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Context-specific signal plasticity of two common bottlenose dolphin ecotypes (*Tursiops truncatus*) in Far North waters, New Zealand

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Abstract

Common bottlenose dolphin (*Tursiops truncatus*, referred to hereafter as bottlenose dolphin) fission-fusion groupings are temporary in nature, lasting from minutes to hours, necessitating efficient signal exchange. The selective pressures and contexts acting on signal exchange, such as ecotype variation, are not well understood. The objectives of the current study are three-fold to: 1) quantify the density, distribution and abundance of bottlenose dolphin ecotypes and identify the nature and areas of spatial overlap between the two in Far North waters; 2) examine aspects of mechanical signal exchange based on biotic and abiotic factors; and 3) estimate the effect of key ecotype specific contexts on group multimodal signal exchange. This thesis applies a holistic approach to the assessment of signal exchange in ecotypes using the highly social bottlenose dolphin as a model genus. Additionally, this body of work provides the first comprehensive assessment of oceanic bottlenose dolphin distribution, abundance, and behaviour ecology and the first ecotype spatial and behavioural overlap within New Zealand waters.

Knowledge of population size, social behaviour, threats, and ability to integrate new individuals is required to define management units. Although it has long been recognised that the *nationally endangered* coastal bottlenose dolphin is not resident in the Bay of Islands but genetically part of a North East coast population, no studies have quantified bottlenose dolphin distribution in Far North waters outside of the Bay of Islands. This study provides the first systematic analysis of detectability, distribution, and spatial overlap of both the coastal bottlenose dolphin and the previously unquantified oceanic bottlenose dolphin in Far North waters. Results suggest Far North waters are important for the coastal bottlenose dolphin, supported by a higher average density (0.620 individuals/kilometre) than that reported for the coastal bottlenose dolphin in other areas of the North East coast population. The importance of assessment outside areas of commercial interest is further reinforced in this study. The Bay of Islands local abundance is not reflective of the coastal bottlenose dolphin in the wider area, as indicated by the higher Far North waters estimates of 212.8% (Austral Summer) and 196.1% (Austral Winter). With no previous density or abundance estimates for oceanic bottlenose dolphin in New Zealand, no comparisons can be drawn with other studies or historic research. However, the distance sampling-based population estimate of 3,634 (SE = 152) indicates oceanic bottlenose dolphin abundance is much higher than the 389 (SE = 108) coastal bottlenose dolphin abundance estimate in Far North waters, even though their distribution is

seasonal with detection only in austral Summer and Autumn. Kernel density also indicates the representative ranges (95 % kernel range) of the coastal bottlenose dolphin are smaller than the oceanic bottlenose dolphin, extending over a total area of $\sim 794 \text{ km}^2$ and $\sim 1,003 \text{ km}^2$, respectively. This study further suggests these ecotypes should be described as largely parapatric and non-resident in nature, with a minimal spatial overlap of only 7.4 % of Far North waters surveyed ($\sim 196 \text{ km}^2$). This is further supported by no sightings of the two ecotypes within the same survey zone on the same day ($n = 372$ bottlenose dolphin sightings) during the present study.

Behaviour can further add insight into the partitioning and variation of parapatric units within a species. In Far North waters, whilst research on surface behaviour has been previously conducted in the Bay of Islands, behavioural assessment in wider areas and based on a holistic assessment of multiple signal forms is lacking in the literature. This study, however, applies a systematic sampling technique and integrated analysis to identify trends in signal exchange use. This is done by examining multiple behavioural modes (states and events, surface and subsurface) concurrently. This ultimately provides an additional method for quantifying group behavioural plasticity as a result of covariates acting on parapatrically occurring bottlenose dolphin groups. In one assessment, cues were taken from avian acoustic research to accurately quantify and analyse ecotype variation in call repertoire. In support of the parapatric definition, call repertoire was correctly assigned to ecotype, with an 89.4% success rate ($n = 31,432$ calls). Of all parameters examined, 71.4% exhibited significant variation, with harmonics and contour inflections used significantly more in oceanic bottlenose dolphin. Both Dynamic Time Warping in Luscinia and Hidden Markov Models add reliable insight into the categorisation of key signal parameters and important tools for the primary assessment of differences in bottlenose dolphin behaviour within Far North waters. Including the full behavioural repertoire of oceanic bottlenose dolphin and coastal bottlenose dolphin through Hidden Markov Models adds additional insight to the possible drivers behind the divergence in the call parameters noted. It is notable that signal parameters are not influenced by the same key drivers for both ecotypes. This is an important finding in a species in which most communication exchanges involve acoustic signals in some form.

The formation of interspecific groupings has the largest effect on social signal exchange in oceanic bottlenose dolphin of all covariates considered. The response magnitude is associated with group parameters, for example, the ratio of individuals (e.g. pilot whales (*Globicephala*

sp.) to oceanic bottlenose dolphins) and the behaviour and/or overall size of the focal group. These aspects in turn determine the effect of participation in interspecific groups on oceanic bottlenose dolphin behaviour. Oceanic bottlenose dolphins in interspecific groups with pilot whales display higher call plasticity, both in the time and frequency domain, utilising significantly higher measures for 66.7% of parameters, including longer and more complex calls (increased number of harmonics and inflects), than in intraspecific oceanic bottlenose dolphin groups. Signal adaptation is more evident when oceanic bottlenose dolphins and pilot whales are directly interacting with each other during social events. During socialising states, the predominant subsurface event type observed is aggression (59.4%, $n = 233$). As the ratio of pilot whales to oceanic bottlenose dolphins increases, the use of long-distance signal exchange decreases. This suggests that the observed decreases in interspecific similarity of whistle parameters during social interactions may act to increase the ability to differentiate species-specific rather than whole group signal exchange cues. Although species-specific call differentiation is likely heightened by variation in gross morphology, phylogeny and geographical constraints, frequency domain characteristic overlap between oceanic bottlenose dolphins and pilot whales. The detected adjustments in signal structure away from intermediate values may suggest a decrease in the increment in this overlap. Support is given to the theory that signal exchange might be modified not only as a result of group behaviour state but also due to the signaller's motivational state (i.e. stress). While the full biological effects of changes in whistle rates and parameters remain uncertain, these changes add initial insights to the dynamics of interspecific groupings.

Number of vessels had largest effects on coastal bottlenose dolphin social signal exchange, with response magnitude significantly related to group composition (ex. with or without calves) and use of other signal exchange behaviours (ex. tactile type and rate). The response is also influenced by acoustic parameters considered (frequency or call rate). The highest coastal bottlenose dolphin density area, the Bay of Islands, contains the highest proportion of groups with calves and the highest level of vessel traffic in Far North waters. Groups with calves favour sounds typically used for short-distance signal exchange, appearing to increase the use of mechano-reception in the presence of vessels. Overall, coastal bottlenose dolphins are more likely to: (1) leave the low-call-rate state in the presence of one to two vessels (within 300m); (2) leave the high-call-rate state when three or more vessels (adults only), or two or more vessels in the case of groups with calves, are within 300m; and (3) stay in a relatively silent state when more than three vessels are present. Furthermore, coastal bottlenose dolphins are

more likely to (1) leave the low-call-rate state when contact rate is low; (2) leave the high-call-rate state when contact rate is high; and (3) stay in a relatively silent state when contact rate is high. This suggests an inverse relationship exists between call rate and contact rate, i.e. as possible vessel effect increases, vocalisation-mediated coordination decreases, and mechano-mediated coordination increases with a lower threshold for groups with calves than groups without. Several drivers of elevated signal exchange rates have been suggested in the presence of vessels. These include an increased motivation for individuals to stay close together, a changed group cohesion and amplified arousal. However, this study adds new insights with the quantification of multi-modal signal exchange in the presence of vessel. This has not been the focus of previous research in any of the bottlenose dolphin populations in New Zealand.

Distribution, density, and abundance is now available for both bottlenose dolphin ecotypes, with multimodal group behaviour in ecotype specific contexts additionally quantified. As such, supplementary monitoring and reviews of the coastal bottlenose dolphin and oceanic bottlenose dolphin parapatric populations in New Zealand are essential. Pre-emptive rather than reactive conservation is recommended to effectively manage both bottlenose dolphin ecotypes separately and efficiently in New Zealand waters.

Dedication

This thesis is dedicated to my role-models and parents, Sue and Chris Peters, who taught me that almost any task, no matter how overwhelming it may appear, can be accomplished with passion, determination, and discipline to see a project through to its completion.

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Abbreviations

AIC	Akaike's Information Criterion
AIC _c	Akaike's Information Criterion with correction for small samples
ANOVA	Analysis of variance
BSS	Beaufort Sea state
Non-Bay of Islands	Cavalli Islands, Doubtless Bay, Whangaroa Harbour, Wider Survey
CV	Co-efficient of variation
CI	Confidence interval
CSV	Comma-separated values
CV	Mean cross-validated (log) likelihood
dB	Decibels
°C	Degrees Celsius
DOC	Department of Conservation
DNA	Deoxyribonucleic acid
EAC	East Auckland current
k	Fleiss' Kappa statistic
GIS	Geographic information system
GPS	Global Positioning System
GSI	Global silhouette index
ID	Identification
IUCN	The International Union for Conservation of Nature and Natural Resources
kHz	Kilohertz
km	Kilometres
knts	Knots
MMPA	Marine Mammal Protected Area
MMPR	Marine Mammal Protection Regulations
llk	Maximum log likelihood
m	Metres
ms	Millisecond
min	Minute
MCDS	Multi-covariate distance sampling
spp.	Multiple species
NZ	New Zealand
RV	Research vessel
SST	Sea surface temperature
sp.	Species unknown
SD	Standard deviation
SE	Standard error
NIWA	The National Institute of Water and Atmospheric Research
TTCh	Time to change
wgt	Akaike's Information Criterion weight

Chapter 1

General Introduction



Researchers conducting a focal follow on common bottlenose dolphin (*Tursiops truncatus*) in the Bay of Islands, New Zealand. Photo credit: L. Smith.

1.1 Introduction

Understanding how populations behave and interact within specific areas and contexts is crucial for applied conservation. This thesis is focused on these themes, with the all-encompassing objective of advising adaptive management. The density, abundance, distribution and spatial overlap of two focal common bottlenose dolphin ecotypes (coastal and oceanic, *Tursiops truncatus*) in Far North waters, New Zealand (NZ), are initially investigated to provide context for subsequent questions posed. The signal exchange of bottlenose dolphins within this region is the primary focus of this thesis. The overall goal is to add insight to the possible interactions of the two ecotypes and the common and unique contexts that may affect the group behaviour of each ecotype (e.g. interspecific groupings for oceanic bottlenose dolphins and coastal vessel traffic for coastal bottlenose dolphins).

In this introductory chapter, the history of signal research, behavioural correlates and current definitions are described as per contemporary literature. Further to this, the bottlenose dolphin, more specifically the two ecotypes found in Far North waters, NZ, is described as a model genus for signal exchange research. Finally, the motivation and configuration of this thesis are outlined at the end of the chapter.

1.2 Current and historical signal research

Knowledge of how species exchange signals with both their own species and others has come from a variety of data collection techniques (see Brumm, 2013 for review). Data have been collected from captive (e.g., Caldwell & Caldwell, 1968; Esch et al., 2009b; Reiss & McCowan, 1993) and wild populations (e.g., Aubin et al., 2000; Krützen et al., 2005; Mann et al., 2008; Morisaka et al., 2005a; Marino & Frohoff, 2011).

1.2.1 Signals in space - distribution, density and abundance

Many studies reveal that animal signals, most notably the frequency and temporal patterns of acoustic signals, vary depending on the context in which the signal is produced. This is to ensure signals are unfailingly transmitted (Morton, 1975; Wiley & Richards, 1978). In terrestrial scenarios, environments such as forest, edge and grassland habitats can act as selection pressures on signals used (Morton, 1975). Another example is buildings and ambient noise affecting bird song in urban environments, resulting in geographic distinction (Ryan & Brenowitz, 1985). The use of environmentally plastic vocalisations also occurs in mammals.

Pygmy marmosets (*Cebuella pygmaea*) adapt their calls (usually in an inverse relationship) depending on characteristics of their acoustic environment to reduce transmission loss, masking and distortion of the signal (De La Torre & Snowdon, 2002). In comparison to the wealth of data surrounding terrestrial environmental call adaptation, little is known about the topic for aquatic animals.

Air and water vary considerably in their physical properties, which results in sound propagating faster and further in water than in air. Numerous marine species, including, but not limited to, crustaceans, fish and marine mammals, utilise long-range communication signals to overcome ambient noise levels (Tyack, 1998). Ambient noise includes wave, wind, surf, human activity, and biological noise from other animals (Au & Banks, 1998; Dahl et al., 2007). In “louder” habitats, species, including cetaceans, produce adapted signals to maximise transmission efficiency. For instance, a beluga whale (*Delphinapterus leucas*) uses higher frequency and intensity biosonar signals when placed in louder contexts (Au et al., 1985). The same behaviour has also been observed in other species, including bottlenose dolphins and false killer whales (*Pseudorca crassidens*) (Au, 1993; Au et al., 1974). As in terrestrial environments, if acoustic characteristics differ among habitats, this may cause geographical variation in signal modalities.

1.2.2 Behavioural context

When recording behaviour, methods include aerial (Friedman et al., 2013; Karnowski et al., 2016), surface (Connor et al., 2017; Christiansen et al., 2017; Noren & Hauser, 2016), and/or underwater observations (Bräger et al., 1999; Cusick & Herzing, 2014; Filatova, 2006; Guerra et al., 2014; Kuczaj et al., 2015; Miles & Herzing, 2003; Pearson et al., 2017; Simon et al., 2010; Vollmer et al., 2015).

Analysis of behavioural observations within a population’s home range provides a more thorough understanding of how a population is using an area. As is common in the study of cetacean area utilisation, this thesis explores the surface behaviour of bottlenose dolphins through predominant group activity. Marine mammal behaviours are grouped into categories by researchers. In the literature, the most often utilised by researchers are states, e.g., travelling, socialising, feeding, diving, and resting (Osterrieder et al., 2017; Shane, 1990b). Feeding (López & Shirai, 2006) and travelling (Shane, 1990b) are the most observed behaviours on average, or feasibly the most readily recognised (Lynn, 1995). Beyond surface behavioural

state observations, social behavioural repertoires of cetaceans have been a strong research focus in the literature (e.g., Clegg et al., 2017; Connor et al., 2017). For social species, the reliable exchange of information is a fundamental daily need (Altmann, 1967; Cullen, 1972; Smith, 1977), as social groupings would not be maintained if it was not present (Marler, 1977; Otte, 1974).

1.2.3 Signal exchange

Defining *signal exchange* has not been consistent in the study of behaviour, as it depends on the study context. However, these definitions have in common that a transfer of information occurs. The application in this thesis requires expansion of the definition of signal exchange. To illustrate, Kimura (1993) confines the signal receiver to the species of the signalling individual. This definition is not appropriate for use in marine mammals, as both intra- and interspecific signal exchange has been documented, e.g., Indo-Pacific bottlenose dolphin and Atlantic spotted dolphins (*Stenella frontalis*) (Dudzinski, 1996; Herzing, 1997; Herzing et al., 2003; Kaplan & Reiss, 2017).

A definition with an adaptive component which is more applicable for cetaceans is given by Vauclair (1996), where signal exchange is defined as “an information exchange amongst the sender and receiver utilising specific signal codes” and, in most cases, aiding in meeting the shared biological needs of individuals within a social group (e.g., reproduction, defence from predators, prey acquisition, and promotion of group cohesion). Further to this, the three vital components of signal exchange are: 1) a signaller; 2) a signal; and 3) a signal recipient. If any one of these three aspects does not occur, the signal exchange is not considered complete (Vauclair, 1996).

Once signal exchange has been defined, it is important to consider mitigating factors pertaining to the group composition of interacting individuals. Group coordination does not occur by chance: information exchanges that inform participants about each other and/or their environment aids coordination (e.g., Krebs et al., 1981; Miller et al., 2004). For social species, it is important to accurately anticipate and predict the behaviour of conspecifics, thus the act of one individual having an effect on another and vice versa is termed social interaction (Paulos, 2004). Signal exchange is a collective suite of tools for co-adaptation, which is ultimately responsible for preserving association and thus assisting in perpetuating existence (Paulos, 2004).

Ultimate and proximate benefits may be achieved through signal exchange. At the ultimate level, signals may function to increase the reproductive success of individuals as a result of the defence of key territories (e.g., Gosling & Roberts, 2001); young socialisation (e.g., Rendell & Whitehead, 2001); or non-antagonistic sexual interactions (e.g., Dulac & Torello, 2003). Ultimately, the exchange of signals works to improve survival and reproduction prospects. At the proximate level, day-to-day needs are satisfied through the use of signal exchange, such as prey location (e.g., Mougeot & Bretagnolle, 2000) or predator threats (reviewed in Laidre & Johnstone, 2013). Additionally, signal exchange may function as a mediation tool in social encounters within a group (e.g., Connor et al., 2006) and result in information beneficial to subsequent interactions.

1.2.3.1 Signal types

Signal types vary substantially. Signallers may exploit photic (visual), chemical (taste and olfaction), mechanical (tactile and acoustic), or electromagnetic channels, or a combination thereof, to transfer information (Herman & Tavalga, 1980; Paulos, 2004; Reynolds & Rommel, 1999; Yunker & Herman, 1974). The ability to employ a signal type is determined by the sender and receiver's ability and the propagation of the signal in the environment (e.g., in mechanical acoustic signals, Figure 1.1). For example, kangaroo rats (*Dipodomys heermanni*) use mechanical signals in the form of ground vibration through foot-drumming. The non-vocal acoustic signal indicates individual identity as female and willingness to interact (Shier & Yoerg, 1999). There are two forms of stimulus used here, the main type being acoustic, but additionally the receiving individual may also take cues from the photic channel once at the entrance to the burrow. The use of these signals from inside a burrow necessitates a signal that can be perceived when not in a direct line of sight and airborne signal propagation is restricted. The need of the signaller to stay safe within a burrow may drive the evolution of a signal that can be perceived with minimal danger.

Signals can be used as a single mode of transfer or concurrently with other signal types. In most species, photic signals are the primary mode of non-vocal information transfer. Photic signalling (as in the above example) is defined as a signal that can be visually perceived, including body posture, facial displays, gestures, and body movements (Andrew, 1963; Chevalier-Skolnikoff, 1982; DeCourcy & Jenssen, 1994; Goodall, 1986; Lovern & Jenssen, 2003; Van Hooff, 1967).

