	1992	1995	1997	1998	1999	2000	2001	2002	2003	2004	2005	Total
I152						1						1
I153						1						1
I154						1						1
I194						1						1
I196						1						1
I197						1						1
I49						1	3			3	4	11
I61						1	4					5
I76						1	2	1		4	5	13
I142						2	1	1		3	5	12
I163						2				4	4	10
I41						2	3					5
I83						2	2	1		3	4	12
I177						3		1				4
I21							1	1	1	3	3	9
I36							1	1	1	2	2	7
I56							1	1	1	4	5	12
I91							1	1	3	2	4	11
I14							1	1				2
I168							1	1				2
I176							1	1				2
I181							1	1				2
I65							1	1				2
I78							1	1				2
I97							1	1		3	3	8
I107							1		1			2
I12							1		1			2
I145							1		1	4	4	10
I158							1		1	2	1	5
I75							1		1	3	3	8
I89							1		1	3	4	9
I104							1		2	2	3	8
I164							1		2	2	2	7
I1							1			4	5	10
I108							1					1
I111							1			2	3	6
I112							1					1
I113							1					1
I13							1					1
I144							1					1
I146							1					1
I147							1					1
I148							1			1		2
I149							1					1
I150							1					1
I155							1					1
I156							1					1

APPENDIX D: Cont.

ID	1992	1995	1997	1998	1999	2000	2001	2002	2003	2004	2005	Total
I16							1					1
I161							1					1
I165							1					1
I166							1					1
I178							1					1
I182							1					1
I185							1					1
I186							1					1
I19							1				3	4
I20							1					1
I25							1			5	2	8
I31							1					1
I32							1			4	3	8
I35							1					1
I40							1				4	5
I50							1					1
I53							1					1
I58							1					1
I6							1					1
I62							1					1
I68							1					1
I69							1					1
I70							1					1
I72							1					1
I74							1					1
I81							1				1	2
I84							1			1		2
I85							1					1
I86							1			3	4	8
I88							1					1
I93							1			1	2	4
I94							1					1
I2							2	1	1	3	3	10
I42							2	1	1	2	6	12
I59							2	1	1	3	4	11
I87							2	1	1	3	3	10
I28							2	1	2			5
I92							2	1	2	3	6	14
I3							2	1				3
I46							2	1		4	2	9
I143							2		1	1	4	8
I15							2		1	5	5	13
I4							2		1	2	6	11
I60							2		1	7	4	14
I105							2					2
I106							2			4	2	8
I109							2			9	2	13

APPENDIX D: Cont.

ID	1992	1995	1997	1998	1999	2000	2001	2002	2003	2004	2005	Total
I110							2			1	1	4
I118							2			3	5	10
I122							2					2
I124							2					2
I126							2					2
I127							2			2	6	10
I134							2			3	6	11
I151							2			2	3	7
I154							2			1	3	6
I157							2			11	2	15
I163							2			3		5
I167							2					2
I17							2			3	2	7
I173							2			3		5
I177							2			1		3
I179							2			2	1	5
I18							2					2
I19							2			2	4	8
I117							3	1	1	3	4	12
I147							3	1	2	3	4	13
I123							3	1		1		5
I190							3	1		3	6	13
I129							3		1	3	4	11
I155							3		1	10		14
I137							3			3	3	9
I15							3					3
I171							3			3	3	9
I148							4		1	6	5	16
I166							4		1	4		9
I1174							4					4
I164							4					4
I1103								1	1	3	3	8
I160								1	1			2
I130								1	1			2
I196								1	1	4		6
I138								1	2		3	6
I1100								1		3	3	7
I1101								1		2	7	10
I1102								1		4	3	8
I1159								1				1
I1162								1				1
I139								1		3	5	9
I145								1		3	5	9
I182								1		3	3	7
I198								1				1
I199								1				1
FP002									1			1

APPENDIX D: Cont.