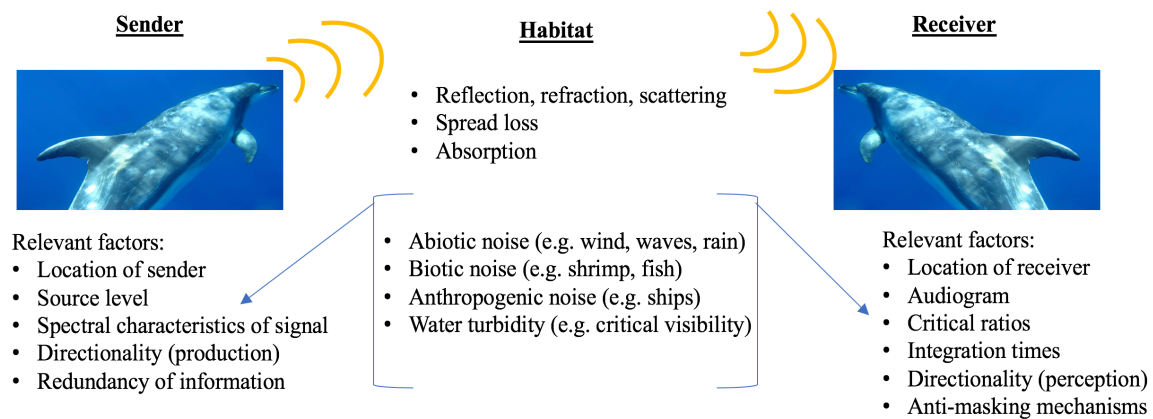


Figure 1.1: Relevant factors that affect signal exchange when using the primary mode of communication (auditory) in marine environments (adapted from Erbe et al., 2016).

1.2.4 Signal exchange in dolphins

Dolphin group social structure is complex and flexible (Dudzinski, 1998; Rossbach & Herzing, 1999; Paulos, 2004; Paulos et al., 2008a & b; Slooten, 1994; Smolker et al., 1992). Dolphins can utilise mechanical (tactile contact), photic (postures), and acoustic (vocal and non-vocal) signal types, or a multi-modal arrangement to propagate information (Dudzinski, 1998; Dudzinski et al., 2002; Herman & Tavorla, 1980; Pryor, 1990; Reynolds & Rommel, 1999). The classification of vocal and non-vocal signals across species is not above critique (refer to Hauser, 1996; Hinde, 1972; Scherer & Ekman, 1982; Siegman et al., 1987). However, in this thesis, a practical distinction in the essential meanings of these two terms is provided in relation to this body of work.

1.2.4.1 Vocal signal exchange

Mechanical vocal production is the best long-range oceanic signal exchange system (Colosi, 2016) and vocal behaviour is considered the predominant mode of signal exchange for cetaceans (for review see Herzing & Johnson, 2015). Vocal signal exchange is loosely described as “sounds produced by expelling air from the lungs, first past some sort of vibrating mechanism and then one or more resonating chambers or tubes” (Smith, 1977, p.31, as applied in Paulos, 2004), which includes a range of sounds utilised by different species (e.g., dolphin whistles).

Dolphins have an extensive repertoire of vocal signals ranging from 0.2 – 150 kHz with most energy <96 kHz (Tyack & Clark, 2000) in three groupings: tonal whistles, pulsed sounds, and burst-pulse sounds (Figure 1.2; Richardson et al., 1995).

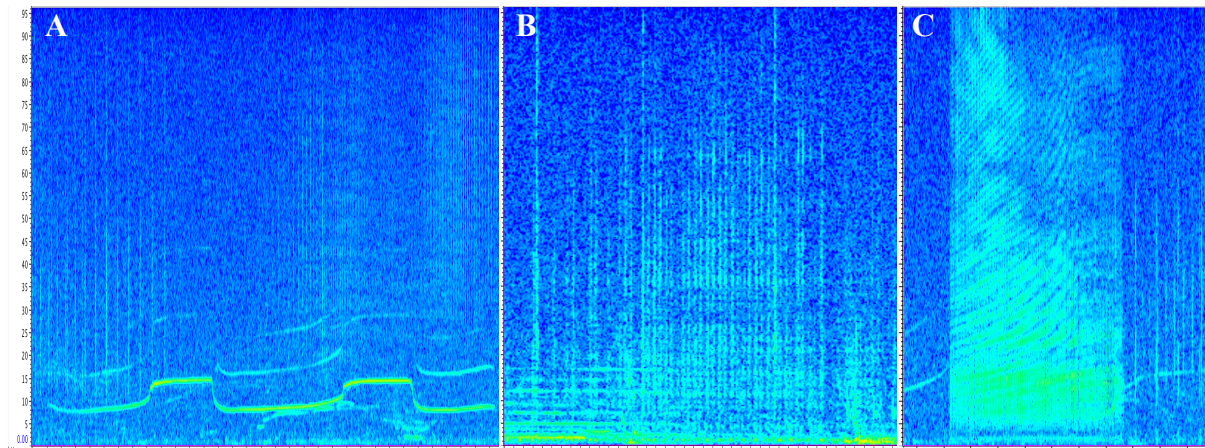


Figure 1.2: Spectrographic examples featuring the main energy of a) tonal whistles, b) pulsed sounds and c) burst-pulse sounds. Examples are from bottlenose dolphin (*T. truncatus*) in Far north waters, New Zealand.

Whistles can be categorised as narrow-band signals ranging from 2 – 25 kHz. They are utilised in reunions of mother/calf, alloparental care, courtship, and a range of affiliative and/or agonistic/aggressive circumstances (Caldwell & Caldwell, 1977; Dudzinski, 1996; Herzing, 2000; Hiley et al., 2017; King et al., 2016; Paulos, 2004; Smolker et al., 1993). Pulsed sounds are mostly produced during echolocation, but could additionally be produced during social interactions, e.g., prey acquisition, courtship, conflict resolution, and play (Evans, 1973; Herzing, 2000; Norris, 1969; Paulos, 2004). Current literature suggests context dependency acts on burst-pulse sounds, e.g., during social situations (specifically sexual activity) or the final stages of prey acquisition (Tyack & Clark, 2000). A mechanical function, beyond the acoustic element, may occur with a tactile element such as pleasure or pain (intensity dependence) perceived by the receiver (Herzing, 2000). However, the ultimate and proximate function/s of dolphin vocalisations have not been quantified.

The odontocete whistle repertoires are highly variable inter- and intra- species, with geographical, group and/or individual differences documented (Rendell et al., 1999). Intra-population, variability is highest when related to complexity or individual identity, for example, duration, inflections, or steps (Morisaka et al., 2005a; Rendell et al., 1999). Overall, individuals living in fluid societies exhibit increased whistle repertoire variation compared to those living in stable groups. Stable groups, however, can produce group-distinct repertoires, termed dialects (Filatova et al., 2017; Tyack, 1986). At the individual level, the most significant vocalisation is represented by the signature whistle. This type of whistle exhibits a stereotypical shape (or contour) which is based on the other signature whistles present in the community (Fripp et al., 2005; King & Janik, 2013) and typically develops within the first year after birth,

remaining stable throughout the lifetime of the individual (Sayigh et al., 2007; Tyack, 1997).

Studies have examined the correlation between acoustic behaviour and behavioural state at the group level (Dawson, 1991; Simon et al., 2007; Sjare & Smith, 1986; Taruski, 1979), suggesting that the call type and rate varies with behavioural state and signal function. Signal function is affected by a variety of parameters, including the signalling environment, conspecific identity, and sender/receiver internal physiology (see Kremers et al., 2016 for review). Additionally, the internal state of signalling individuals has been assessed using a motivation-structural rules hypotheses (MS) (Morton, 1977). MS rules assume that mutual signal exchange mutually benefits both individuals involved, that signals are kept informative through evolution acting on them, and that there is no arbitrary structure in vocalisations (Morton, 1977). The conclusion drawn from MS rules is, in summary, that comprehension of vocalisations is independent of physical structures. Examples include low frequency sounds being perceived as aggressive, while high-frequency sounds portray an invitation or a submissive motivational state. Morton (1977) further considered proximity and motivation as factors of importance in relation to causation and progression of signals. No matter the proximate causes, Morton (1977) concluded that, in dolphins, the link between behaviour and the structure of vocalisations provides information on the potential functions of certain classes of vocal behaviour, as in other social animals (refer to Dunlop, 2017; Perrtree et al., 2016).

1.2.4.2 Non-vocal signal exchange in dolphins

Non-vocal signal exchange is defined as signal exchange involving messages other than those produced vocally (DeVito & Hecht, 1990). Non-vocal signal exchange thus involves body parts not utilised in vocal sound production and may be photic, mechanical, acoustic or chemical. There is minimal evidence in the current literature to support chemical signal use in captive (e.g., Corkeron et al., 1990; Shane, 1977) and semi-wild (e.g., Dill et al., 2003) dolphins, and such evidence is non-existent in wild populations. Thus, non-vocal signal exchange in cetaceans may be photic (i.e., posture) or mechanical (i.e., touch - pectoral fin of one individual physically touching another individual, or a non-vocal sound - jaw clap or tail slap). Jansen and Jansen (1969) found that odontocete adults lack olfactory nerves, bulbs, and peduncles. Thus, the use of chemical signals can only include those passed through taste. Captive dolphins (e.g., Corkeron et al., 1990; Shane, 1977) and semi-wild dolphins (e.g., Dill et al., 2003) have shown food preferences, indicating the use of taste.

1.2.4.2.1 Photic signals

Water turbidity can limit visibility, and therefore the effectiveness of photic signals for aquatic animals (Chivers et al., 2013). The visual acuity of delphinids is good both above- and sub-surface (Dawson, 1991; Delfour & Marten, 2006; Madsen & Herman, 1980). The complexity of photic signals is apparent across species, ranging from passive and simple (i.e. posture displays, colour patterns, or water column orientation), to complex sequences of behaviours. Complex sequences are utilised to indicate species, movement, and reproductive condition, amongst other things (Herman & Tavolga, 1980; Würsig et al., 1990). Species with conspicuous markings, e.g., dusky dolphins (*Lagenorhynchus obscurus*) and killer whales, also benefit from two forms of photic reception as colouring reinforces movements and postures (Würsig et al., 1990). For example, leaps in dusky dolphins may signal prey has been located, with colouration reinforcing the signal as being from a conspecific (Würsig & Würsig, 1980). Un-patterned species may also use pigmentation, dorsal fin shape/size, and scarring as passive photic cues to identify “friend or foe” and individual identity, such as mature vs immature individuals (Dudzinski et al., 2002; MacLeod, 1998; Würsig et al., 1990). An example of the latter is the patterning of spotted dolphins, where the spots become denser as the individual matures (Herzing, 1997; Perrin, 1969; Perrin et al., 2009). Members of the group may utilise these coloration patterns in conjunction with dorsal fin shape to ascertain individual identity. It has also been suggested that scarring may function in the same way, with individuals with more scars being perceived as more likely to be older, larger, and more likely to engage in aggressive encounters, thus signalling that the individual is a potential threat (MacLeod, 1998; Pryor & Shallenberger, 1990).

Photic short-range signal exchange are complex and can be employed in affiliative or aggressive exchanges (Tyack, 2000). Modification of these signals may occur as a result of signaller context, e.g., age of the individual or angle of approach (Dudzinski, 1998). Examples in the literature include the S-shaped posture utilised by males in an agonistic encounter, which is suggested to function as a threat display (Caldwell & Caldwell, 1977; Defran & Pryor, 1980; Tavolga, 1966). S-shaped posture is defined as an individual positioned with its torso flexed and head up (Caldwell & Caldwell, 1977). The S-shape posture, when occurring in concordance with an oblique approach angle and genital region presentation, may portray a *play* context, illustrating the complexity of photic signal exchange (Dudzinski, 1998). Additionally, age could modify the production and perception of signals. Sub-adult spotted

dolphins utilise an S-posture during aggressive activity, while the same signal is utilised during play by juveniles (Dudzinski, 1998; Paulos, 2004).

Additional photic signals linked to aggressive or threatening signals include: a head-on approach, shaking of the head, and jaw opening/closing (Figure 1.3, Herman & Tavalga, 1980). Contrary to this, conflict resolution, sub-ordination, and pacification may be signalled by facing away (Caldwell & Caldwell, 1972). Further, in agonistic encounters, closing of the mouth and a lateral swimming position may be employed (Caldwell & Caldwell, 1977). Finally, insights from captivity illustrate submissive photic displays, such as turning the head to look away (Pryor, 1990), flinching, and moving/orientating body away from aggressor (Samuels & Gifford, 1997; Paulos, 2004; Würsig et al., 1990).



Figure 1.3: Jaw opening/closing photic signal in bottlenose dolphin (*T. truncatus*) in Far North waters, New Zealand.

1.2.4.2.2 Mechanical tactile signals

Dolphins have highly innervated skin sensitivity (Palmer & Weddell, 1964); therefore, mechanical perception is a viable mean of short-range signal exchange. The eyes and blowhole are particularly sensitive, akin to lips and fingers in primates (Connor & Peterson, 1994). Literature focusing on mechanical tactile signals in dolphins abounds: rubbing and touching using flukes, pectoral, and dorsal fins to another individual's body is relatively frequently observed during social interactions (e.g., Connor, 1990; Dudzinski et al., 2012; Kaplan & Connor, 2007; Östman, 1994; Shane, 1990b; Tamaki et al., 2006). Aggressive interactions have a high rate of mechanical tactile contacts characterised by more overt movements, including butting, biting, ramming, and raking (Brown & Norris, 1956; Norris, 1967; Östman, 1990;

Scott et al., 2005; Slooten, 1994). Contact behaviours and non-vocal auditory signals are often combined, e.g., jaw clapping or tail slapping in aggressive interactions (Mann & Smuts, 1999; Östman, 1990; Paulos 2004). Tactile signals can be adapted to maximise information transfer through the type/location and intensity of touch. Mechanical contact behaviour and signal transfer in Atlantic spotted dolphins has been recorded as predominantly affiliative (Dudzinski, 1998; Paulos, 2004). This includes body-body rubbing, petting (pectoral fin-fin), petting/rubbing (pectoral fin-body), and simple body-body contact (with no movement, Figure 1.4, Dudzinski, 1998; Paulos, 2004). Additionally, the contact was more likely between members of the same gender and age class, suggesting recognition of individual parameters within a group (Dudzinski, 1998).



Figure 1.4: Contact behaviour defined as A) *rubbing* in coastal bottlenose dolphin (*T. truncatus*) and B) *petting* in oceanic bottlenose dolphin and false killer whales (*Pseudorca crassidens*), in Far North waters, New Zealand.

Adaptations to enhance functionality of tactile signals have even been suggested. For example, in Commerson's dolphin (*Cephalorhynchus commersonii*), pectoral fins are characterised with

saw-tooth serrations on the leading edge. When males had only one serrated pectoral fin, the majority of contact emanated from the serrated fin, possibly functioning to enhance stimulation (Johnson & Moewe, 1999). Contact signalling may have a communicative function, with a contact eliciting a reciprocal response (Dudzinski, 1998; Herzing, 2000; Paulos, 2004; Sakai et al., 2003). On the other hand, dolphins could utilise group members for hygiene or stimulation similar to the way they make contact with the ocean floor or alternate objects. All the above functions could also be possible at the same time.

Mechanical tactile signals are not restricted to intra-specific interactions. Both affiliative and agonistic behaviours have been observed during inter-specific exchanges of wild bottlenose dolphin with humans (Dudzinski et al., 1995) and humpback whales (*Megaptera novaeangliae*) (Deakos et al., 2010). The behaviours observed were predominantly affiliative (inquisitive), yet, in the case of interactions with humans, when swimmers exited the water aggressive behaviours were also noted (Dudzinski et al., 1995). While the communicative function of behaviours is still unclear, the interactions noted may function similarly to the social rubs and hierarchical sorting observed in affiliative contexts between conspecifics. Determining true signal exchange can be problematic, particularly as tactile behaviour can hold many functions beyond that of signal exchange.

1.2.4.2.3 Non-vocal acoustic signals

When discussing signal exchange, non-vocal acoustic signalling is also applicable. Non-vocal acoustic behaviour includes sound production in any way other than using a vocal pathway (e.g., a jaw clap, breach, or tail slap). In dolphins, this is primarily the result of an audible displacement of water and has been related to circumstances of aggression, discipline, or attention (Pryor, 1990).

Dominant individuals have been observed utilising tail slaps as warning signals (Shane et al., 1986) and in scenarios where individuals were disturbed or annoyed, such as a boat approaching (Lusseau, 2007; Würsig & Würsig, 1979). Within bottlenose dolphin groups, aerial behaviours function as short-range exchange signals, including the aggressive displays observed in other studies (Connor & Smolker, 1996). Another example, the jaw clap, has both photic and mechanical (non-vocal acoustic) properties (first described by McBride & Hebb, 1948). A dolphin opens its jaws, showing teeth, then snaps the jaw shut, expelling water and producing a loud, percussive sound. A posture often accompanies the jaw display, such as an

arch of the back while facing the receiver of the signal. If the receiver responds by not retreating, the individual performing the display may charge (Caldwell & Caldwell, 1977; Saayman & Tayler, 1973). Non-vocal acoustic signals are linked with affiliation/recruitment and agonistic (annoyed/disturbed) contexts (Dudzinski et al., 2002; Paulos, 2004).

1.2.5 Bottlenose dolphin as a model species for studying signal exchange

Marine mammal behaviour, and particularly bottlenose dolphin behaviour, is multifaceted and variable. Prior research has indicated that behaviour is not affected by one single factor, but rather “dictated by a complicated web of interacting elements” (Shane, 1990a, p. 261). Throughout their reasonably long life span, this highly adaptive group of species demonstrates a recurring capability to learn and modify their behaviours to optimise survival (Shane, 1990b), exhibiting a “large degree of behavioural plasticity” (Pace et al., 1998, p. 2).

1.2.5.1 Adaptability and variation

The *Tursiops*’ taxonomic status has long been contentious, despite being the focus of many studies. Morphological variations have resulted in more than 20 different species or subspecies within the genus being suggested (Hershkovitz, 1966), though full clarity is yet to be achieved. Currently, bottlenose dolphin species officially recognised are *T. truncatus* and *T. aduncus* (Indo-Pacific bottlenose dolphin), with an additional species, the *T. australis* (Burrnun dolphin), described recently in Australian waters (Charlton-Robb et al., 2011). The Committee on Taxonomy for marine mammal species and subspecies does not currently accept the latter (Committee on Taxonomy, 2016). The establishment of an accepted global threat status for bottlenose dolphin remains impeded by their wide-ranging distribution and unresolved taxonomic status (Reeves & Leatherwood, 1994; Reeves et al., 2003). The International Union for Conservation of Nature and Natural Resources (IUCN) Red List classifies bottlenose dolphin as *Least Concern*, while the Indo-Pacific bottlenose dolphin is listed as *Data Deficient* (Reilly et al., 2015). A globally threatened classification for bottlenose dolphin is not suggested by any current evidence. This is not the case in regional and local populations, which can be identified as threatened as a result of anthropogenic factors, such as habitat degradation, hunting, fisheries interaction, and disturbance of biologically vital behaviours (e.g., Peters & Stockin, 2016; Reeves et al., 2003; Wells & Scott, 1999). In NZ, only *T. truncatus* are documented (Figure 1.5), and as such the use of the term bottlenose dolphin in this thesis refers only to *T. truncatus* and not *T. aduncus* or *T. australis*.