ID	1992	1995	1997	1998	1999	2000	2001	2002	2003	2004	2005	Total
FP003									1		1	2
FP004									1			1
Q003									1	4	5	10
Q020									1	3	3	7
Q023									1	6		7
Q070									1	3	4	8
Q084									1	3	3	7
Q102									1	3	5	9
Q107									1	4	3	8
Q109									1	3	2	6
Q112									1	5	4	10
Q152									1	3	4	8
Q200									1	2	1	4
Q270									1	3	6	10
Q300									1	2	3	6
Q328									1	2	4	7
QC003									1			1
QC005									1			1
PS001									2	2	2	6
PS005									2	1	4	7
Q002									2	6		8
Q061									2	4	7	13
Q083									2	3	2	7
QC004									2			2
Q001									4	6	4	14
Q176									4	3	4	11
Q004										1	1	2
Q269										1	2	3
Q412										1	2	3
Q460										1	3	4
Q505										1	3	4
Q202										1	4	5
Q411										1	4	5
Q465										1	4	5
Q495										1	4	5
Q218										1	5	6
Q415										1	6	7
Q450										1	6	7
F001										1		1
F004										1		1
F008										1		1
F021										1		1
F032										1		1
F051										1		1
F060										1		1
Q006										1		1
Q048										1		1

APPENDIX D: Cont.

ID	1992	1995	1997	1998	1999	2000	2001	2002	2003	2004	2005	Total
Q056										1		1
Q075										1		1
Q115										1		1
Q160										1		1
Q183										1		1
Q286										1		1
Q376										1		1
Q451										1		1
Q463										1		1
Q484										1		1
Q211										2	3	5
Q261										2	4	6
Q280										2	4	6
Q054										2	5	7
Q217										2	7	9
Q041										2		2
Q043										2		2
Q343										2		2
Q045										3	1	4
Q317										3	1	4
Q138										3	2	5
Q255										3	3	6
Q125										3	4	7
Q241										3	4	7
Q326										3	4	7
Q064										3	5	8
Q110										3	5	8
Q040										3	6	9
Q124										3	7	10
Q111										3		3
Q293										3		3
F062										4	1	5
Q028										4	2	6
Q095										4	2	6
Q155										4	2	6
Q039										4	4	8
Q065										4	5	9
Q175										4	7	11
F065										4		4
Q030										4		4
Q163										4		4
Q035										5	2	7
Q147										5	2	7
Q340										5	2	7
F045										5	5	10
Q068										5	7	12
Q161										5		5

APPENDIX D: Cont.

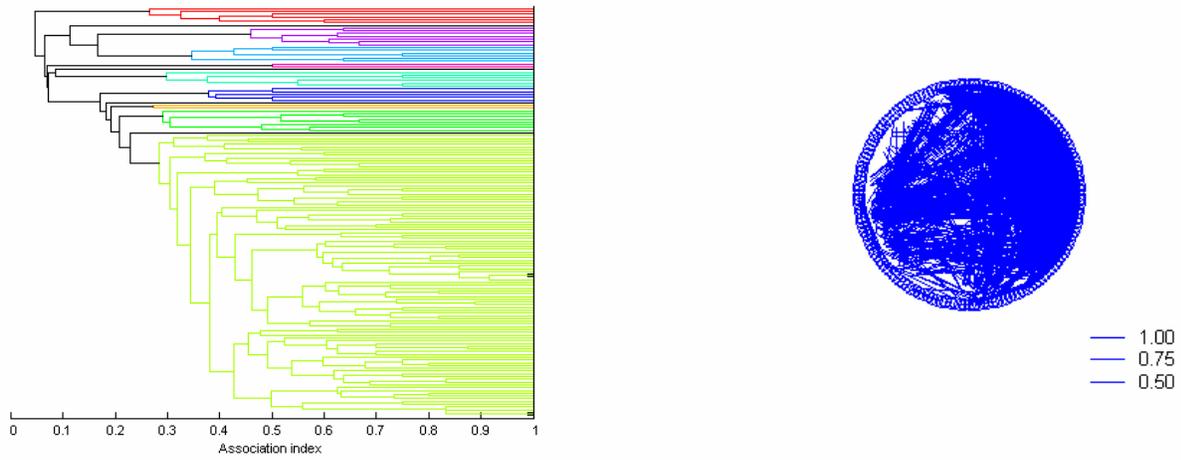
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Q140										7	4	11
FPA013											1	1
FPA014											1	1
FPA023											1	1
FPA032											1	1
PES029											1	1
PES044											1	1
PES058											1	1
PES078											1	1
PES079											1	1
PES080											1	1
PES093											1	1
PES190											1	1
POU309											1	1
POU364											1	1
QCS006											1	1
QCS045											1	1
QCS058											1	1
QCS071											1	1
QCS097											1	1
QCS098											1	1
QCS111											1	1
QCS123											1	1
QCS163											1	1
QCS170											1	1
QCS182											1	1
QCS186											1	1
QCS205											1	1
QCS283											1	1
QCS293											1	1
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FPA018											2	2
FPA020											2	2
FPA022											2	2
PES004											2	2
PES201											2	2
QCS094											2	2
QCS104											2	2
QCS168											2	2
QCS176											2	2
PES007											3	3
PES011											3	3
PES022											3	3
PES136											3	3
QCS025											3	3
QCS106											3	3

APPENDIX D: Cont.

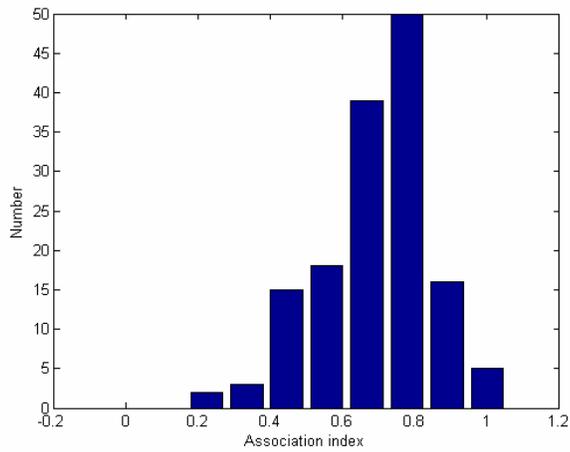
ID	1992	1995	1997	1998	1999	2000	2001	2002	2003	2004	2005	Total
QCS141											3	3
QCS196											3	3
QCS289											3	3
QCS292											3	3
QCS294											3	3
QCS044											4	4
QCS193											4	4
QCS077											6	6

APPENDIX E: SOCPROG 2.3 Results for Simple Ratio Index

All



a.)



b.)

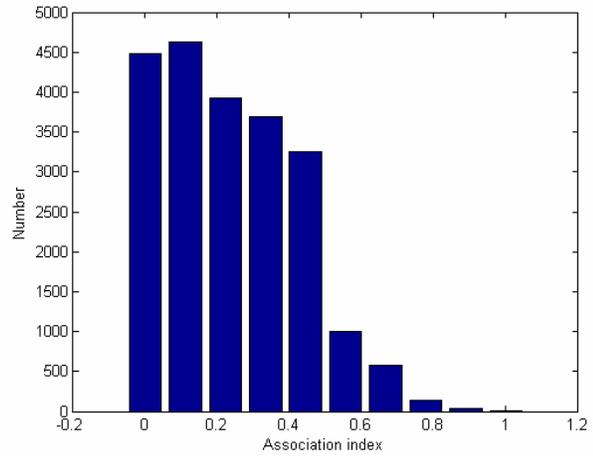
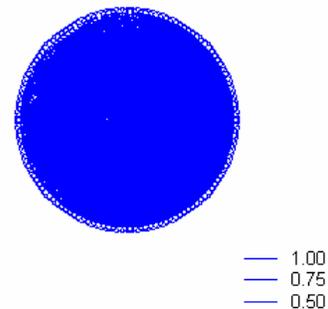
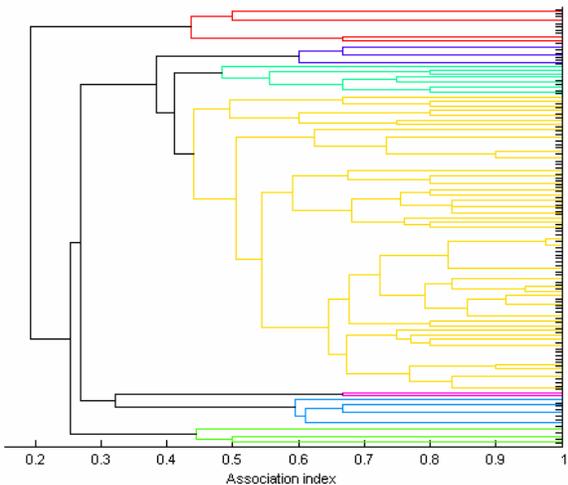
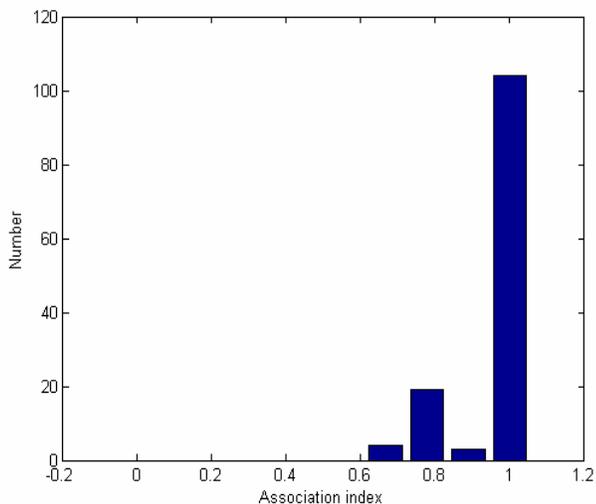