T. truncatus appears to have, on one or multiple occasions, adapted to environmental conditions within different home ranges and thus several different forms or “ecotypes” exist (Figure 1.5). Duffield et al. (1983) first used the terms offshore and inshore to describe *T. truncatus* ecotypes with different distributions and haematology in Western North Atlantic waters (WNA). Additionally, genetic distinctions between WNA ecotypes have been discovered from mitochondrial and nuclear DNA (e.g., Curry & Smith, 1997; Dowling & Brown, 1993; Hoelzel et al., 1998). Prey preference, parasitic load (Mead & Potter, 1995), and satellite-linked radio telemetry have also been utilised to differentiate WNA ecotypes (Wells & Scott, 1999). The WNA is the only ecotype classification to date clearly supported by genetic evidence. In all other areas studied to date, a lack of evidence has resulted in an inability to differentiate habitat use and ecotype specialisation in its true form; NZ is no exception to this (as discussed in section 1.3.2). In this regard, this thesis refers to the well-recognised, near-shore form termed the coastal ecotype and the lesser known open-water dwelling form referred to as the oceanic ecotype. Though it must be noted no assumption is made that true ecotype specialisation exists (i.e., the true offshore ecotype).

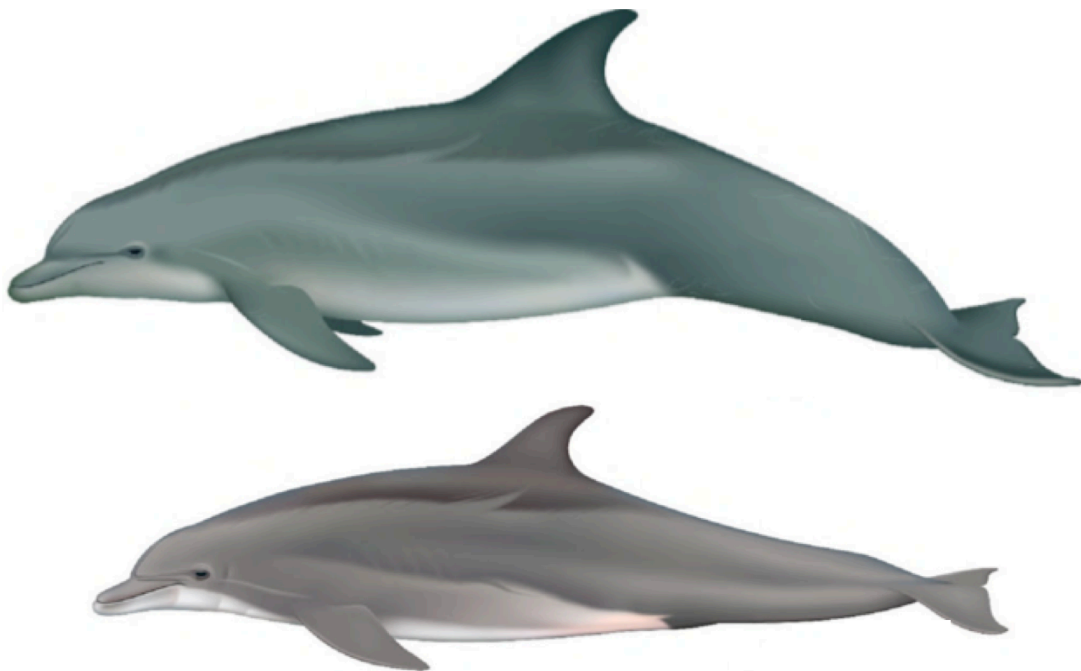


Figure 1.5: Ecotypes of common bottlenose dolphins (*T. truncatus*); top: Offshore/Oceanic adult, bottom: Coastal adult. Adapted from Jefferson et al. (2008).

The coastal bottlenose dolphin is smaller in size than the oceanic bottlenose dolphin in WNA and the Gulf of Mexico (Curry, 1997) and larger in Eastern North Pacific waters (adult size range - 1.9 – 3.6 m, up to 650 kg, Walker, 1981). Hersh & Duffield (1990) suggest that this may occur as a result of adaptation to the local environment. A smaller size in coastal

environments facilitates manoeuvrability in shallow waters (Hersh & Duffield, 1990). It is worth noting that taxonomic uncertainty may have confused morphological classification (Reeves et al., 2004).

Bottlenose dolphin ecological flexibility is a fundamental reason populations are exposed to anthropogenic impacts (Reeves et al., 2003; Wells & Scott, 1999). Their ranges include documented use of fiords, harbours, estuaries, bays and rivers where most human activities occur (Leatherwood & Reeves, 1990; Wells & Scott, 1999). Their adaptability is reinforced by the wide range of population structures and sizes observed, such as small resident groups with restricted ranges (e.g., Wells et al., 1987; Wilson et al., 1997), mobile coastal populations (e.g., Defran et al., 1999), and large transient pelagic groupings (Leatherwood et al., 1988). Population sizes range from 50 – 150 individuals (e.g., Williams et al., 1993; Wilson et al., 1999) to 2,000 – 7,000 individuals (e.g., Forcada et al., 2004; Preen et al., 1997). Ecological restrictions seem to drive social structure; as demonstrated by the dynamic relationships observed in fission-fusion societies of the sub-tropics (Connor et al., 2000) that are set aside for long-term close associations in cool temperate latitudes (Currey et al., 2008; Lusseau et al., 2003).

1.2.5.2 Complex social structure

Bottlenose dolphin society is described as fission/fusion in which individuals move between small groups that continually change in composition and behaviour (Connor et al., 2000; Würsig & Würsig, 1977). Behaviour changes and group size may depend on habitat, sex ratios, and associations. Social groupings of bottlenose dolphins can include associations with other species. Inter-specific groups of birds and coral reef fishes have been extensively documented (e.g., Bonin et al., 2009; Farine et al., 2015; Goodale et al., 2015). Whilst less research on mixed-species groups in mammals exists, it has still been documented across a range of taxa, e.g., ungulates (Fitzgibbon, 1990; Keast, 1965; Sinclair, 1985), primates (Chapman & Chapman, 2000; Cords, 1987, 1990a, 1990b; Gartlan & Struhsaker, 1972; Peres, 1992a, 1992b, 1993; Whitesides, 1989), and cetaceans (Corkeron, 1990; Frantzis & Herzing, 2002; Herzing & Johnson, 1997; Sheldon et al., 1995; Weller et al., 1996; Zaeschmar et al., 2014).

Associations may vary in function and duration, with both aggressive and non-aggressive associations described. For cetaceans, non-aggressive associations of bottlenose dolphin are best described with Indo-Pacific humpback dolphins (*Sousa chinensis*) (e.g., Corkeron, 1990;

Stensland et al., 1998). Evidence shows that aggressive associations primarily originate from harassing behaviour by false killer whales (*Pseudorca crassidens*) and pilot whales, which have been described on bottlenose dolphins in Costa Rica (Acevedo-Gutiérrez et al., 1997) and NZ (Zaeschar et al., 2014), and sperm whales (*Physeter macrocephalus*) near the Galapagos Islands (Palacios & Mate, 1996). Hybrids with other delphinids as a result of these associations have also been documented, including the false killer whales (e.g., Nishiwaki & Tobayama, 1982), Guiana dolphin (*Sotalia guianensis*, Caballero & Baker, 2010), long-beaked common dolphin (*Delphinus capensis*, Zornetzer & Duffield, 2003), pilot whales (Sylvestre & Tasaka, 1985), Risso's dolphin (*Grampus griseus*, Shimura et al., 1986), and rough-toothed dolphin (*Steno bredanensis*, Dohl et al., 1974). Despite the reported commonality of these associations, the proximate and ultimate causes remain unquantified (Reeves et al., 2003), resulting in difficulty in interpreting events.

An extensive temporal variety in interspecific associations, from minutes to years, has been observed (e.g., Fulling et al., 2011; Jefferson et al., 2006; May-Collado, 2010; Smultea et al., 2014; Zaeschar et al., 2013). Short-lived associations are the most documented (e.g., Herzing & Johnson, 1997; Migura & Meadows, 2002; Psarakos et al., 2003). Assessment of long-term associations is, however, difficult in gregarious interspecific groupings (Cords & Würsig, 2014). Research primarily focusses on a single individual joining a larger group of heterospecifics (e.g., Baraff & Asmutis-Silvia, 1998; Bearzi, 1996; Jefferson et al., 1991; Stensland et al., 2003). Again, data are not-exhaustive regarding the drivers of these associations, limiting the discussion of reasons for association persistence. Most authors assume participants gain an evolutionary benefit by for inter-specific groupings (Heymann & Buchanan-Smith, 2000; Whitesides, 1989). Functional explanations primarily include the general group theory dilution effect of foraging success and predator avoidance (Acevedo-Gutiérrez, 2008; Cords & Würsig, 2014; Stensland et al., 2003). Conversely, mixed groups do not need to always be driven by a functional explanation (Stensland et al., 2003), e.g., resource and habitat sharing in pursuit of a common interest, such as the case of the Indo-Pacific humpback dolphin and bottlenose dolphin foraging sympatrically compared to resource partitioning in the sympatric Australian snubfin dolphin (*Orcaella heinsohni*) and Indo-Pacific humpback dolphin (Parra, 2006). Finally, no all-inclusive mixed species association definition is accepted in the literature and examples are very extensive, making comparisons between different studies difficult. In this thesis, an interspecific group is defined as groups “where two

or more species are seen in such close association that they can be regarded as members of the same group” (Stensland et al., 2003, p. 206).

1.2.6 NZ Bottlenose dolphin as a model species for studying signal exchange

T. truncatus is the sole species of bottlenose dolphin recognised in NZ waters, with 2 distinct ecotypes: a coastal, shallow, warm-water type (coastal bottlenose dolphin) and an oceanic, deep, colder-water (oceanic bottlenose dolphin) type (Figure 1.6). Historically, research has focussed on the coastal bottlenose dolphin (e.g., Constantine, 2001; Currey et al., 2008; Dwyer et al., 2014a and b; Hartel et al., 2014; Lusseau, 2003; Merriman et al., 2009; Tezanos-Pinto et al., 2013). Ecotypes are distinguished based on morphological differences in size and colour, with the larger and darker oceanic ecotype additionally displaying scars believed to be from oceanic cookie cutter shark bites (*Isistius* sp.; Constantine 2002; Dwyer & Visser, 2011; Figure 1.6). Little is known about the oceanic form, meaning a definitive body size, group size, and distribution range is not available, though recent contributions to the current NZ oceanic bottlenose dolphin literature is described in section 1.3.1.2. Both ecotypes are referred to in this thesis and the signal use of each provides a novel comparison opportunity.



Figure 1.6: Gross morphological variation of bottlenose dolphins (*T. truncatus*) in New Zealand, left) coastal and right) oceanic bottlenose dolphin ecotype.

There are three geographically discrete populations of coastal bottlenose dolphins recognised in NZ waters (Baker et al., 2010; Figure 1.7). They are described as distinct due to the low gene flow levels amongst them (Tezanos-Pinto et al., 2009). The predominant population locations documented are: 1) the North Island’s North-East coast (Constantine, 2002); 2) the Marlborough Sounds (Merriman et al., 2009); and 3) Fiordland in the South Island (Webb, 1973). New hotspots are still being described, including Great Barrier Island (Dwyer et al., 2014b), Stewart Island (Brough et al., 2015), and the Kermadec Islands (Baker et al., 2010; Baker et al., 2016).

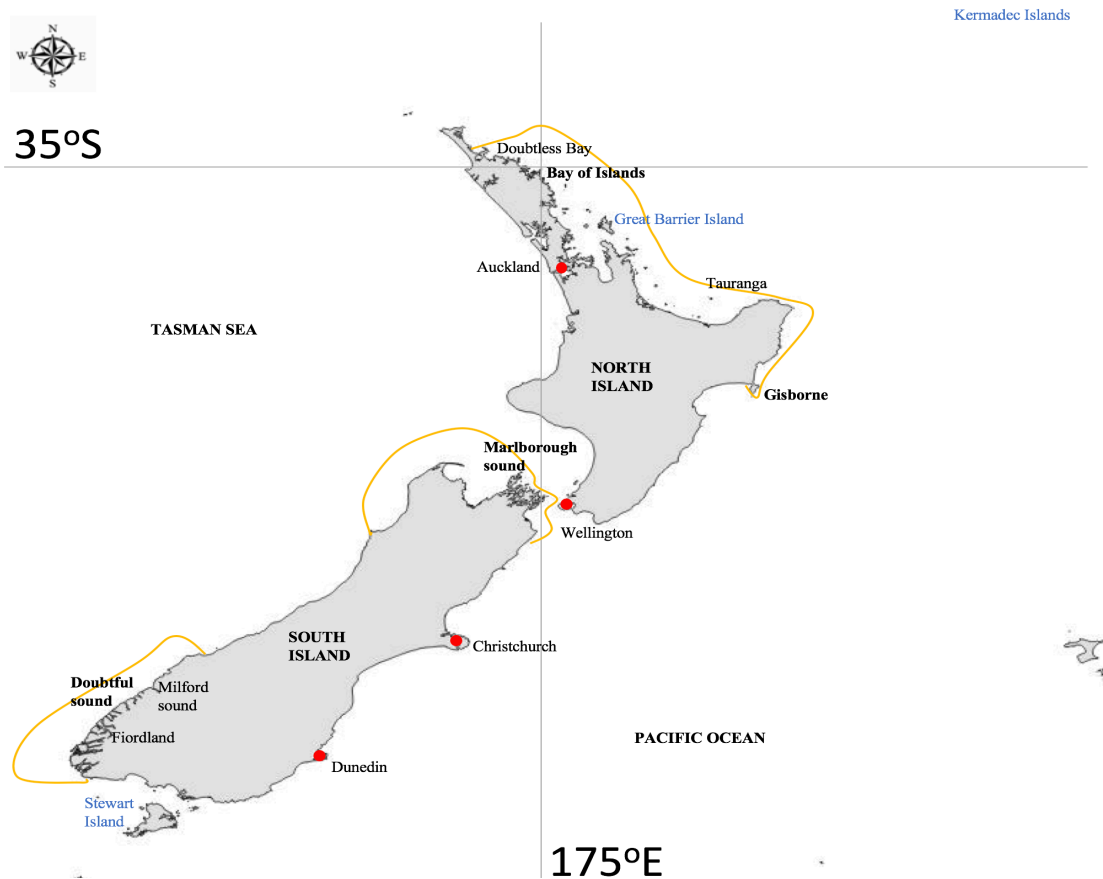


Figure 1.7: Presumed discontinuous distribution of coastal bottlenose dolphins (*T. truncatus*, inside orange line) from live sighting data, New Zealand. Additionally, new hotspots are shown (blue).

NZ bottlenose dolphins have varied spatial and temporal habitat use, with all spatial research focussed on coastal bottlenose dolphins only (Baker et al., 2010). The Fiordland population (Doubtful Sound) utilises fiords seasonally, with more summer and autumn sightings in inner fiords. The outer fiord sites are frequented more in winter and spring (Elliott et al., 2011). Bottlenose dolphins around the North Island do not follow this pattern, predominantly occurring in inshore warmer waters during winter and spring and further offshore in deeper/cooler waters during summer and autumn (Dwyer et al., 2014b; Hartel et al., 2014; Peters & Stockin, 2016). Suggested drivers of this distribution include variation in prey distribution (both populations), and/or Fiordland dolphin groups with calves seeking warmer waters in winter. The Marlborough Sounds bottlenose dolphin population shows no seasonal variation (Merriman, 2007).

The North Island North-East Coast population extends between Doubtless Bay – Tauranga (Constantine, 2002). Individuals are occasionally sighted outside of this core area, including the North Island’s west coast (Tezanos-Pinto et al., 2013). Whilst the range is comprehensively documented, research across it has not been even or inclusive of all areas, with the Bay of

Islands region, where bottlenose dolphin tourism is well established, being the primary focus (Constantine, 2001; Constantine et al., 2004). In Northland, outside of the Bay of Islands only limited and opportunistic data, have been published (Constantine, 2001) prior to this thesis, even in directly adjacent areas.

1.3 Study region of this thesis

The Far North waters are on the North-North-East coast of NZ and comprise largely varied habitats, i.e. open coastline, sheltered harbours, and areas of high and low vessel usage (Figure 1.8). The Far North waters extend ~105 km along the Northland coast. The coastline consists of numerous bays, estuaries, and sandy beaches. Primarily, cliffs are described as greywacke and sandstone rock (Tortell, 1981).

All surveys were conducted in waters less than 150m deep, where bottom type ranges from fine to coarse and rocky (Morrison et al., 2010). Four partially sheltered primary sites were selected: Bay of Islands, Doubtless Bay, Cavalli Islands, and Whangaroa Harbour. The Bay of Islands has a 15km wide entrance to the bay, which is delineated by Ninepin (Tikitiki Is.) and Cape Brett/Piercy Is. (Motukokako Is., 35°18'S and 174°16'E). The Bay of Islands is made up of a large bay with 144 islands described (Figure 1.8), and an average water depth of ~12m around the inner islands and ~50m in the outer bay. Doubtless Bay is a semi-circular embayment (34°55'S and 173°28'E; Figure 1.8). Doubtless Bay encompasses the area of coastline between Knuckle Point to the north and Berghan Point to the south, which forms the 10.7km mouth of the bay. The coastline comprises rocky headlands and sandy beaches (Kerr & Grace, 2005). The bathymetry of Doubtless Bay is predominantly a gently shelving seafloor, to a depth of approximately 70m at a central point between Knuckle and Berghan Points (Kerr & Grace, 2005). The Cavalli Islands is a cluster of islands 3 km east of Matauri Bay (on the mainland; 34°97'S and 173°96'E; Figure 1.8). The Cavalli Islands includes the main island of Motukawanui and six smaller Islands. Between the Islands the water depth averages ~10m and in the outer bay water depth averages ~50m. Whangaroa is demarcated by Tauranga Bay and False Head, which forms the 1km mouth of the bay (35°01'S and 173°45'E). Inside the harbour are three islands, of which the largest is Milford Island. The inner harbour has an average water depth of ~8m and the outer harbour water depth averages ~21m. The adjoining waters between Whangamumu and Doubtless Bay were also surveyed (referred to as Wider Survey). In areas outside the boundaries of sheltered bays, the principally rocky and exposed shorelines fall sharply to > 50m close to the coast (Morrison et al., 2010; Kerr & Grace, 2005).