Figure a.) Maximum coefficient of association plot, b.) Non-diagonal association plot, both based on a weekly sampling period, (simple ratio index) for all individuals photographed four or more times in the Marlborough Sounds from 1997-2005. Number = the number of coefficients of association.

LARGE



a.)



b.)

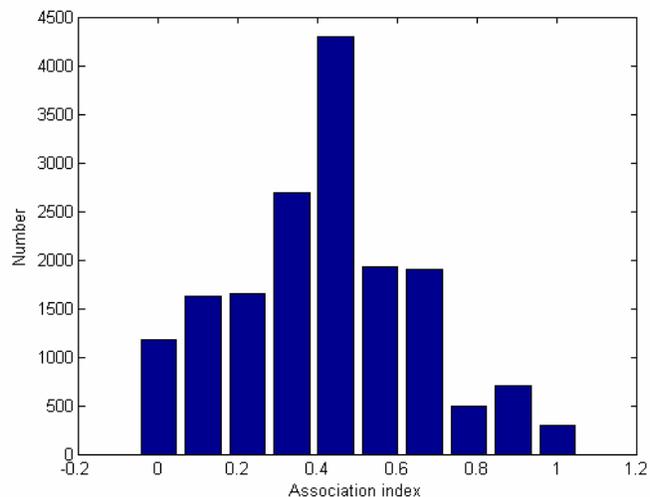
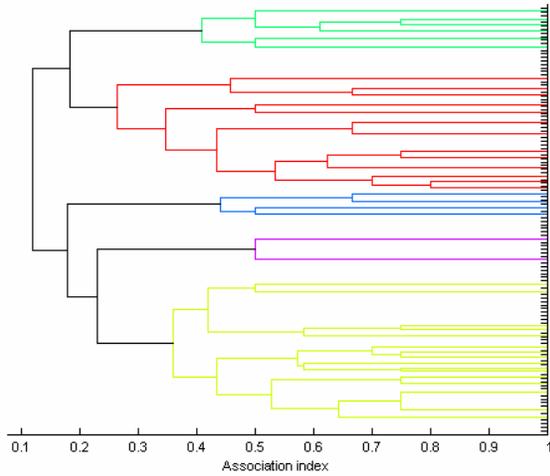


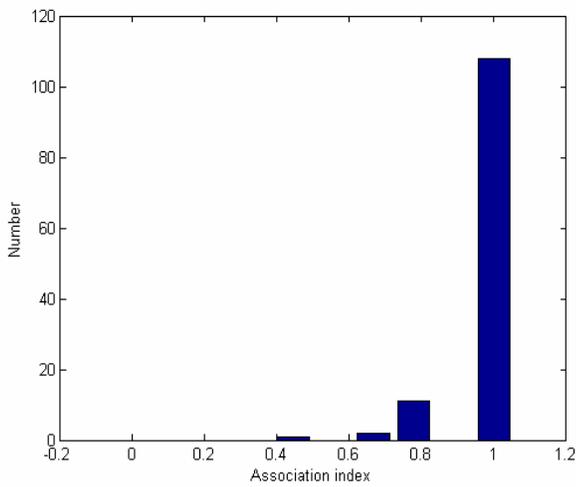
Figure a.) Maximum coefficient of association plot, b.) Non-diagonal association plot, both based on a weekly sampling period, (simple ratio index) for all individuals photographed four or more times occurring in large groups (greater than 61) in the Marlborough Sounds from 1997-2005. Number = the number of coefficients of association.

MEDIUM



— 1.00
— 0.75
— 0.50

a.)



b.)