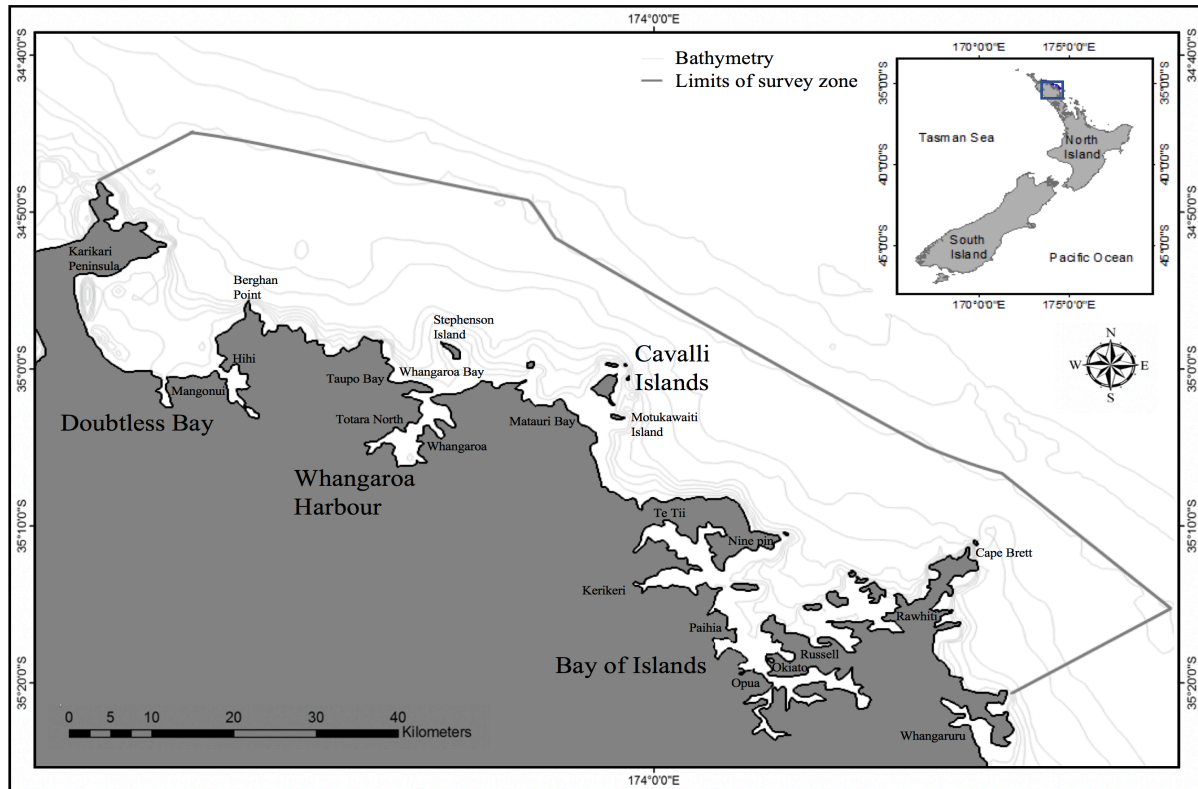


Figure 1.8: Study site in Far North waters. Bathymetric lines show 5 – 250 meters depth seabed gradient.

The Far North waters are heavily affected by the interaction between surface winds and tidal currents. Additionally, physical barriers, i.e., headlands and islands, can result in the development of local upwellings. In Far North waters, the principal oceanic current is the East Auckland Current, a warm subtropical current originating from the Eastern Australian Current (EAC, Stanton et al., 1997). The EAC migrates southward along the Northland east coast as far as the Bay of Plenty (Kerr & Grace, 2005). Water temperatures in the EAC area are $\sim 22^{\circ}\text{C}$ – 14°C in austral summer (peaking in February) and winter respectively, with the lowest temperatures in July/August; Kerr & Grace, 2005). Variability in the current temperature and timing is observed and this is primarily linked to the Southern Oscillation El Niño/La Niña phases.

The Far North waters are a productive marine ecosystem (Zeldis et al., 2005; Ocean Survey 20/20 Bay of Islands coastal survey) and are biodiversity-rich in megafauna, including seabirds (Gaskin & Rayner, 2013; Marchant & Higgins, 1991) and thirty-five species of marine mammals (within the 12 nmi limit) (Baker et al., 2010; Baker et al., 2016; Constantine et al., 2004; Peters & Stockin, 2013; Visser, 1999; Visser, 2007). Three threatened species are amongst the most often encountered in inshore and offshore waters: Bryde's whale

(*Balaenoptera edni*), bottlenose dolphin, and orca. This body of work concentrates on the most-encountered species in the Far North waters, namely the bottlenose dolphin.

1.3.1 Current knowledge of bottlenose dolphins in the study region

1.3.1.1 Coastal bottlenose dolphins in Far North waters

Within Far North waters the Bay of Islands, as part of the North-East coast population home range, has been the focus of many studies. Long-term studies are suitable for the area due to frequent sightings of individuals, year-round occurrence, and dolphin-related tourism in the area (Constantine, 2002; Constantine & Baker, 1997; Mourão, 2006; Ryding, 2001; Tezanos-Pinto, 2009; this study).

Research began in Bay of Islands waters in 1993 with a photo-identification study. Following this, Constantine (1995) built on the work by S. Baker and initiated the first assessment of coastal bottlenose dolphin behavioural responses to permitted tour-boat operators. The results indicated the need for further investigation into the population dynamics, local and global abundance, habitat use and dolphin/tour-boat interactions in the Bay of Islands, therefore Constantine's 2002 study began. Subsequently, the life histories, biology, and behaviour of approximately 408 coastal bottlenose dolphins have been documented (Berghan et al., 2008; Constantine et al., 2004; Hartel et al., 2014; Mourão, 2006; Peters & Stockin, 2016; Ryding, 2001; Tezanos-Pinto et al., 2009).

The population dynamics of the local Bay of Islands coastal bottlenose dolphin was investigated through the assessment of group size, composition, and calf mortality (Constantine, 2002). Constantine's results suggested coastal bottlenose dolphin groups averaged 15 individuals; in line with populations at similar latitudes (Constantine, 2002). The local population (446 adults (CI = 418 – 487) from closed mark-recapture) is described as non-resident, due to resighting rates suggesting no resident dolphins occur in the Bay of Islands (Constantine, 2002). However, it was noted that the home ranges of coastal bottlenose dolphins differ, as evidenced by variable individual resighting rates (30% of coastal bottlenose dolphins are sighted only once per lunar month; Constantine, 2002). Coastal bottlenose dolphin behaviour was also variable with decreased resting in the presence of dolphin watching and swimming vessels. Moreover, dolphins appeared to avoid swimmers, depending on their placement around the coastal bottlenose dolphin group (Constantine, 2001; Constantine et al., 2004).

Outside of the Bay of Islands (in Far North waters) Constantine conducted 13 random surveys, 2 of which resulted in 3 coastal bottlenose dolphin encounters (Constantine, 2002). Additional photographs were also shared from the local Bay of Islands community. These photographs were cross-referenced with the Bay of Islands catalogue, resulting in 62 matches of individual dolphins. This led Constantine to conclude that this North-East coast coastal bottlenose dolphin population is a geographically closed population. Additionally, it was suggested that most coastal bottlenose dolphins used the Bay of Islands at some point in their lifetime. Subsequent comparison with the Hauraki Gulf (240 km further south) coastal bottlenose dolphin catalogue, resulted in 59% of the Hauraki Gulf ($n = 162$) individuals also being documented in the Bay of Islands (Berghan et al., 2008). The results suggested a greater population size than initially predicted by Constantine (2002) and/or home-range preferences that vary by individual with overlapping preferred sites (e.g., Bay of Islands and Hauraki Gulf, Berghan et al., 2008).

Coastal bottlenose dolphins in the Bay of Islands have a social group structure described as fission-fusion, with social affiliations resembling resident populations, such as in Doubtful Sound (Fiordland; e.g., Lusseau et al., 2003) and Sarasota Bay (USA, e.g., Wells, 1991). Long-term associations lasting up to 10 years have been documented within this social structure (Mourão, 2006). Though, no male alliances have been documented, unlike in the *Tursiops* spp. in Shark Bay (Connor et al., 2017). Nonetheless, social structures have been documented, both long- and short-term (Mourão, 2006).

Tezanos-Pinto (2009) investigated the local Bay of Islands coastal bottlenose dolphin population structure and genetic diversity, alongside two other NZ populations (Marlborough Sound and Fiordland), to define their boundaries. That study focussed on the Bay of Islands subpopulation to assess dolphin group dynamics, habitat use, and abundance, and, finally, female reproductive parameters to determine the viability of coastal bottlenose dolphins in the Bay of Islands on the long-term. The results indicated a very dynamic habitat use pattern with frequent, occasional, and infrequent visitors (Tezanos-Pinto 2009), with non-uniform use within these groups. Changes in habitat use supported the suggestion that the Bay of Islands coastal bottlenose dolphin population is experiencing high calf mortality and local abundance decline (Tezanos-Pinto, 2009; Tezanos-Pinto et al., 2013; Tezanos-Pinto et al., 2015). Despite this finding, coastal bottlenose dolphins are regularly recorded in Bay of Islands waters, suggesting that, whilst there are less dolphins, they are regularly using the bay (Tezanos-Pinto

et al., 2013). Thus, varied habitat use, possible mortality, and reduced recruitment may explain the local decline indicated.

1.3.1.2 Oceanic bottlenose dolphins in Far North waters

A paucity of data relating to the oceanic bottlenose dolphin form currently exists in NZ. Most recently, Zaeschmar et al. (2013; 2014) added to the literature by documenting the oceanic bottlenose dolphin in respect of its association with the false killer whales and pilot whales in Far North waters. They are spotted seasonally in deeper North-East NZ waters in the austral summer – autumn months (Zaeschmar et al., 2013), yet are considered distinct from the coastal bottlenose dolphin population despite no genetic divergence detected (Tezanos-Pinto, 2009). To date, no confirmed inter-ecotype exchange has been observed (despite long-term coastal bottlenose dolphin research, e.g., Constantine et al., 2004; Peters & Stockin, 2016; Tezanos-Pinto et al., 2013; this study), though possible interactions during mating season have been suggested from unpublished photo-identification in the Bay of Islands (referred to in Tezanos-Pinto, 2009).

Zaeschmar et al. (2013) began to investigate the association of the oceanic bottlenose dolphin with the false killer whales through his examination of the ecology of the latter. The bottlenose dolphins were categorised as oceanic due to the stereotypical scarring and robust morphology noted. In most encounters with false killer whales, they were associated with bottlenose dolphins (91.5%, $n = 43$), illustrating that mixed species associations are common for oceanic bottlenose dolphins in Far North waters (December – May, Figure 1.10; Zaeschmar et al., 2013). Additionally pilot whales were nearby/interacted with the group in two encounters (Figures 1.9 and 1.10; Zaeschmar, 2014).

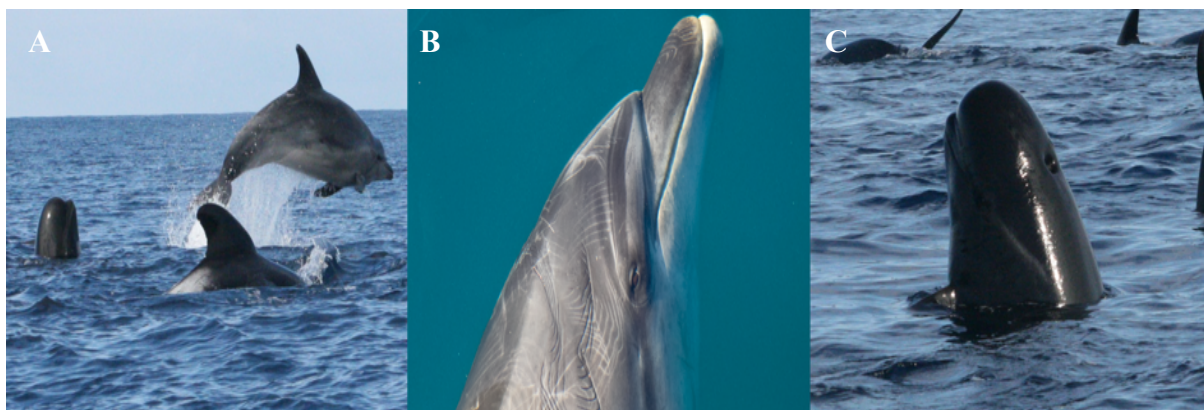


Figure 1.9: Inter-species groupings in New Zealand, A) pilot whale(s) (*G. sp.*) and bottlenose dolphin (*T. truncatus*) in a mixed grouping, centre and right images show the rostrum characteristic of B) bottlenose dolphins and C) pilot whales, respectively. Photograph B © T. Guerin.

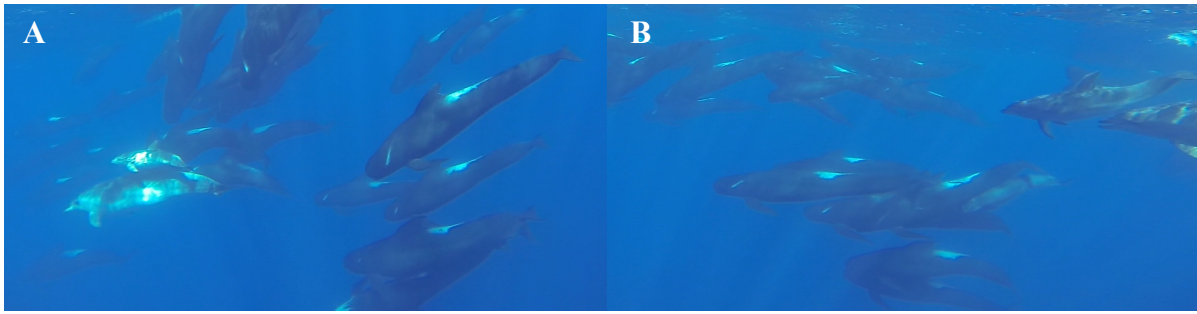


Figure 1.10: Inter-species groupings of bottlenose dolphins (*T. truncatus*) and pilot whales (*G. sp.*) in New Zealand, A) bottlenose dolphin calf with presumed adult bottlenose dolphins and pilot whales; and B) pilot whale calf with presumed adult pilot whales and bottlenose dolphin.

1.4 Thesis structure and rationale

In Far North waters, cetaceans encounter a variety of behavioural drivers. Insight into the density, distribution, and signal behaviour of the bottlenose dolphins utilising Far North waters is necessary to comprehend the possible population level effects. Understanding this region is especially important, given the documentation of two bottlenose dolphin ecotypes, nursery groups observed in both populations, high documented calf mortality, and a local Bay of Islands coastal bottlenose dolphin population in decline (Constantine et al., 2004; Tezanos-Pinto et al., 2013, 2015).

The current research seeks to quantify context specific signal plasticity of bottlenose dolphin ecotypes utilising Far North waters. For the first time, systematic surveys were conducted focusing on a range of strata across Far North waters. Moreover, this doctoral thesis utilises a synthesis of novel analytical techniques to examine the ecological parameters encountered by parapatrically occurring *Tursiops* frequenting Far North waters, including both surface and subsurface behaviour.

This thesis presents and examines data collected during fieldwork and empirical analytical conducted by C. Peters. Four research chapters (Chapters 2 – 5) are presented, with introductory and concluding chapters (Chapters 1 and 6, respectively). Each chapter builds on the next, resulting in unavoidable repetition. Where achievable, this is reduced. The scope of each chapter is as follows:

- **Chapter 1** contains background details of the core thesis topics. The concept of the bottlenose dolphin as a model genus of signal exchange is introduced. A literature review of the types and use of signal exchange by bottlenose dolphins and current research on bottlenose dolphin behaviour is presented. This is followed by a current knowledge

summary of bottlenose dolphin ecotypes in New Zealand and the study region. This chapter was written by C.H. Peters and improved by edits and suggestions provided by K.A. Stockin and E. Martinez.

- **Chapter 2** examines the geographic distribution, density, and abundance of the bottlenose dolphin in coastal and pelagic Far North waters. Data were collected year-round during a systematic three-year study. Relative densities were examined in relation to abiotic and biotic factors. A distance sampling methodology allowed for spatial surface density analysis. Finally, the spatial and temporal overlap of bottlenose dolphin ecotypes was investigated to inform Chapters 3 – 6. Data collection and analysis for this chapter was performed by C.H. Peters. Assistance and advice regarding spatial analysis and statistics was provided at the Centre for Research into Ecological and Environmental Modelling, St. Andrews, Scotland. The chapter was written by C.H. Peters and improved by edits and suggestions provided by K.A. Stockin.

The following questions were explored:

- 1) What geographic distribution and density patterns of bottlenose dolphin ecotypes occur in both inner and outer Far North waters?
- 2) Does bottlenose dolphin abundance vary as a function of season, stratum, and ecotype in Far North waters?
- 3) Is there a measurable spatial overlap of coastal and oceanic bottlenose dolphins in Far North waters?

- **Chapter 3** quantifies the call repertoire of bottlenose dolphin groups detected during systematic surveys in Far North waters. Repertoire call variation is examined in a multi-faceted manner. Spatial variation and influence on acoustic behaviour is analysed and compared between the call repertoires of ecotypes. Data collection and analysis for this chapter was performed by C.H. Peters. Training and assistance in the application of freeware Luscinia was received from W. Webb, and statistical advice was provided by M.D.M. Pawley. The chapter was written by C.H. Peters and improved by edits and suggestions provided by K.A. Stockin, E. Martinez and M.D.M. Pawley.

The following questions were explored:

- 1) Is semi-automated categorisation and comparison of call contours using the software Luscinia applicable to bottlenose dolphins?

- 2) Are coastal bottlenose dolphin and oceanic bottlenose dolphin calls acoustically distinct and do they differ in call rate?
 - 3) Can calls from Far North waters be acoustically categorised as belonging to either the coastal- or oceanic-type?
- **Chapter 4** describes the signal exchange between oceanic bottlenose dolphins detected during systematic surveys in Far North waters. Assessing the behavioural repertoire of dolphins in a multi-faceted manner to include photic (postural and spacing) and mechanical (tactile and call) signalling allows the examination of functional signal exchange parameters at a group level. Additionally, the influence of factors specific to oceanic bottlenose dolphin, such as mixed-species aggregations, is examined. Data collection and analysis for this chapter was performed by C.H. Peters. Training and assistance in the application of freeware Luscinia was received from W. Webb and statistical advice was provided by C. Amiot. The chapter was written by C.H. Peters and improved by edits and suggestions provided by K.A. Stockin and E. Martinez.

The following questions were explored:

- 1) Does the formation of interspecific groupings with pilot whales (*Globicephala sp.*, pilot whales) affect the call behaviour of oceanic bottlenose dolphin groups?
 - 2) How do vocal parameters change in relation to biotic and abiotic factors in intra- and inter-specific groupings?
 - 3) Is multimodal signal exchange utilised in intra- and inter-specific groupings?
- **Chapter 5** investigates the signal exchange of coastal bottlenose dolphin groups detected during systematic surveys in Far North waters. The methods mirror those used in Chapter 4. Additionally, the influence of factors specific to coastal bottlenose dolphin, such vessel presence, is examined. Data collection and analysis for this chapter was performed by C.H. Peters. Statistical advice was provided by C. Amiot. The chapter was written by C.H. Peters and improved by edits and suggestions provided by K.A. Stockin, E. Martinez and M.B. Orams.

The following questions were explored:

- 1) Do coastal bottlenose dolphins modify call rate, frequency, and/or duration as a response to vessel noise, and/or are there photic and mechanical behaviour changes?

If so:

- 2) How is coastal bottlenose dolphin call rate, frequency, and/or duration modified as a response to vessel noise and/or photic and mechanical behaviour changes?
 - 3) How does the use of tactile (mechanical), posture (photic), and call (mechanical) signal exchange parameters change in relation to one another in different vessel scenarios?
 - 4) Does group composition (i.e. groups with and without calves) result in altered signal exchange in different vessel scenarios?
- **Chapter 6** discusses the key research findings of the whole thesis by summarising and synthesising the research chapters. The research significance is identified and outlined by the conservation management context. Further research suggestions are outlined for *Tursiops* in Far North waters and to populations throughout New Zealand. This chapter was written by C.H. Peters and improved by edits and suggestions provided by K.A. Stockin and E. Martinez.