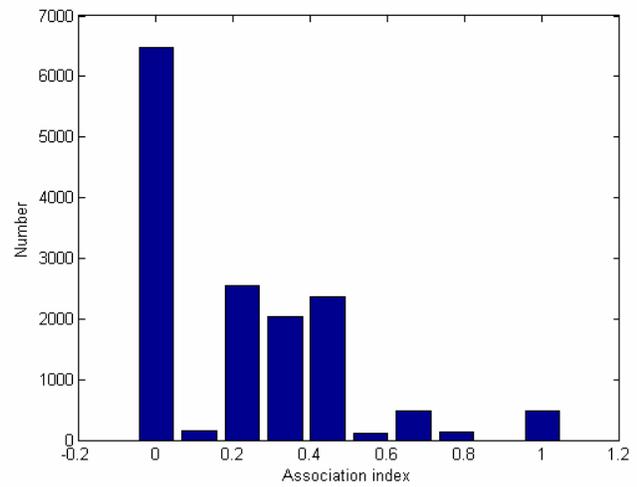
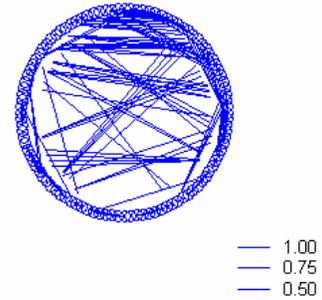
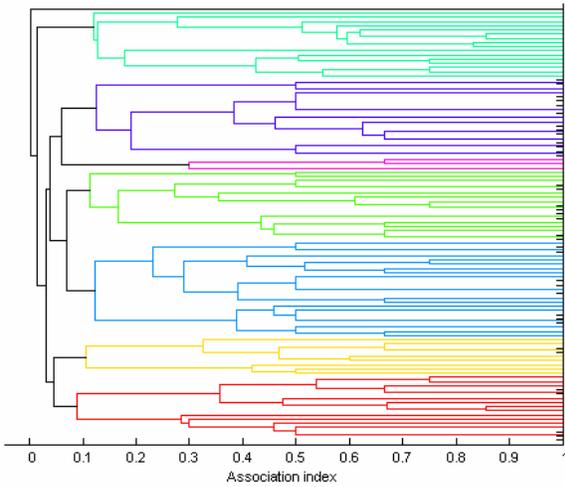
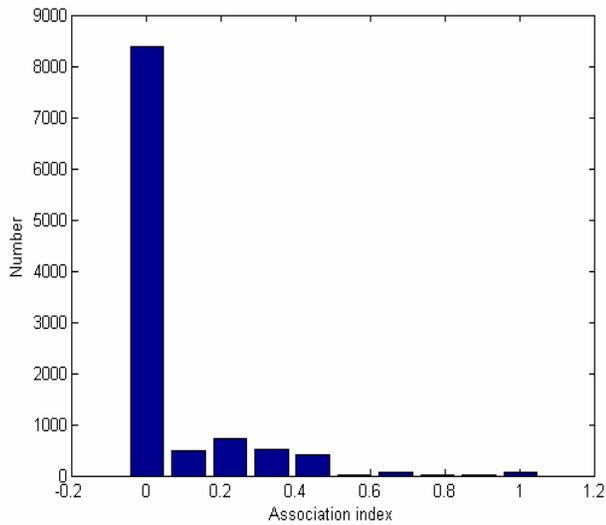


Figure a.) Maximum coefficient of association plot, b.) Non-diagonal association plot, both based on a weekly sampling period, (simple ratio index) for all individuals photographed four or more times occurring in medium groups (26-60) in the Marlborough Sounds from 1997-2005. Number = the number of coefficients of association.

SMALL



a.)



b.)

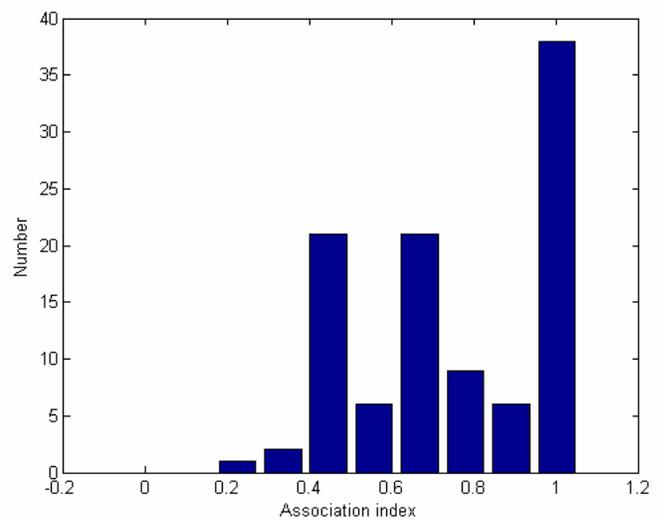


Figure a.) Maximum coefficient of association plot, b.) Non-diagonal association plot, both based on a weekly sampling period, (simple ratio index) for all individuals photographed four or more times occurring in small groups (less than 25) in the Marlborough Sounds from 1997-2005. Number = the number of coefficients of association.