Chapter 2

Density, distribution and abundance of parapatric common bottlenose dolphin (*Tursiops truncatus*) ecotypes in Far North waters, New Zealand



Common bottlenose dolphin (*Tursiops truncatus*) adults and calves/neonates in Far North waters, New Zealand.

2.1 Introduction

There is a growing need to provide context to complex scientific questions. As a starting point, knowledge of population's spatial use and size is needed to evaluate conservation status and prioritise management actions. This is the case particularly in Far North waters, New Zealand where two known ecotypes, the coastal and oceanic common bottlenose dolphins (*Tursiops truncatus*, referred to hereafter as bottlenose dolphin), are exposed to human activities. Coastal bottlenose dolphins are the target of human activity in the form of tourism, which causes disturbance (Peters & Stockin, 2016). In one area of Far North waters, the Bay of Islands, the local population has also been documented as in decline, with high calf mortality and possible displacement from the local area (Tezanos-Pinto, 2009; Tezanos-Pinto et al., 2013; Tezanos-Pinto et al., 2015).

The size and spatial use of populations needs to be quantified across Far North waters. Studies encompassing robust density and population estimates of marine organisms have relied on distance sampling methodologies for decades (e.g., Beavers & Ramsey, 1998; Burnham et al., 1980; Forcada et al., 2004; Goyert et al., 2016; Hammond et al., 2013; Laake et al., 1997; Slooten et al., 2004; Williams et al., 2017). Distance sampling provides a suite of techniques which enable absolute density to be estimated based on the measured distances from the observer to each observed animal across a representative or complete section of a population's known range (e.g., Buckland et al., 2001; Fouchet et al., 2016; Goyert et al., 2016; Sollmann et al., 2016). Progressively, conservation management requires more than abundance estimates from sighting surveys, including the relation of estimates to spatial variables reflecting topography or habitat. By incorporating detection probability changes as a function of covariates, the resulting density estimates can be compared across populations, species, age groups, locations, sexes, etc (Buckland et al., 2009; Buckland et al., 2015). This results in an improved population context for the management of environments and the animals within it.

To date any possible interaction between the two bottlenose dolphin ecotypes remains unquantified. The most frequently studied species in Far North waters is the coastal bottlenose dolphin (Peters & Stockin, 2016). Our preliminary understanding of coastal bottlenose dolphins originates primarily from within Bay of Islands waters (Takou Bay to Whangamumu (Latitude 34°51 to 35°05'S, Longitude 173°16 to 174°28'E), see Fig. 2.1 for Far North waters boundaries). Earlier research focuses on behaviour (e.g., Constantine et al., 2004), anthropogenic effects (e.g., Constantine, 2001, 2002; Constantine et al., 2004; Snell, 2000),

and population structure/abundance (e.g., Tezanos-Pinto, 2009; Tezanos-Pinto et al., 2013; Tezanos-Pinto et al., 2015). The occurrence and density of the coastal bottlenose dolphin in the Bay of Islands have also been linked to environmental parameters (Hartel & Constantine, 2014). Conversely, occurrence, distribution, and density have received no previous assessment in Far North waters beyond the Bay of Islands, despite a 10-year permit moratorium for the whole area being established until 2026 (Mangawhai Harbour to Cape Reinga (Latitude 36°05' to 34°25'S, Longitude 174°36' to 172°41'E)). As a result, limited scientific literature exists in relation to the coastal bottlenose dolphin in Far North waters prior to this study. Further to this, no systematic spatial or behavioural assessment of the oceanic bottlenose dolphin anywhere in New Zealand has occurred to date. Instead, current understanding of oceanic bottlenose dolphin occurrence originates only from a description of their association with false killer whales (*Pseudorca crassidens*) (Zaeschmar, 2014; Zaeschmar et al., 2014; Zaeschmar et al., 2013).

Boat-based line-transect surveys were conducted in inner and outer Far North waters to address the lack of data on both bottlenose dolphin ecotypes and to identify possible ecotype spatial overlap. Further to this, concerns over the local decline of the coastal bottlenose dolphin in the Bay of Islands necessitated a stratified design to provide a thorough assessment of surrounding areas (Peters & Stockin, 2016; Tezanos-Pinto et al., 2013). The aim was to describe density, spatial use and distribution overlap of bottlenose dolphins in Far North waters and provide information on previously unstudied regions, including Whangaroa Harbour, Cavalli Islands, Doubtless Bay, and wider survey (described in Chapter 1, section 1.3). The specific chapter objectives were to:

- 1) Present the first geographic distribution and density patterns of bottlenose dolphin ecotypes occurring in both inner and outer Far North waters;
- 2) Describe bottlenose dolphin density and abundance as a function of season, stratum, and ecotype in Far North waters; and
- 3) Define the spatial overlap of the coastal and oceanic bottlenose dolphin in Far North waters.

2.2 Materials and methods

2.2.1 Survey methods

Line transect surveys were conducted in Far North waters (Figure 2.1) year-round from March 2013 to September 2015, between sunrise and sunset. Lines were grouped into 4 coastal strata

(Whangaroa Harbour, Cavalli Islands, Doubtless Bay, Bay of Islands) and 1 open ocean stratum (wider survey). Taking into account shoreline complexity and navigation hazards, parallel transects were established, spaced 500 m apart for sheltered areas and 5 km apart for open areas (Buckland et al., 2001; Ronconi & Burger, 2009). The systematic line transects evenly covered Far North waters and were delimited by the 5 and 150 m (seaward boundary) depth contours (as per Ronconi & Burger, 2009). All transects were orientated perpendicular to shore (Buckland et al., 2016). Transect coverage was dependent on available good weather days per month, thus regular interval coverage was not achievable, though all transects were covered each month over the sampling period.

Data were collected from Research vessel *Te Epiwhania*, a 5.5 m Stabicraft with a 100 hp four-stroke engine (Appendix 2.1). Owing to the eye height of *Te Epiwhania* (1.5 – 2 m above the water surface) surveys were conducted in good weather conditions (Beaufort Sea State (BSS) ≤ 3) and in good visibility (≥ 1 km) (as per Dwyer et al., 2016). Surveys were discontinued in precipitation or fog, or if the BSS exceeded the acceptable limit. Survey transects were selected at the beginning of the day dependent on weather/sea conditions and the already completed survey effort in each zone within that month (the aim being to cover most areas, where possible, within any given month, Figure 2.1, as per Dwyer et al., 2016). Travel direction was based on sea conditions and wind direction, with vessel speed maintained at approximately 13 knots (knts) in accordance with published methods (Barlow, 2006; Cañadas & Hammond, 2008; Dwyer et al., 2016).

At the onset of each survey, start time on the water, unique observer number, observer assignments, tides, and environmental conditions (e.g., visibility, swell height and BSS) were recorded (as per Ronconi & Burger, 2009). The vessel was then operated at survey speed and *on effort* survey mode commenced. Subsequently, variables were logged at 15 min intervals: BSS, swell height, observer field of view, and glare (De Boer et al., 2008). Observational and environmental data were collected using an Acer Iconia B1 tablet computer with associated Garmin GLO GPS device. CyberTracker (CyberTracker Conservation, Version 3.296+) software was programmed to record continuous GPS tracks (with recordings every 30s).

Paired observers surveyed from the bow. Each observer scanned an allocated vessel side from directly ahead to 90° abeam (Mack et al., 2002). During *on effort* survey mode, dolphins were detected by naked eye and confirmed by binoculars. Once detected data were collected by the lead observer following distance sampling protocols. This included recording group radial

distance from the transect line (at detection), angle of sighting and group size (Buckland et al., 2001; Ronconi & Burger, 2009). The recommended methodology of reticules (Bushnell Marine 7x50 Waterproof Binoculars with Digital Compass) from horizon or alternate fixed point (if horizon is not visible) and angle were employed (Buckland et al., 2001; Dick & Hines, 2011; Ronconi & Burger, 2009).

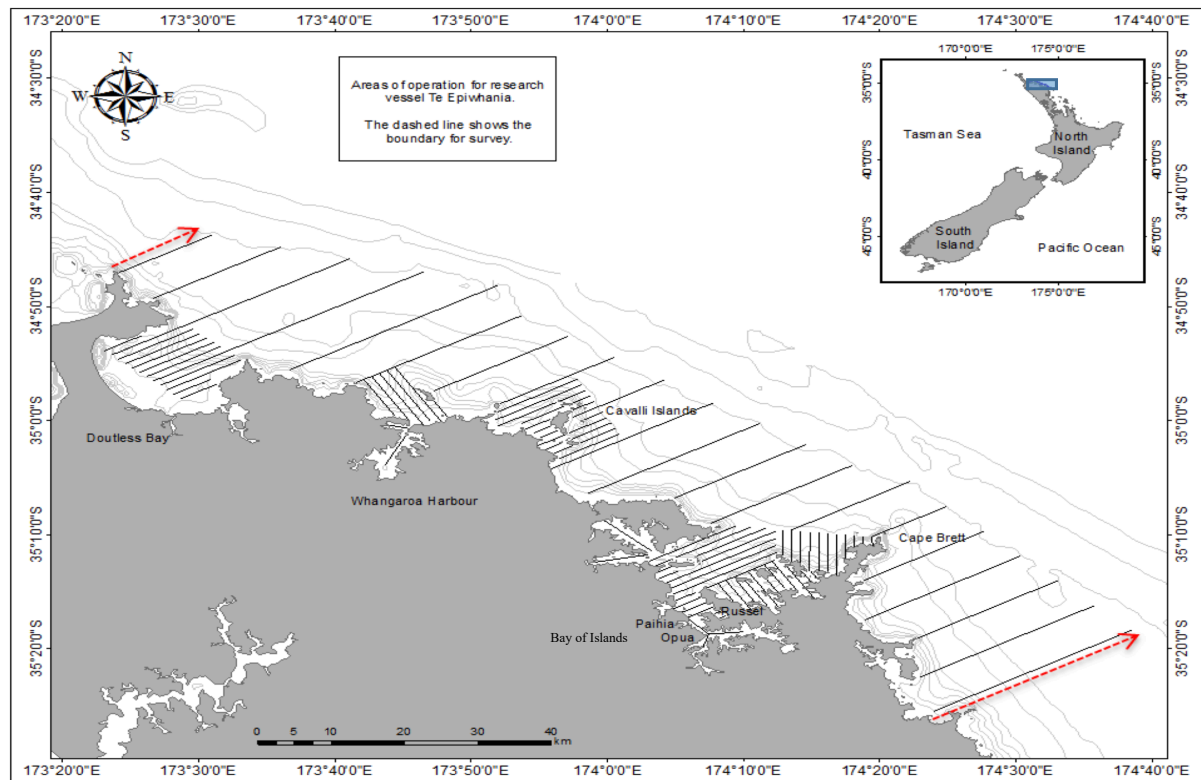


Figure 2.1: Designated systematic survey design utilised March 2013 – September 2015, in Far North waters, New Zealand.

Observers were trained in the use of the binoculars, however only the lead observer took measurements to minimise inter-observer error. To allow the rapid transfer of a sighting to the lead observer, other observers underwent distance estimation training. This was achieved with a stern buoy line with three buoy markers spaced at 10m, 25m, and 50 m behind the research vessel (Ronconi & Burger, 2009). This test was utilised for the first two weeks of each season, or until observers could estimate distance to $\pm 10\text{m}$, and was used again periodically at least twice per month. To prevent fatigue, observers rotated their positions every hour or at each *on effort* survey point. Standard sighting cues, including splashing, fins breaking surface waters, vessel behaviour, and the presence of birds were used to detect dolphin groups (Constantine et al., 2004; Lusseau et al., 2003). CHP remained consistent across all years and was the primary observer.

Once a group was located, all observers were focused on data collection pertaining to the focal group encountered (Mann, 1999). As such, no further *on effort* survey mode was initiated as no search effort was undertaken for new groups during this time. In line with the Marine Mammal Protection Regulations (1992) Part 3, which follow Section 28 of New Zealand's Marine Mammals Protection Act (1978), the research vessel was operated to minimise disturbance to natural behaviour of any marine mammal. This was achieved by manoeuvring at a constant idle or *no wake* speed, within 300 m of any marine mammal, so that no animal was separated from the focal group (e.g., Dwyer et al., 2016; Stockin et al., 2008).

During an encounter, abiotic parameters, including water depth ($\pm 0.1\text{m}$), SST (sea surface temperature) ($\pm 0.1^\circ\text{C}$), and BSS were recorded using an on-board depth sounder, a hand-held digital thermometer, and visual observations, respectively (e.g., Stockin et al., 2009). Biotic parameters pertaining to group size, composition, behaviour, and associated species were logged respective to time and GPS coordinates (as above). Species and ecotype were confirmed at the onset of data collection. External morphological separation of the 2 ecotypes was deemed an appropriate criterion for classification (Visser et al., 2010; Zaeschmar, 2014). Oceanic bottlenose dolphins are described as comparatively more robust and with extensive scarring in most cases, with most scarring presumed to be cookie cutter shark (*Isistius* spp.) bite scarring (Constantine, 2002; Dwyer & Visser, 2011). In contrast, coastal bottlenose dolphin do not usually exhibit cookie cutter shark scarring (Constantine, 2002) and are smaller in body size, with paler colouration.

Dolphins were considered as being in a group when individuals (of any number) were recorded as in apparent association, with the same direction of movement and < 5 body length apart (Constantine, 2002; Constantine et al., 2004; Shane, 1990). For this study, when dealing with groups larger than 40 individuals, focal-sub groups were sampled. The groups size collected for each sub-group was preferentially used to calculate total encounter group size if required. Subsequent groups were considered independent if separated by > 5 km or sighted > 30 min after the previous sighting, to minimise resampling (as per Dwyer et al., 2016; Stockin et al., 2009). Where possible, additional confirmation was provided via photo-identification of individual bottlenose dolphins, conducted using a Nikon D90 camera fitted with a AF-S VR ZOOM-NIKKOR 70 – 300MM F4 – 5.6G IF-ED lens (e.g., Dwyer et al., 2016).

Group sizes were logged according to three categories: the absolute *minimum* number of dolphins counted (further validated with the minimum dolphins identified through photo-

identification), the absolute *maximum* number of individuals believed to be in the group (cross validated with other higher platforms where possible) and the *best estimate* for the group size (Dwyer et al., 2016). When estimating group size two separate sampling occasions were utilised: 1) from the trackline at first sighting systematically scanning the group from one side to the other and 2) on approach to count the individuals (and where applicable sub-groups). All observers provided an estimate of group size and a consensus estimate for ‘best’ group size was used (as per Flach et al., 2008). For analytical purposes, group composition was dependent on the occurrence or nonexistence of immature individuals (i.e. adult only, adults with juveniles, adults and/or juveniles with calf/neonate groups). Group size estimates were further defined into two larger categories of mixed (any combination of adults accompanied by juveniles and/or calves and/or neonates) and adult only groups (Appendix 2.2).

Behaviour was included as a factor which could affect detectability. To determine the predominant behavioural state of the focal group, a left-to-right scan of all individuals was completed. This method reduced potential bias towards conspicuous individuals/behaviours and included the entire group (as recommended by Mann, 1999). Predominant behaviour protocol assumes the behaviour observed at the surface is representative of the behaviour occurring under the surface (Baird & Dill, 1996). States were created to be “mutually exclusive and cumulatively inclusive” of the behavioural budget of dolphins (Pirotta et al., 2014, p. 51). Behavioural states’ definitions are based on previous studies to maintain consistency (Appendix 2.2). To minimise the potential bias when group members do not all behave in a uniform manner, the 50 % rule was applied (Lusseau, 2003). When > 50 % of individuals were displaying a behavioural state category this was selected (as per Dyer et al., 2016). Additionally all recordable behaviours were documented if an equal section of the focal group were observed displaying alternate behaviours (Stockin et al., 2009; e.g., Dwyer et al., 2014b).

Following the completion of observational data collection, the research vessel navigated to the original track line, returning to *on effort* survey mode to search for further independent groups. Identical protocols were applied over consecutive months and years.

2.2.2 Data analysis

A multi-scale approach was applied to all analyses. The latest tools, techniques, and analytical methods utilised three distinctive processes to test for density, distribution and spatial overlap between ecotypes in Far North waters. First, detection functions were investigated for each

ecotype. Second, density and abundance were estimated by incorporating modelled covariates which affect detection function. This was done at a global and *stratum* level (Bay of Islands, Cavalli Islands, Whangaroa Harbour, Doubtless Bay and wider survey) for each ecotype. Finally, spatial concordance across all encounters was quantified using kernel utilisation distribution of core and representative ranges at the global level for each ecotype.

2.2.2.1 Removal of data deficient and temporally correlated sightings prior to analysis

Austral seasons used were summer (December, January, February), autumn (March, April, May), winter (June, July, August) and spring (September, October, November). Diurnal categories were created to account for the varying length of daylight across the year and biological relevance. To that effect, time was calculated as an index of day light hours (as per Lundquist et al., 2012). The time between a data point and sunrise was divided by daylight length (time of sunset – time of sunrise) to create a percentile of total daylight hours. Each data point clustered into morning (< 0.33), midday ($0.33 - 0.66$), or afternoon (> 0.66) (as per Lundquist et al., 2012). After categorisation any temporally correlated (i.e., same day) sightings were removed. Additionally data verification removed data-deficient sightings (e.g., no angle, distance not measured and uncertainty regarding species sighted) prior to analysis.

2.2.2.2 Data analysis for distance sampling

All transect and sighting data were exported from a CyberTracker (version 2.356+, CyberTracker Conservation, 2013) database to Microsoft Excel and CSV spreadsheets. Only *on effort* sightings were included in the data analysis. Methods followed Buckland et al. (2001) and Ronconi & Burger (2009). Key equations required to understand this study are provided in the following sections (see also Buckland et al., 2001 for comprehensive distance-sampling theory and equations). A fundamental equation is presented in order to allow the interpretation of results (complete distance-sampling equations can be found in Buckland et al., 2001). DISTANCE software was not employed in the estimation of overall density or abundance as a result of the non-standard stratification survey design, replaced instead by free statistical software R (R Core Development Team, 2014, RStudio for Mac version 1.0.136).

2.2.2.2.1 Detection function analysis for density and variance estimation

Data analysis included model selection, detection function analysis, multi-covariate distance sampling and inference. Overall, analysis followed Marques & Buckland (2003), which

extends the approach of the ‘key + series adjustment’ methodology (Buckland, 1992). For the oceanic bottlenose dolphin it was predicted that detection function would be qualitatively different for mixed groups (oceanic bottlenose dolphin and pilot whales (*Globicephala* sp.)) vs. single species groups, so DFs were fitted stratified by mixed or single species. The estimated mean density of each year was computed from the effort-weighted mean of the year-specific estimates (as per Williams & Thomas, 2007). Global mean density in the region was computed from the area-weighted average of *stratum* estimates. The delta method was applied to compute variances and t-based, log-normal, two-sided and 95 % confidence limits (equations 3.72 – 3.76 of Buckland et al., 2001; Williams & Thomas, 2007). The analysis of each ecotypes’ data began by accounting for the need to truncate the largest distances, as no sighting selection or truncation was undertaken during data collection. The minimal truncation required to the minimum possible series expansion terms were fitted and then rounded to the nearest 100m (as per Williams & Thomas, 2007).