APPENDIX F: Original results from SOCPROG for comparisons.

Population (individuals observed 4 or more times)

Simple Ratio Index

1. Sampling period: Day

Restrictions: No restrictions

Association: Group association; Day; grouped in sampling period

Association index = Simple ratio

Permute groups within samples

Number of individuals = 148

Number of random permutations = 1000; number of flips per permutation = 100

Real association indices:

all: mean = 0.21264; s.d. = 0.17245; CV = 0.81099

non-zero elements: proportion = 0.79776; mean = 0.26655; s.d. = 0.15136; CV = 0.56784

SD(typical group size) = 18.71433

Degenerate matrix: cannot be permuted

Random association indices (mean over permutations):

all: mean = 0.00021; s.d. = 0.00017; CV = 0.00081

non-zero elements: proportion = 0.00080; mean = 0.00027; s.d. = 0.00015; CV = 0.00057

SD(typical group size) = 0.01871

p-values (large p indicates large real value compared to random values):

all: mean = 0.00100; s.d. = 0.00000; CV = 0.00000

non-zero elements: proportion = 0.00100; mean = 0.00100; s.d. = 0.00000; CV = 0.00000

SD(typical group size) = 0.00100

2. Sampling period: Day/7 (Weekly)

Restrictions: No restrictions

Association: Group association; Day; grouped in sampling period

Association index = Simple ratio

Permute groups within samples

Number of individuals = 148

Number of random permutations = 1000; number of flips per permutation = 100

Real association indices:

all: mean = 0.23982; s.d. = 0.19121; CV = 0.79728

non-zero elements: proportion = 0.79776; mean = 0.30062; s.d. = 0.16598; CV = 0.55213

SD(typical group size) = 18.71433

Random association indices (mean over permutations):

all: mean = 0.23950; s.d. = 0.18538; CV = 0.77404

non-zero elements: proportion = 0.82394; mean = 0.29069; s.d. = 0.16381; CV = 0.56353

SD(typical group size) = 17.82847

p-values (large p indicates large real value compared to random values):

all: mean = 0.80800; s.d. = 1.00000; CV = 1.00000

non-zero elements: proportion = 0.00100; mean = 1.00000; s.d. = 0.98700; CV = 0.00100

SD(typical group size) = 1.00000

APPENDIX F: Continued

3. Sampling period: Month

Restrictions: No restrictions

Association: Group association; Day; grouped in sampling period

Association index = Simple ratio

Permute groups within samples

Number of individuals = 148

Number of random permutations = 1000; number of flips per permutation = 100

Real association indices:

all: mean = 0.34933; s.d. = 0.25951; CV = 0.74288

non-zero elements: proportion = 0.79776; mean = 0.43789; s.d. = 0.21363; CV = 0.48786

SD(typical group size) = 18.71433

Random association indices (mean over permutations):

all: mean = 0.36551; s.d. = 0.21771; CV = 0.59566

non-zero elements: proportion = 0.90422; mean = 0.40425; s.d. = 0.19177; CV = 0.47437

SD(typical group size) = 12.75666

p-values(large p indicates large real value compared to random values):

all: mean = 0.00000; s.d. = 0.99900; CV = 0.99900

non-zero elements: proportion = 0.00000; mean = 1.00000; s.d. = 1.00000; CV = 0.97800

SD(typical group size) = 1.00000

4. Sampling period: Year

Restrictions: No restrictions

Association: Group association; Day; grouped in sampling period

Association index = Simple ratio

Permute groups within samples

Number of individuals = 148

Number of random permutations = 1000; number of flips per permutation = 100

Real association indices:

all: mean = 0.40644; s.d. = 0.28543; CV = 0.70226

non-zero elements: proportion = 0.79776; mean = 0.50948; s.d. = 0.22276; CV = 0.43724

SD(typical group size) = 18.71433

Random association indices (mean over permutations):

all: mean = 0.43835; s.d. = 0.24629; CV = 0.56190

non-zero elements: proportion = 0.90864; mean = 0.48243; s.d. = 0.21332; CV = 0.44218

SD(typical group size) = 11.74303

p-values(large p indicates large real value compared to random values):

all: mean = 0.00000; s.d. = 1.00000; CV = 1.00000

non-zero elements: proportion = 0.00100; mean = 1.00000; s.d. = 0.99900; CV = 0.11000

SD(typical group size) = 1.00000

APPENDIX F: Continued

Small Groups

5. Sampling period: Day/7

Restrictions: No restrictions

Association: Group association; Date; grouped in sampling period

Association index = Simple ratio

Permute groups within samples

Number of individuals = 104

Number of random permutations = 1000; number of flips per permutation = 100

Real association indices:

all: mean = 0.07003; s.d. = 0.15908; CV = 2.27152

non-zero elements: proportion = 0.21733; mean = 0.32225; s.d. = 0.18755; CV = 0.58201

SD(typical group size) = 5.00070

Random association indices (mean over permutations):

all: mean = 0.07102; s.d. = 0.16103; CV = 2.26748

non-zero elements: proportion = 0.21815; mean = 0.32556; s.d. = 0.18977; CV = 0.58288

SD(typical group size) = 5.08220

p-values (large p indicates large real value compared to random values):

all: mean = 0.05100; s.d. = 0.06800; CV = 0.75800

non-zero elements: proportion = 0.17700; mean = 0.06200; s.d. = 0.21900; CV = 0.47900

SD(typical group size) = 0.09400

Medium Groups

degenerate matrix will not permute

Large Groups

6. Sampling period: Day/7

Restrictions: No restrictions

Association: Group association; Date; grouped in sampling period

Association index = Simple ratio

Permute groups within samples

Number of individuals = 130

Number of random permutations = 1000; number of flips per permutation = 100

Real association indices:

all: mean = 0.42499; s.d. = 0.23231; CV = 0.54661

non-zero elements: proportion = 0.92952; mean = 0.45722; s.d. = 0.20814; CV = 0.45523

SD(typical group size) = 5.61980

Random association indices (mean over permutations):

all: mean = 0.42501; s.d. = 0.23186; CV = 0.54555

non-zero elements: proportion = 0.93065; mean = 0.45668; s.d. = 0.20809; CV = 0.45566

SD(typical group size) = 5.54712

p-values (large p indicates large real value compared to random values):

all: mean = 0.58300; s.d. = 0.86700; CV = 0.85800

non-zero elements: proportion = 0.10600; mean = 0.90600; s.d. = 0.62100; CV = 0.31400

SD(typical group size) = 0.85700

APPENDIX F: Continued

Population (individuals observed 4 or more times)

Half Weight Index

1. Sampling period: Day

Restrictions: No restrictions

Association: Group association; Day; grouped in sampling period

Association index = Half weight

Permute groups within samples

Number of individuals = 148

Number of random permutations = 1000; number of flips per permutation = 100

Real association indices:

all: mean = 0.31847; s.d. = 0.22907; CV = 0.71929

non-zero elements: proportion = 0.79776; mean = 0.39921; s.d. = 0.18315; CV = 0.45879

SD(typical group size) = 18.71433

Degenerate matrix: cannot be permuted

Random association indices (mean over permutations):

all: mean = 0.00032; s.d. = 0.00023; CV = 0.00072

non-zero elements: proportion = 0.00080; mean = 0.00040; s.d. = 0.00018; CV = 0.00046

SD(typical group size) = 0.01871

p-values (large p indicates large real value compared to random values):

all: mean = 0.00000; s.d. = 0.00000; CV = 0.00100

non-zero elements: proportion = 0.00000; mean = 0.00100; s.d. = 0.00000; CV = 0.00000

SD(typical group size) = 0.00000

2. Sampling period: Month

Restrictions: No restrictions

Association: Group association; Day; grouped in sampling period

Association index = Half weight

Permute groups within samples

Number of individuals = 148

Number of random permutations = 1000; number of flips per permutation = 100

Real association indices:

all: mean = 0.42610; s.d. = 0.28933; CV = 0.67902

non-zero elements: proportion = 0.79776; mean = 0.53412; s.d. = 0.21733; CV = 0.40690

SD(typical group size) = 18.71433

Random association indices (mean over permutations):

all: mean = 0.45282; s.d. = 0.23737; CV = 0.52425

non-zero elements: proportion = 0.90277; mean = 0.50161; s.d. = 0.19485; CV = 0.38845