Detection function analysis was completed prior to multi-covariate distance sampling (MCDS). The models (and series expansion terms) explored for detection function of each ecotype were: half-normal (cosine or hermite-polynomial) and hazard-rate models (cosine or simple-polynomial). Model fit (covariate explanatory power) and ranking was investigated with: (1) AIC_c , Akaike’s information criterion with correction for small sample size; (2) ΔAIC_c , the difference in AIC_c of a fitted model and the smallest AIC_c of any model; and (3) *wgt*, the AIC_c weight, indicates the best model from the models investigated (Burnham & Anderson, 2002; Forcada et al., 2004; Ronconi & Burger, 2009; Williams & Thomas, 2007).

2.2.2.2.2 Multi-covariate distance sampling models of estimated abundance

In standard line-transect sampling, an assumption is made the detection probability of a focal species $g(y)$ is solely a function of the sighting distance, y , from the transect line, and heterogeneity in the detection probabilities due to covariates other than distance is ignored. In this study, regardless of the volume of data collected and in common with most surveys conducted on vessels, substantial heterogeneity in probability of detection (beyond that explained by distance from the transect line) is present. Additionally, it is beneficial to model variables other than distance due to the likelihood that density is correlated with detection probability. Furthermore, detection probability changes across strata but inadequate detections in some strata may necessitate a global detection function. The potential to reduce bias in relative abundance indices by modelling covariates therefore exists (Marques, 2001; Marques

& Buckland, 2003; Buckland et al., 2004).

R distance analysis permits several key functions plus series expansion terms to be included when modelling the detection function (Ronconi & Burger, 2009). Bias in *stratum*-specific estimates due to heterogeneity can be eliminated by building on the global detection function model separately by *stratum*. Further to this, $g(y)$, and thus detection, can be modelled as a function of covariates. Both strategies were employed in this study for the coastal bottlenose dolphin. For the oceanic bottlenose dolphin, given the lack of sightings outside of the wider survey *stratum*, only global data were tested with no stratification. These were added individually to the top-ranked global detection function model. The top three ranking covariates for each model were then considered concurrently and added to the base global model.

Including covariates in a detection function necessitates the estimation of 1) the joint density of y and 2) further explanatory covariates \underline{z} (Buckland et al., 2004). Here the y and z are assumed independent of one another (as a result of random line placement), and therefore the equation is factorised as (Buckland et al., 2004):

$$\mathcal{L}_{y,z}(\underline{\theta}) = \mathcal{L}_z(\underline{\theta})\mathcal{L}_{y|z}(\underline{\theta}) = \left[\prod_{i=1}^n \frac{P_a(\underline{z}_i)\pi(\underline{z}_i)}{P_a} \right] = \left[\prod_{i=1}^n \frac{g(y_i, \underline{z}_i)\pi(y_i|\underline{z}_i)}{P_a(\underline{z}_i)} \right], \quad (1)$$

where $\pi(y|\underline{z})$ is the conditional probability density function of y given \underline{z} , and

$$P_a(\underline{z}_i) = \int_0^w g(y, \underline{z}_i) \pi(y|\underline{z}_i) dy. \quad (2)$$

Given ecotype independence of y and \underline{z} , then $\pi(y|\underline{z}_i) = \pi(y)$ and $\mathcal{L}_{y|z}(\underline{\theta})$ involves only the probability density function of y which can be assumed as known, as per with conventional distance sampling. In this case, the detection function parameter vector θ and $g(y,z)$ can be estimated from $\mathcal{L}_{y|z}(\underline{\theta})$ with no additional assumptions about the distribution of z .

2.2.2.2.3 Overall and seasonal estimation of density and abundance

Maximum likelihood estimation of N with a Horvitz-Thompson-like estimator, using $P_a(\underline{z}_i)$ is used in the inclusion probability. Assuming coverage probability P_c is constant, the abundance estimator is:

$$\hat{N} = \frac{1}{P_c} \sum_{i=1}^n \frac{1}{\hat{P}_a(\underline{z}_i)}, \quad (3)$$

where $\hat{P}_a(\underline{z}_i)$ is found by evaluating equation (2) using the estimated detection function parameter vector $\hat{\underline{\theta}}$.

When animals are detected in groups, and n groups are detected, equation (3) estimates group abundance. Individual abundance was estimated by multiplying this \hat{N} by estimated mean group size for the ecotype and stratum, $\hat{E}[s]$.

An unbiased estimate of ecotype mean group size was calculated using the Distance software default method. This was done using the group size natural logarithm, $\ln(s)$, regressed on the group distance from the transect line when sighted. The predicted $\ln(s)$ value on the transect line was subsequently back-transformed to provide the required estimate (following Williams & Thomas, 2007). Group-size bias was tested, following Ronconi & Burger, 2009, by examining correlations of group size with y , $g(x)$, for a range of truncation distances. When group-size bias was identified, regression methodology determined unbiased group size estimates for density calculations. This was utilised in subsequent analyses (following Buckland et al., 2001; Ronconi & Burger 2009).

MCDS conducted for both ecotypes tested for the effects of: *time of day* (daylight quartile), *year* (2013 – 14/2014 – 15), *season* (spring, summer, autumn, winter), *stratum* (Bay of Islands, Cavalli Islands, Whangaroa Harbour, Doubtless Bay, Global), *observer* (unique ID), *depth* (water depth, m), *sea state* (BSS 0-1, 2-3), *group size*, *initial behaviour* (forage, mill, rest, social, travel, dive), *sighting cue* (splashing, fins breaking surface waters, vessel behaviour and presence of birds), *distance from shore* (km), and *group type* (coastal bottlenose dolphin, oceanic bottlenose dolphin only, mixed) on the estimation of each ecotype's detection function. On a broad scale, *group size* was classified as ≤ 20 or > 20 animals for bottlenose dolphins. Fine scale analysis classified dolphin group size into nine categories. For both ecotypes (focal and sub-groups) this was 1 – 5, 6 – 10, 11 – 15, 16 – 20, 21 – 25, 26 – 30, 31 – 35, 36 – 40 and > 40 . *Year* was considered at two levels (2013 – 14 / 2014 – 15), to provide two comparable variables and reduce bias created from categorising the data. One observer was excluded (Observer 2) because $n < 5$ observations.

When evaluating the relative importance of covariates, automatic selection of adjustment terms is not appropriate, therefore models were manually manipulated to allow no adjustment terms (Buckland et al., 2016; DISTANCE User's Manual, p. 119, 2015). Moreover, the inclusion of

covariates in MCDS will change the shape of the detection function at different values of the covariate, therefore a scale parameter was utilised to preserve the detection function shape while allowing the scaling to change for each covariate (DISTANCE User's Manual p. 117, 2015). A set of competing models, which included perpendicular distances (x) and all possible combinations of additional covariates (up to 3), were tested (Forcada et al., 2004). Once covariates were included density and abundance estimates were calculated with area weighted averages and the delta method (as per section 2.2.2.2.1).

2.2.2.2.4 Spatial distribution

The spatial modelling (density surface modelling) of line transect data to estimate abundance was introduced by Hedley et al. (1999). This was expanded by Hedley & Buckland (2004) and MacKenzie & Clement (2014a & b). Separate density surface models were generated to estimate the seasonal distribution of bottlenose dolphin per *stratum* and globally. For each season, the top-ranked detection function model (full dataset) was used to develop the density surface models. Covariates in the density surface models included location (easting and northing), depth and distance from shore. Analyses were performed with statistical software R, utilising bespoke coding and R package dsm (v.2.2.13).

Transect lines were segmented (into sections ~1 km long × ~1 km wide) using ArcGIS 10.0. A 1 x 1 km cell prediction grid was utilised to acquire the easting and northing coordinates (exact segment's centroid) and distance from shore (MacKenzie & Clement, 2014a). A cell was *stratum*-associated if its centroid fell within the predefined *stratum* boundaries. Bespoke code and dsm package (v.2.2.13) were utilised in free statistical software R (R Core Development Team, 2014, RStudio for Mac version 1.0.136). Dolphin abundance within each segment was estimated based upon the number of dolphins (groups and individuals), the estimated detection function and estimates of global availability (following Buckland et al., 2004; MacKenzie & Clement, 2014a; MacKenzie & Clement, 2014; 2016). Thus calculated as:

$$\hat{N}_i = \sum_{j=i}^{n_i} \frac{S_{ij}}{E(p.(S_{ij}))} \quad (4)$$

Where \hat{N}_i is estimated abundance for segment i, n_i is the number of groups detected in the segment, S_{ij} is the number of individuals in the j th group within the segment and $E(p.(s_{ij}))$ is the expected detection probability of a size S_{ij} group.

A generalised additive model (GAM) modelled the abundance estimate (including covariates) for each segment (the bivariate spline term utilised was the coordinates for each segment following MacKenzie & Clement (2014)). Standard errors were acquired for detection function and density surface models using a parametric bootstrap (100 repetitions was deemed appropriate and accommodated detection function and density surface models uncertainty as per Manly, 2006). No simplification attempts were undertaken on the GAM results, i.e., removal of covariates which had minimal effect on the prediction surface. Implementation followed methods described in MacKenzie & Clement (2014):

1. Fit a density surface models of available groups
2. Determine group locations through a random Poisson point process, with intensity provided by the density surface models from step 1.
3. Produce group-size frequency estimates and tables.
4. Generate detection estimates (using detection function) from the bootstrapped dataset.
5. Estimate *stratum* specific availability by selecting a random logit-normal distribution value.
6. Integrate estimates from step 3-5 to refit the density surface models to generate a predicted density surface (individual level).
7. Sufficiently repeat steps 1-5. GAM bootstrapped density surface models standard deviation was utilised in the estimation of standard errors for corresponding quantities in the real data.

Relative densities are expressed in maps of the density surface models. The estimated cell and/or stratum density is relative to the global density. This approach identified higher or lower locations of relative density that are “robust to the magnitude of absolute abundance estimates” (MacKenzie & Clement, 2014, p. 24):

$$\frac{\hat{N}_k/A_k}{\hat{N}/A} \quad (5)$$

Areas with values over 1 suggest the associated densities are higher than the global average. Additionally, relative density can translate as the fraction of the Far North waters population within a grid cell, k , relative to the proportion Far North waters covered, A , inside that grid cell, A_k , i.e. (MacKenzie & Clement, 2014):

$$\frac{\hat{N}_k/\hat{N}}{A_k/A} \quad (6)$$

2.2.2.4 Concordance in space use

A probability density function, the utilisation distribution, is used to describe bottlenose dolphin ecotypes relative use of space within Far North waters, founded on group locations (Van Winkle, 1975). To produce a coastal bottlenose dolphin and oceanic bottlenose dolphin utilisation distribution estimate, all grid cell point density (as per section 2.1.2.2.3.5.) was developed (Parra, 2006). Additionally, the ArcView-Animal Movement Analyst extension was employed to estimate a ecotype specific fixed kernel utilisation distribution (as per Parra, 2006). Kernel utilisation distribution ranges were calculated at 50 % (core area) and 95 % (representative range) occurrence probability due to their robustness (as per Parra, 2006; Worton, 1989). This was achieved utilising smoothing parameters obtained through the least squares cross-validation procedure (following Parra, 2006; Seaman et al., 1999). Density surface model estimates are calculated at the group level (considering the number of groups and individual numbers within the group), therefore, utilisation distributions were calculated for coastal bottlenose dolphin and oceanic bottlenose dolphin using the locations of groups rather than individual animals. Methods were similar to Ingram & Rogan (2002), Parra (2006), and Wilson et al. (1997), applying ‘Design I’ of Thomas & Taylor (1990). ‘Design I’ was chosen as ecotype level estimates are created.

Due to the data being restricted to part of the Far North waters, and group density utilised for analysis, all kernel ranges were at the group level for the area surveyed. To quantify shared space of coastal bottlenose dolphin and oceanic bottlenose dolphin, the area overlap (PAO, %) between the 95 % kernel range of both ecotypes were generated as (following Atwood & Weeks, 2003; Parra, 2006 and modified after Cagnazzi, 2010):

$$PAO = \left(\frac{A_{Oh,Sc}}{A_{Oh}} \times \frac{A_{Oh,Sc}}{A_{Sc}} \right)^{0.5}, \quad (7)$$

where $A_{Oh,Sc}$ is the area of ecotype overlap. The 95% kernel range area is A_{Oh} for coastal bottlenose dolphin and A_{Sc} for oceanic bottlenose dolphin. Through this analysis an initial estimate of spatial distribution and overlap by ecotypes. The probability of using areas of overlap (utilisation distribution) is not yet considered. For example, range could overlap by 50 % but comprise the least used areas for both ecotypes. Shared/overlapping areas could otherwise be utilised heavily by coastal bottlenose dolphins and less oceanic bottlenose dolphins, or vice versa. This needed to be accommodated and spatial concordance (i.e., use of spaces) quantified. To this end, correlation (Spearman’s coefficient of rank correlation, r_s) of

utilisation distributions pairs of coastal bottlenose dolphin and oceanic bottlenose dolphin groups from all grid cells was examined (Parra, 2006). Grids where ecotypes have a matching utilisation distribution will result in $r_s = 1$ and grids with full discordance between ecotypes will produce $r_s = -1$ (Doncaster, 1990).

2.3 Results

2.3.1 Data for distance sampling

2.3.1.1 Realised survey effort

On effort transects covered a total of 36,728 km between March 2013 and September 2015 (Figure 2.2, Table 2.1). Survey effort covered 100 % of planned survey in Cavalli Islands (*Stratum* 2), Whangaroa Harbour (*Stratum* 3), and Doubtless Bay (*Stratum* 4). In Bay of Islands (*Stratum* 1), 98 % of planned effort was realised due to oyster (*Crassostrea Gigas*) farms preventing access to two planned lines. Owing to distance of travel from port and fuel availability, extrema transects were eliminated in wider survey (*Stratum* 5) resulting in 93 % planned effort realised. Surveys were conducted in Far North waters in all months of the study period. Survey effort was not consistent across all years, but all areas were covered each season (Figure 2.2).

Table 2.1: Annual survey area and effort in Far North waters, New Zealand March 2013 – September 2015. Stratum 1 = Bay of Islands, Stratum 2 = Cavalli Islands, Stratum 3 = Whangaroa Harbour, Stratum 4 = Doubtless Bay and Stratum 5 = wider survey, Tran = transect.

Stratum	Year	Total area (km ²)	Tran #	Tran repeated all seasons	Total tran length (no duplication, km)	Total tran length (duplication, km)
1	2013	241	58	Y	240	4,456
	2014			Y		4,453
	2015			Y		4,457
2	2013	152	22	Y	125	1,579
	2014			Y		1,580
	2015			Y		1,579
3	2013	64	8	Y	58	698
	2014			Y		699
	2015			Y		691
4	2013	135	21	Y	132	1,594
	2014			Y		1,596
	2015			Y		1,596
5	2013	2,071	18	Y	309	3,983
	2014			Y		3,887
	2015			Y		3,880
Total	N/A	2,663	127	N/A	864	36,728

Chapter 2 – Density, abundance and distribution of parapatric common bottlenose dolphin
(*Tursiops truncatus*) ecotypes in Far North waters, New Zealand

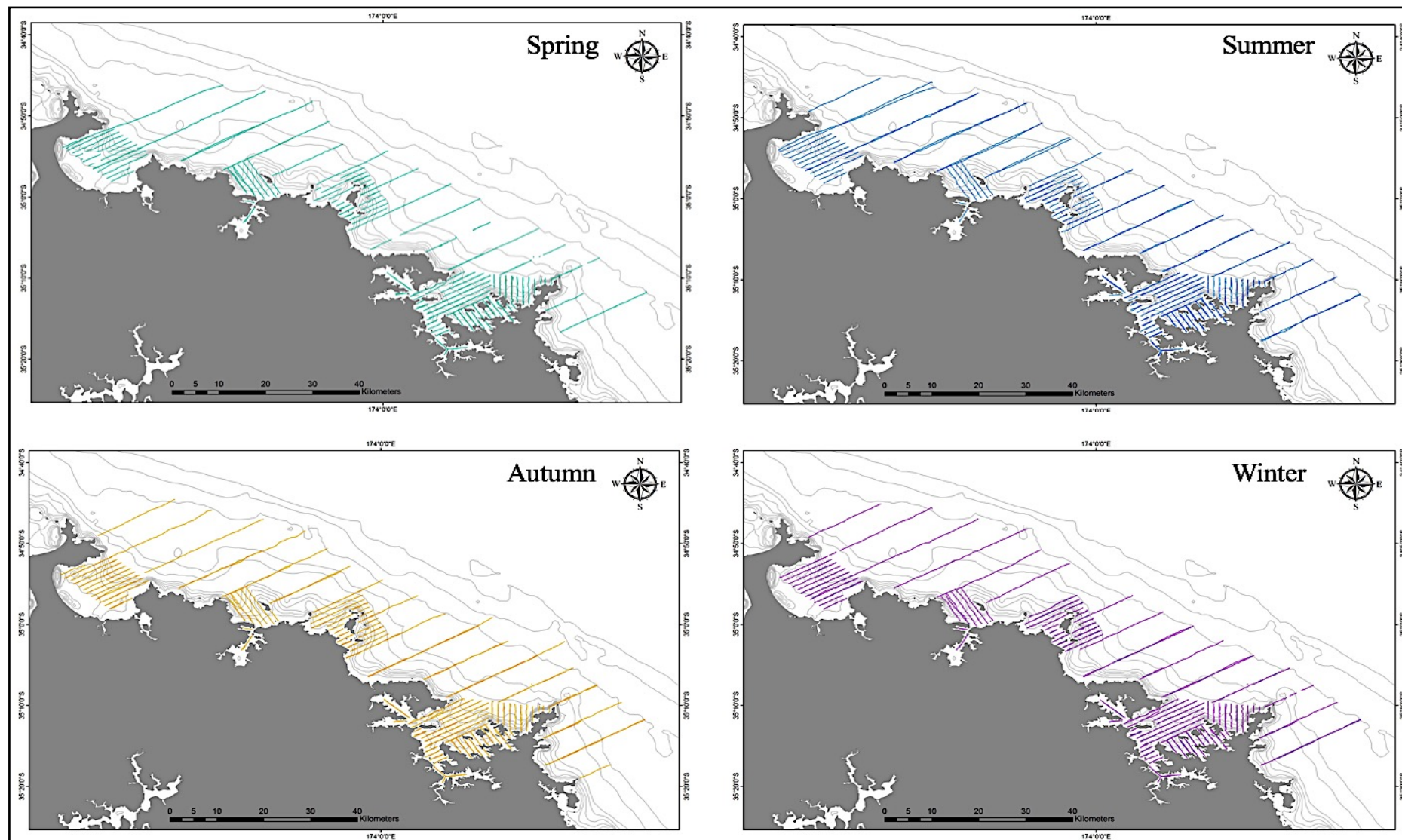


Figure 2.2: Seasonal search effort in Far North waters, New Zealand March 2013 – September 2015. Coloured lines illustrate realised on-effort vessel survey per austral season. Bathymetry is represented with pale grey lines, data courtesy of NIWA.

Overall, summer received the most survey effort (26.3 % of survey days) (Table 2.2). An additional 16,122 km of *off effort* tracks were driven in the Far North waters region. This consists of an amalgamation of group observations duration, collecting photo-identification, and transitioning to/from transects and launch point (Opua/Waitangi bridge boat ramp, shown in Figure 2.1).

Table 2.2: Seasonal survey effort in each stratum in Far North waters, New Zealand March 2013 – September 2015. Stratum 1 = Bay of Islands, Stratum 2 = Cavalli Islands, Stratum 3 = Whangaroa Harbour, Stratum 4 = Doubtless Bay and Stratum 5 = wider survey.

	Summer	Autumn	Winter	Spring	Total
Survey days	64	59	62	58	243
Km on effort Stratum 1	3,356	3,337	3,327	3,346	13,366
Km on effort Stratum 2	1,191	1,185	1,168	1,194	4,738
Km on effort Stratum 3	542	502	503	541	2,088
Km on effort Stratum 4	1,238	1,157	1,188	1,203	4,786
Km on effort Stratum 5	3,006	2,889	2,902	2,953	11,750
Km on effort Total	9,333	9,070	9,088	9,237	36,728

Both oceanic bottlenose dolphins and coastal bottlenose dolphins were recorded during *on effort* survey, resulting in a total of 372 bottlenose dolphin groups detected, 90.3 % of which were coastal bottlenose dolphin (n = 336). Each ecotype was treated separately in the distance sampling analysis. An additional 2,021 coastal bottlenose dolphin groups (1722 in Bay of Islands) and 4 oceanic bottlenose dolphin groups were recorded during *off effort* survey, these sightings were not included in the subsequent analysis. Varied sampling effort is accounted for in the distance sampling analysis.

2.3.1.2 Dolphin sightings

A total of 228 groups of coastal bottlenose dolphin, 15 oceanic bottlenose dolphin and an additional 21 mixed groups (32 subgroups on 16 independent days, Appendix 1.1, Figure 2.3) *on effort* encounters were included in the survey analysis (following removal of data see 2.2.2.1., Figure 2.3, Table 2.3). The sample size for both ecotypes exceeded the suggested minimum of 30 detections from publications for abundance estimation (though an ideal would be 60-80 detections, Buckland et al., 2001). Coastal bottlenose dolphins were detected as far as ~1700 m from the transect line, with 50 % and 95 % recorded inside ~150 m and ~600 m, respectively. Oceanic bottlenose dolphins were predominantly observed in wider survey, but also once in the Bay of Islands (Figure 2.3). Oceanic bottlenose dolphins were detected as far as 1900 m from the transect line, with 50 % and 95 % recorded inside ~230 m and ~870 m, respectively. Mixed groups were most frequently recorded in wider survey, but also twice in

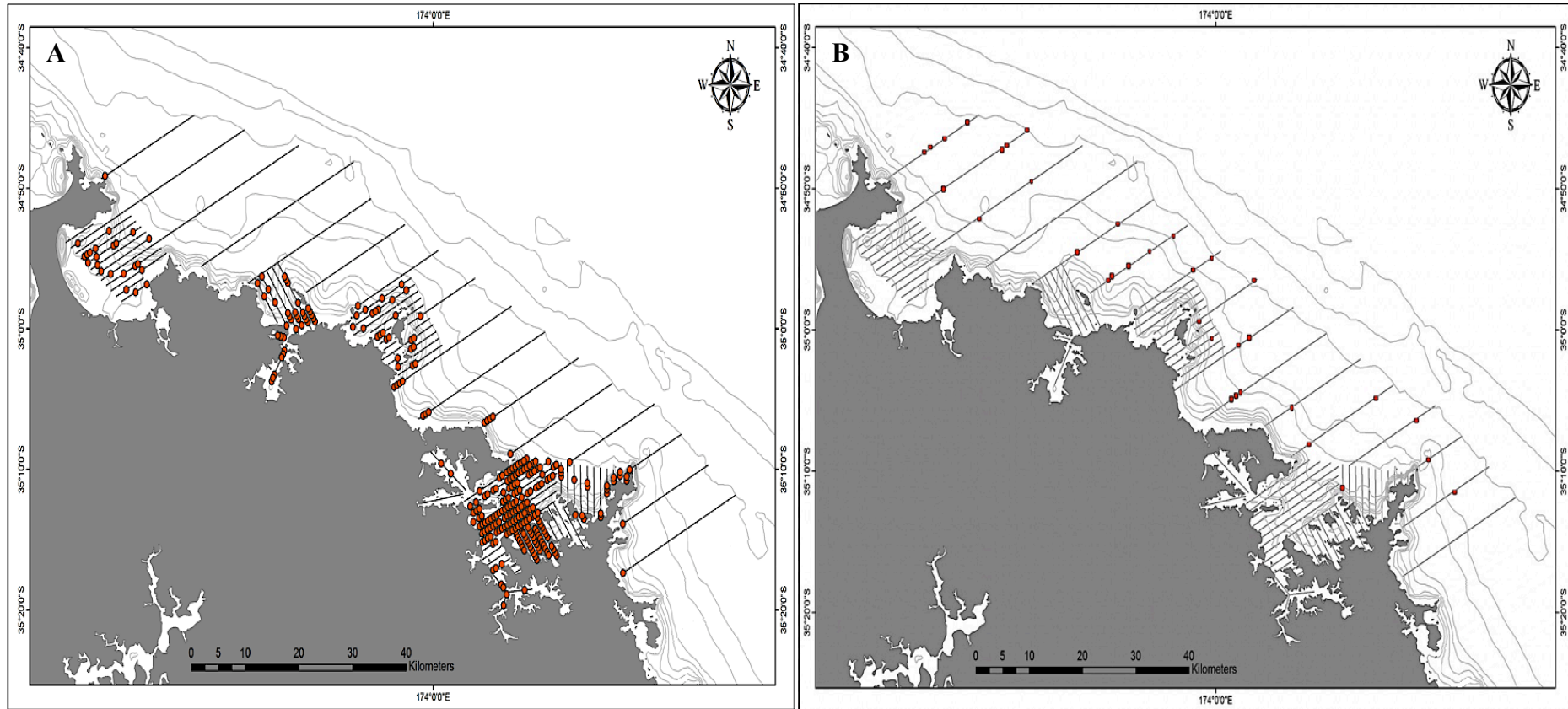


Figure 2.3: The location of *on effort* A) coastal bottlenose dolphin and B) oceanic bottlenose dolphin sightings (*T. truncatus*) and transects driven March 2013 – September 2015, in Far North waters, New Zealand. One orange circle represents a single group sighting. Black lines symbolise survey lines. Bathymetry is represented with pale grey lines, in increments of 5, 10, 20, 30, 40, 50, 100, 150, 200 and 250m, data courtesy of NIWA.

Cavalli Islands (Figure 2.3). Mixed groups were recorded up to 2020 m from the transect line, with 50 % and 95 % of groups within ~380 m and ~990 m, respectively. Note, sightings furthest from the transect line occurred as a result of conspicuous sighting cues, i.e., vessel, jumps, or birds. Seasonal trends in occurrence were seen in raw data, with sightings only occurring in autumn (77.8 %, n = 28) and summer (22.2 %, n = 8).

2.3.1.3 Removal of data deficient and temporally correlated sightings prior to analysis

A number of bottlenose dolphin sightings were removed as a result of data verification before density, abundance, and distribution were calculated (Table 2.3).

Table 2.3: The group sightings of common bottlenose dolphin utilised in full analyses from a dataset collected March 2013 – September 2015, in Far North waters, New Zealand. Brackets illustrate the percentage of raw group sightings the verification step denotes. Key: Stratum 1 = Bay of Islands, Stratum 2 = Cavalli Islands, Stratum 3 = Whangaroa Harbour and Stratum 4 = Doubtless Bay.

Type	Stratum	Raw sightings	Uncertain ID	Missed data	Correlated	Truncated to w (m)	Final
Coastal ecotype	Global	336	2 (0.6)	1 (0.3)	102 (30.3)	3 (1)	228
	1	223	1 (0.4)	1 (0.4)	102 (45.7)	2 (1)	117
	2	26	0	0	0	0	26
	3	39	0	0	0	1 (3)	38
	4	22	0	0	0	0	22
	5	26	1 (4)	0	0	0	25
Oceanic ecotype	Global	36	0	0	0	2 (6)	34
	1	1	0	0	0	0	1
	2	2	0	0	0	0	2
	3	0	0	0	0	0	0
	4	0	0	0	0	0	0
	5	33	0	0	0	2 (6)	31

2.3.2 Detection function analysis for density and variance estimation

The survey design was stratified (Figure 2.2), however a pooled-data detection function following global investigation was created and used to produce stratum specific estimates due to sample size. The top four detection function models (as ranked by AIC_C) for each ecotype's global dataset are presented in Table 2.4 and the data fit in Table 2.5. For coastal bottlenose dolphins the top-ranked model for global data utilised a key function with Half-normal relationships to distance and a series expansion with a cosine adjustment term. The top-ranked model for oceanic bottlenose dolphins global data utilised a key function with Half-normal relationships to distance and a series expansion with a simple polynomial adjustment term. In

both ecotypes the AIC_C weight is predominantly linked to the top two models, and less weight is carried by other models; therefore, the top model was used in subsequent MCDS.

Table 2.4: Top AIC_C-ranked models for the detection function of bottlenose dolphins (*T. truncatus*). Detection function model components; *wgt* = AIC_C model weight, *-2l* = twice the negative log-likelihood and Adj = number of adjustment terms. Note: group size effected all estimates.

Ecotype	Strata	Model	No. of parameters		AIC _C	<i>wgt</i>	<i>-2l</i>	Effective strip width (km)
			Key	Adj				
Coastal	Global	Hn + cos	1	0	0.00	0.41	354.71	0.299
		Hn + her-poly	1	0	1.09	0.23	361.54	0.291
		Hr + cos	2	0	2.32	0.08	385.02	0.280
		Hr + sim-poly	1	0	2.47	0.07	387.26	0.293
Oceanic	Global	Hr + sim-poly	1	2	0.00	0.52	260.12	0.302
		Hr + cos	2	0	2.89	0.17	281.03	0.293
		Hn + her-poly	1	0	3.02	0.03	285.54	0.291
		Hn + cos	1	0	3.47	0.02	312.91	0.294

Table 2.5: Goodness of fit tests and associated p-value of the top four ranked models on coastal and oceanic bottlenose dolphin (*T. truncatus*) data collected March 2013 – September 2015, in Far North waters, New Zealand.

Ecotype	Model Rank	Cramer-von Mises	p-value	Kolmogorov-Smirnov	p-value
Coastal	1	0.085	0.666	0.039	0.913
	2	0.061	0.658	0.041	0.537
	3	0.056	0.832	0.031	0.873
	4	0.078	0.721	0.047	0.464
Oceanic	1	0.123	0.536	0.114	0.521
	2	0.131	0.581	0.121	0.534
	3	0.129	0.532	0.118	0.573
	4	0.135	0.541	0.127	0.469

The fitted detection function (detection function) and empirical histogram indicated no systematic concerns regarding a possible lack of fit for the top global model for both ecotypes (Figure 2.4).

2.3.3 Multi-covariate distance models of estimated abundance

2.3.3.1 Group size

The expected *group size* needed to be generated to be included as a covariate (Table 2.6). Stratum specific estimates were generated as the trend in group size also varied by *stratum* for coastal bottlenose dolphin and *group type* for oceanic bottlenose dolphin.

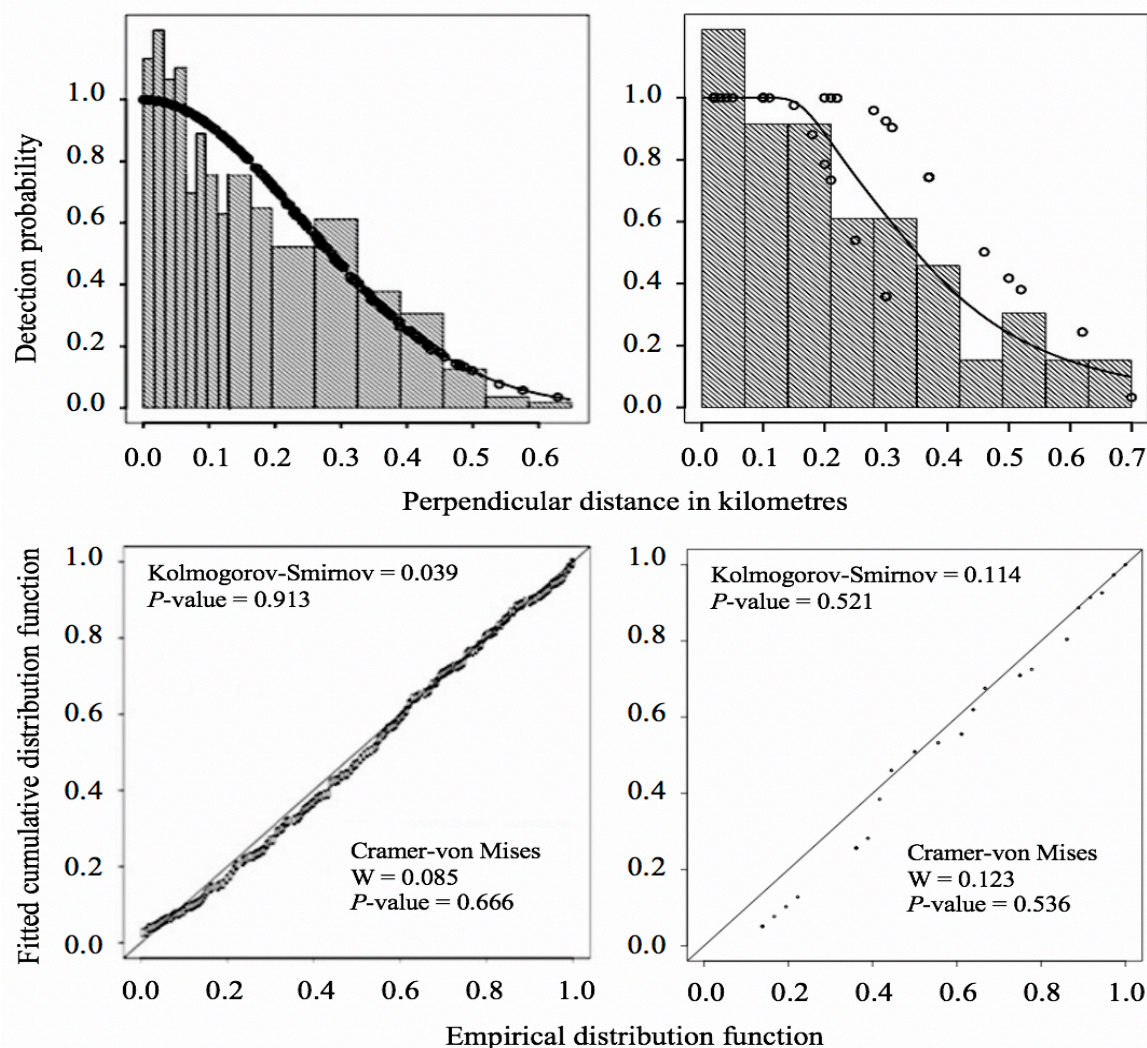


Figure 2.4: Histograms of fitted detection functions (top) and Q-Q plots (bottom) for coastal bottlenose dolphins (left) and oceanic bottlenose dolphins (right) (*T. truncatus*). In constructing the histograms, $1.5\sqrt{\text{number of detections}}$ equally spaced bins were utilised, excluding the four intervals closest to the transect which was further sub-divided into four and subsequent two intervals into two for the Bay of Islands. The first interval was sub-divided in the other stratum to clarify the detection of patterns closest to the transect line (as per Williams and Thomas 2007). The Q-Q plot presents the fitted and empirical cumulative density functions. *Note: top left, two sets of points; 1) oceanic bottlenose dolphin only and 2) oceanic bottlenose dolphin in mixed species groups with pilot whales (*G. sp.*).

Coastal bottlenose dolphin (*Tursiops truncatus*) groups ranged in size from singletons to 48 individuals (mean = 14.6 ± 3.2 standard error (SE), $n = 228$, for New Zealand comparison see appendix 2.3). *Group size* frequency distribution skewed towards smaller groups, however 57.3 % ($n = 189$) of groups contained more than 10 individuals. This provides an explanation of the difference between the mean and the mode group size. Mean *group size* between 2013 and 2015 was smaller than that reported from previous studies. Small groups (< 20 , 62 %, $n = 205$) were more commonly observed than large groups (> 20 , 38 %, $n = 125$). Groups were larger in summer and autumn than in spring and winter (Kruskal-Wallis: $H = 37.14$, $df = 3$, $P = 0.005$).

For coastal bottlenose dolphins, groups were significantly smaller in *Stratum 4* (Kruskal-Wallis: $H = 24.91$, $df = 3$, $P = 0.005$), with a mean observed group size of 9.56 ± 2.2 standard error (SE). All other *strata* had no significant variation in group size (Table 2.6).

Group sizes of oceanic bottlenose dolphins only ranged from 6 to ca. 70 (mean = 55.2 ± 18.8 standard error (SE), $n = 15$). Group sizes of mixed-species groups (both oceanic bottlenose dolphins and pilot whales, *Globicephala* sp.) ranged from 12 to ca. 350 (mean = 299.3 ± 11.6 SE, $n = 21$, Table 2.6). Group sizes for oceanic bottlenose dolphins within mixed-species sub groups (not including pilot whales) ranged from 5 to 34 (mean = 27.3 ± 7.2 SE, $n = 32$, Table 2.6). Larger groups (> 60 , 78 %, $n = 28$) were more commonly observed than smaller groups (< 60 , 22 %, $n = 8$). There was no significant seasonal (Kruskal-Wallis, $Z = 3.21$, $df. = 3$, $P = 0.483$) or annual variation in group size (Kruskal-Wallis, $Z = 4.95$, $df. = 2$, $P = 0.526$).

Table 2.6: Estimated and observed group size and percentage coefficient of variation for bottlenose dolphins (*T. truncatus*) between March 2013 – September 2015, in Far North waters, New Zealand. Additionally, the average, CV (Co-efficient of Variation) based on bootstrap and maximum observed group sizes are presented.

Ecotype	Stratum	Estimated		Observed				
		E(s)	%CV	Mean	%CV	Min	Med	Max
Coastal	Global	14.5	16.1	14.4	16.2	1	12	40
	Stratum 1	14.3	16.0	14.2	15.5	1	13	44
	Stratum 2	13.9	18.4	14.9	22.9	1	13	41
	Stratum 3	12.3	13.1	14.6	23.9	1	14	43
	Stratum 4	7.3	9.1	9.56	12.2	1	7	12
Oceanic	OBDO	56.9	60.1	55.2	68.8	6	48	70
	Mixed groups	271.2	288.6	299.3	341.6	12	159	350
	OBD Mixed groups	24.1	29.2	27.3	28.5	5	23	34

Coastal bottlenose dolphins displayed group-size bias at most truncation distances (Table 2.7). The observed bias was only eliminated for data less than 200 m from the boat. Moreover, Akaike weights showed group size as an important covariate for coastal bottlenose dolphins in all *strata*. Therefore, abundance estimates for coastal bottlenose dolphins must take group-size bias into consideration when calculating $E(s)$.