SD(typical group size) = 12.85618

p-values (large p indicates large real value compared to random values):

all: mean = 0.00000; s.d. = 0.99900; CV = 1.00000

non-zero elements: proportion = 0.00100; mean = 1.00000; s.d. = 1.00000; CV = 0.99400

SD(typical group size) = 1.00000

APPENDIX F: Continued

3. Sampling period: Year

Restrictions: No restrictions

Association: Group association; Day; grouped in sampling period

Association index = Half weight

Permute groups within samples

Number of individuals = 148

Number of random permutations = 1000; number of flips per permutation = 100

Real association indices:

all: mean = 0.49448; s.d. = 0.31079; CV = 0.62851

non-zero elements: proportion = 0.79776; mean = 0.61984; s.d. = 0.20825; CV = 0.33598

SD(typical group size) = 18.71433

Random association indices (mean over permutations):

all: mean = 0.53977; s.d. = 0.25811; CV = 0.47827

non-zero elements: proportion = 0.90800; mean = 0.59447; s.d. = 0.20220; CV = 0.34015

SD(typical group size) = 11.68716

p-values (large p indicates large real value compared to random values):

all: mean = 0.00100; s.d. = 1.00000; CV = 1.00000

non-zero elements: proportion = 0.00100; mean = 0.99900; s.d. = 0.99800; CV = 0.10800

SD(typical group size) = 1.00000

Small Groups

4. Sampling period: Day/7

Restrictions: No restrictions

Association: Group association; Date; grouped in sampling period

Association index = Half weight

Permute groups within samples

Number of individuals = 104

Number of random permutations = 1000; number of flips per permutation = 100

Real association indices:

all: mean = 0.10007; s.d. = 0.20905; CV = 2.08904

non-zero elements: proportion = 0.21733; mean = 0.46047; s.d. = 0.18746; CV = 0.40711

SD(typical group size) = 5.00070

Random association indices (mean over permutations):

all: mean = 0.10116; s.d. = 0.21081; CV = 2.08381

non-zero elements: proportion = 0.21821; mean = 0.46361; s.d. = 0.18872; CV = 0.40707

SD(typical group size) = 5.08015

p-values (large p indicates large real value compared to random values):

all: mean = 0.03800; s.d. = 0.04900; CV = 0.85800

non-zero elements: proportion = 0.15700; mean = 0.06400; s.d. = 0.24900; CV = 0.49300

SD(typical group size) = 0.07400

APPENDIX F: Continued

Medium Groups

degenerate matrix will not permute

Large Groups

5. Sampling period: Day/7

Restrictions: No restrictions

Association: Group association; Date; grouped in sampling period

Association index = Half weight

Permute groups within samples

Number of individuals = 130

Number of random permutations = 1000; number of flips per permutation = 100

Real association indices:

all: mean = 0.55394; s.d. = 0.24343; CV = 0.43946

non-zero elements: proportion = 0.92952; mean = 0.59594; s.d. = 0.19678; CV = 0.33020

SD(typical group size) = 5.61980

Random association indices (mean over permutations):

all: mean = 0.55405; s.d. = 0.24277; CV = 0.43817

non-zero elements: proportion = 0.93061; mean = 0.59536; s.d. = 0.19681; CV = 0.33057

SD(typical group size) = 5.54891

p-values (large p indicates large real value compared to random values):

all: mean = 0.34500; s.d. = 0.87600; CV = 0.86900

non-zero elements: proportion = 0.11200; mean = 0.90200; s.d. = 0.55000; CV = 0.35700

SD(typical group size) = 0.84200

APPENDIX G: SOCPROG model results for standardised lagged association rates.

Models fitted to lagged association rates. For individuals resighted 4 or more times from 1997 to 2005 in the Marlborough Sounds. * marks the best-fit model based on the half weight index.

Model	Equation	QAIC value	Summed log likelihood
Constant companions	a_1	70447.6144	-566658.3089
Casual acquaintances	$a_2 \cdot \exp(-a_1 \cdot t_d)$	70405.3134	-566301.9656
Constant companions + casual acquaintances	$a_2 + a_3 \cdot \exp(-a_1 \cdot t_d)$	* 70403.1606	-566268.5618
Two levels of casual acquaintances	$a_3 \cdot \exp(-a_1 \cdot t_d) + a_4 \cdot \exp(-a_2 \cdot t_d)$	70409.3134	-566301.9656