Distance vs. *group-size* correlations of oceanic bottlenose dolphins indicated high group-size bias across truncation distance bins (Table 2.7). Bias was eliminated for data < 400 m from vessel. Moreover, *wgt* showed group size as an important covariate for oceanic bottlenose dolphins. Therefore, abundance estimates for oceanic bottlenose dolphins must take group-size bias into consideration when calculating $E(s)$.

Table 2.7: Truncation effect on mean group size (GS) of bottlenose dolphins (*T. truncatus*) between March 2013 – September 2015, in Far North waters, New Zealand. Note: Pearson's r correlation tests the correlation between group size and group distance from transect line with truncation bins (as per Ronconi & Burger 2009). Note: significance of Pearson's r with Bonferroni adjustments for multiple comparisons within species: * < 0.05 and ** < 0.01 .

	Truncation distance (m)			
	800	600	400	200
Coastal bottlenose dolphin				
n	331	330	274	186
Mean GS \pm SE	15.7 \pm 0.05	14.8 \pm 0.04	14.4 \pm 0.03	14.0 \pm 0.04
Pearson's r	0.239**	0.103*	0.116*	0.041
Oceanic bottlenose dolphin				
N	15	14	10	8
Mean GS \pm SE	67.8 \pm 0.11	61.0 \pm 0.17	55.9 \pm 0.12	47.2 \pm 0.13
Pearson's r	0.248**	0.233*	0.045	0.041
Mixed groups				
N	21	15	11	10
Mean GS \pm SE	302.3 \pm 0.05	301.7 \pm 0.03	299.2 \pm 0.03	296.2 \pm 0.03
Pearson's r	0.105**	0.072	0.124	0.021

2.3.3.2 Inclusion of covariates

The top-ranked model for each ecotype from the base models, Table 2.4, Section 2.3.2, to which covariates were added (Table 2.8). Covariates included *time of day* (daylight quartile) *year* (2013 – 14/2014 – 15), *season* (spring, summer, autumn, winter), *stratum* (Bay of Islands, Cavalli Islands, Whangaroa Harbour, Doubtless Bay, Global), *observer* (unique ID), *depth* (m), *sea state* (BSS 0-1, 2-3), *group size* (best group size as per section 2.2.2.2.3), *initial behaviour* (forage, mill, rest, social, travel, dive) and *sighting cue* (splashing, fins breaking surface waters, vessel behaviour and presence of birds; Figure 2.5). Different covariates were deemed important for coastal bottlenose dolphins and oceanic bottlenose dolphins.

For coastal bottlenose dolphins no significant variation due to *time of day* or *year* (apart from in *stratum* 4) was observed. The preliminary investigation indicated a need to consider additional covariates (other than distance) in abundance estimates and that covariate effect varied by *stratum*. Similarly, no significant variation due to *time of day* or *year* was observed for oceanic bottlenose dolphins. The preliminary investigation indicated a need to consider additional covariates in density estimates. Additionally, in oceanic bottlenose dolphins akaike weights for individual covariates (Table 2.8) revealed *group type*, *group size* and *season* as the most important covariates. Whilst the supplementary covariates seem to provide some power for explaining detection variation, their inclusion did not markedly alter the Far North waters abundance estimate for oceanic bottlenose dolphins in the area surveyed.

Akaike weights for individual covariates found *stratum*, sighting cue and sea state as the most important covariates for coastal bottlenose dolphins (*Tursiops truncatus*). Although the added covariates seem to add explanatory power to the detection variation, the abundance estimated in Far North waters surveyed does not change considerably. However, when considering individual *stratum* their inclusion does alter the estimated density to varying extents, and thus they are considered further in the subsequent estimation of abundance (Table 2.9). In the Bay of Islands, vessel presence (*sighting cue*) had the most effect on detection (increased) but not for other *stratum*, though other sighting cues did. In the Cavalli islands and Whangaroa Harbour *group size* had the largest effect, whilst in Doubtless Bay initial behaviour had the largest effect.

Table 2.8: Covariate effect on bottlenose dolphin ecotypes (*T. truncatus*) detection March 2013 – September 2015, in Far North waters, New Zealand (following MacKenzie & Clement, 2014). Covariates were added independently and then in combination to the top-ranked global model from base analysis (Table 2.4). Parameters presented are the relative difference in Akaike’s Information Criterion, ΔAIC_c (ΔAIC_c), twice the negative log-likelihood ($-2l$), number of parameters (K), estimated abundance in the area covered by the survey (\hat{N}_s) and its associated standard error (SE).

Ecotype	Stratum	Model	ΔAIC_c	$-2l$	K	\hat{N}_s	SE
Coastal	Global	+ Stratum + depth + sighting cue	0.00	316.55	11	349	74
		+ Stratum	0.05	317.31	6	357	81
		+ Sighting cue	1.27	319.24	3	355	72
		+ Depth	2.66	325.90	6	359	83
		+ Observer	2.69	327.31	25	392	91
		+ Group size	2.71	328.56	12	401	79
		+ Initial behaviour	2.75	343.17	7	403	75
		Base	2.84	354.71	2	407	76
		+ Season	2.85	348.85	6	408	93
		+ Time of day	2.89	355.13	6	408	78
		+ Sea state	2.96	356.78	5	402	73
		+ Year	3.77	358.22	5	405	75
Oceanic	Global	+ Group Type + Group Size + Season	0.00	189.72	19	3634	152
		+ Group Type	0.04	197.34	5	3197	163
		+ Group Size	0.08	205.20	13	3283	168
		+ Season	0.13	222.15	7	3561	196
		+ Observer	0.83	223.04	26	3591	205
		+ Initial Behaviour	0.89	223.31	8	3029	172
		+ Sighting Cue	1.31	248.92	7	3028	203
		+Depth	2.42	248.97	7	3031	159
		+ Sea State	2.79	254.00	6	3032	138
		Base	2.91	260.12	3	3032	181
		+ Year	3.05	285.29	6	3037	193
		+ Time of Day	4.77	291.55	7	3034	162

Table 2.9: Covariate effect on coastal bottlenose dolphin (*T. truncatus*) detection in different stratum March 2013 – September 2015, in Far North waters, New Zealand (following MacKenzie & Clement, 2014). Covariates were added independently and then in combination to the top-ranked global model from base analysis (Table 2.4). Parameters presented are the relative difference in Akaike’s Information Criterion, ΔAIC_C (ΔAIC_C), twice the negative log-likelihood ($-2l$), number of parameters (K), estimated abundance in the area covered by the survey (\hat{N}_s) and its associated standard error (SE).

Stratum	Model	ΔAIC_C	$-2l$	K	\hat{N}_s	SE
1	+ Initial Behaviour + Season + Sighting Cue	0.00	321.21	12	132	23
	+ Sighting Cue	0.05	337.81	3	116	25
	+ Initial Behaviour	1.27	339.06	7	153	23
	+ Season	2.66	340.35	6	130	34
	+ Observer	2.70	342.33	25	132	37
	+ Group size	2.71	345.99	12	137	24
	Base	2.84	354.71	2	140	22
	+ Sea State	2.84	382.02	5	140	30
	+ Season	2.85	397.56	6	139	32
	+ Year	2.96	421.08	5	136	33
	+ Time of Day	3.77	421.37	6	138	37
2	+ Sea State + Depth + Sighting Cue	0.00	293.14	9	95	34
	+ Sighting Cue	0.09	296.03	2	96	36
	+ Depth	0.38	298.53	5	103	32
	+ Sea State	1.02	298.82	4	87	39
	+ Observer	1.17	300.45	24	82	41
	+ Initial Behaviour	1.99	302.17	6	88	35
	+ Group Size	2.15	306.36	11	88	29
	+ Season	2.54	320.58	5	89	37
	Base	2.84	354.71	2	85	29
	+ Year	3.08	360.04	4	85	31
	+ Time of Day	3.21	369.19	5	89	33
3	+ Sea State + Initial Behaviour + Sighting Cue	0.00	271.02	12	124	39
	+ Sighting Cue	0.02	280.53	2	132	31
	+ Initial Behaviour	0.73	291.07	6	127	42
	+ Sea State	1.34	301.46	4	158	18
	+ Observer	1.58	314.68	24	147	23
	+ Depth	1.77	315.21	5	153	30
	+ Group Size	1.92	331.84	11	152	38
	+ Season	2.36	346.20	5	151	34
	+ Year	2.71	350.93	4	157	39
	Base	2.84	354.71	2	157	41
	+ Time of Day	5.35	559.25	5	159	40
4	+ Sighting Cue + Initial Behaviour + Year	0.00	328.44	10	52	26
	+ Sighting Cue	0.35	329.05	2	48	17
	+ Initial Behaviour	0.37	337.13	6	43	23
	+ Year	0.42	341.02	4	47	16
	+ Group Size	1.11	352.36	11	52	16
	Base	2.84	354.71	2	55	20
	+ Observer	2.90	364.04	24	51	21
	+ Season	3.03	395.28	5	50	22
	+ Depth	4.45	400.11	5	54	21
	+ Time of Day	4.58	402.67	5	52	24
	+ Sea State	4.79	405.78	4	51	23

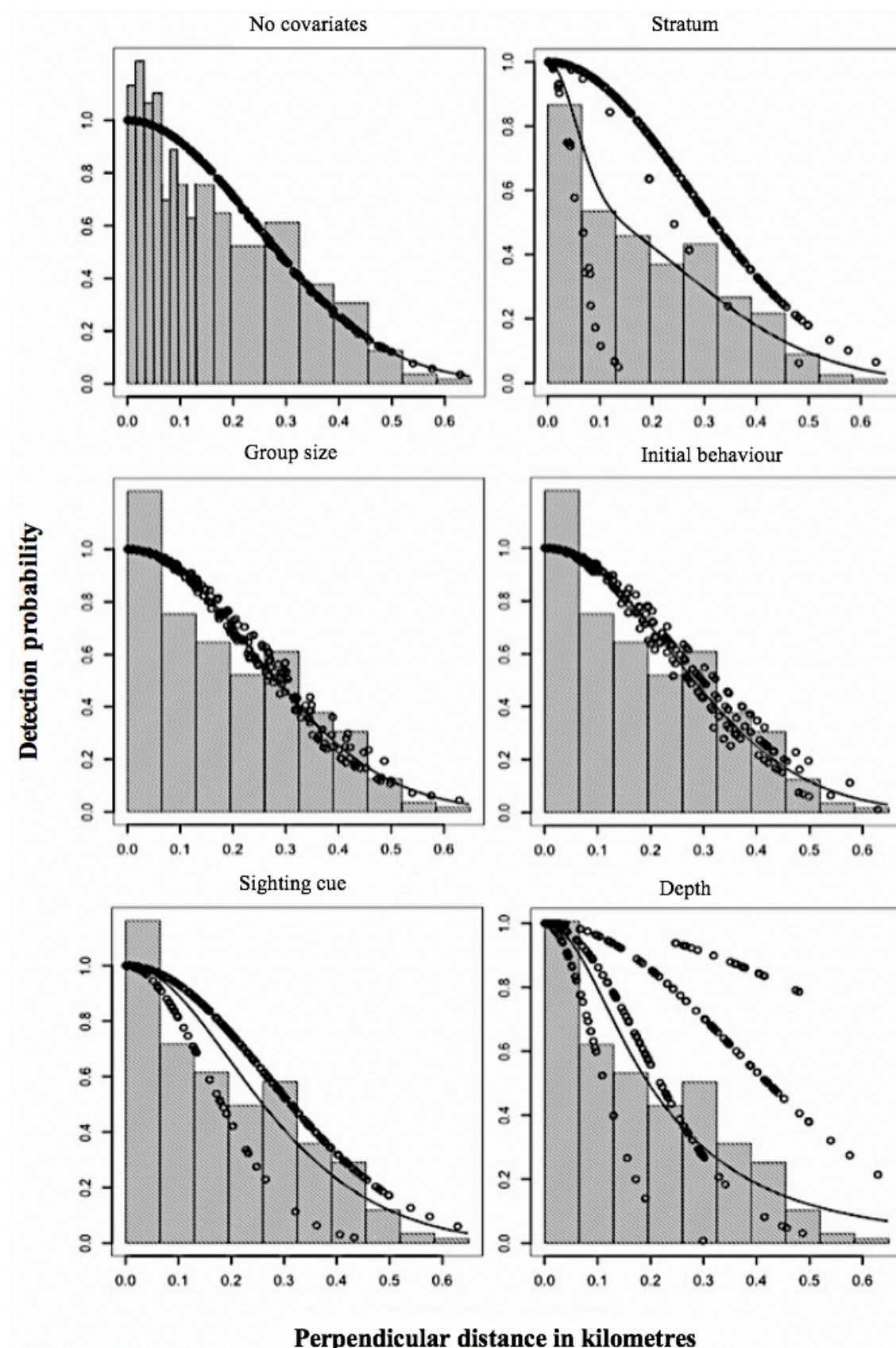


Figure 2.5: Histograms of observed distances and fitted detection functions with covariates added for coastal bottlenose dolphins (*T. truncatus*) March 2013 – September 2015, in Far North waters, New Zealand. *Note: two sets of points for Y/N presence of vessels in Sighting cue and Depth is presented in increments of 50 m (5, 55, 105, 155).

2.3.3.3 Overall and seasonal estimation of density and abundance

Coastal bottlenose dolphin abundance estimates, following correction for covariates and biases, are presented in Table 2.10. Coastal bottlenose dolphin summer abundance in Far North waters (out to 150 m depth) was estimated at 397 (CV: 23 %; 95 % CI: 213 – 482) and 346 (CV: 26 %; 95 % CI: 201 – 495) in winter, making the density in these two seasons the least alike.

Oceanic bottlenose dolphin abundance along the surveyed FN coastline (out to 150 m depth) between 2013 – 2015 was estimated at 3634 (CV: 16 %; 95 % CI: 401 – 6533, Table 2.10). Note, harbours and bays not surveyed in the region are excluded from this estimate. Furthermore, the number of sightings does not allow seasonal breakdown, though it should be acknowledged that this abundance estimate relies on sightings in the summer and autumn months.

Table 2.10: Model averaged seasonal abundance estimates of bottlenose dolphins for each stratum, March 2013 – September 2015, in Far North waters, New Zealand. Given are the estimated abundance of bottlenose dolphin (*T. truncatus*), calculated with the addition of covariates; \hat{N}_k . Note: SE = standard error, L = low, U = upper, Cue = Sighting Cue. Global = all data, Stratum 1 = Bay of Islands, Stratum 2 = Cavalli Islands, Stratum 3 = Whangaroa Harbour, and Stratum 4 = Doubtless Bay. Pale blue shading = oceanic bottlenose dolphin and no colour = coastal bottlenose dolphin.

Season	Stratum	Modelled covariates	\hat{N}_k	SE	L	U
Summer	Global	+ Stratum + Depth + Cue	397	72	213	482
	1	+ Initial Behaviour + Season + Cue	125	19	79	191
	2	+ Sea State + Depth + Cue	82	31	68	102
	3	+ Sea State + Initial Behaviour + Cue	119	41	45	157
	4	+ Cue + Initial Behaviour + Year	39	18	20	66
Autumn	Global	+ Stratum + Depth + Cue	365	81	210	492
	1	+ Initial Behaviour + Season + Cue	103	20	68	181
	2	+ Sea State + Depth + Cue	82	34	60	112
	3	+ Sea State + Initial Behaviour + Cue	121	39	45	184
	4	+ Cue + Initial Behaviour + Year	35	18	18	59
Winter	Global	+ Stratum + Depth + Cue	346	87	201	495
	1	+ Initial Behaviour + Season + Cue	129	20	62	173
	2	+ Sea State + Depth + Cue	87	38	57	107
	3	+ Sea State + Initial Behaviour + Cue	123	35	42	178
	4	+ Cue + Initial Behaviour + Year	30	16	17	63
Spring	Global	+ Stratum + Depth + Cue	349	87	207	401
	1	+ Initial Behaviour + Season + Cue	127	20	66	182
	2	+ Sea State + Depth + Cue	85	35	61	106
	3	+ Sea State + Initial Behaviour + Cue	120	37	44	153
	4	+ Cue + Initial Behaviour + Year	33	17	18	72
All	Global	+ Stratum + Depth + Sighting Cue	3634	152	401	6533

2.3.4 Spatial distribution

2.3.4.1 Coastal bottlenose dolphin spatial distribution

Coastal bottlenose dolphins did not use Far North waters uniformly, instead they were observed in their highest density in the Bay of Islands (Figure 2.6). Approximately 66 % of all sightings were recorded within this *stratum*. A break in sightings occurs between Whangaroa Harbour and Doubtless Bay. Only smaller groups were found in Doubtless Bay. wider survey data were included in this analysis, with a global detection function applied. Sightings were made within a depth range of 2.3 – 143 m (mean = 41.1, Table 2.11). However, most sightings of coastal bottlenose dolphins occurred closer inshore at depths below 20 m (88.5 %, n = 202).

Coastal bottlenose dolphins generally shift inshore over colder months. Whilst most detections occurred inside the 100 m depth contour and less than, or equal to, 6 km from the coast, animals between the Bay of Islands and Cavalli Islands were sighted close to and on this contour on several surveys. This signifies coastal bottlenose dolphins can utilise areas outside of shallow waters (Table 2.11). Coastal bottlenose dolphin showed a strong fine-scale seasonal occurrence in shallow waters (less than 50m) in winter (58.4 %, n = 14) and spring (59.6 %, n = 52) (Mantel $r = 0.167$, $P = 0.001$). In summer and autumn, sightings were more distributed, utilising depths up to 143 m (48.6 %, n = 74 and 44.2 %, n = 29, respectively).

Table 2.11: The mean and maximum distance from shore (km) and depths (m) of survey sightings of coastal bottlenose dolphins (*T. truncatus*) March 2013 – September 2015, in Far North waters, New Zealand. Global = all data, Stratum 1 = Bay of Islands, Stratum 2 = Cavalli Islands, Stratum 3 = Whangaroa Harbour, and Stratum 4 = Doubtless Bay.

			Global	1	2	3	4	5
Summer	Distance offshore (km)	Mean	18.5	19.3	17.2	6.1	10.5	21.4
		Max	25.3	20.0	19.0	7.0	12.0	25.3
Spring		Mean	16.9	16.4	12.7	4.7	8.6	14.8
		Max	19.9	18.8	13.8	5.9	9.2	19.9
Autumn		Mean	18.1	18.5	14.4	6.5	9.7	15.1
		Max	19.3	19.1	19.0	7.2	11.3	18.5
Winter		Mean	16.4	10.8	11.0	4.6	7.1	16.7
		Max	17.0	12.0	15.0	5.0	8.0	17.0
Summer	Depth (m)	Mean	21.3	34.6	22.7	21.6	21.2	39.5
		Max	43.3	42.0	37.0	27.0	28.0	43.3
Spring		Mean	20.2	19.2	21.0	18.5	20.2	46.0
		Max	51.4	23.5	31.4	23.2	26.4	51.4
Autumn		Mean	20.7	22.7	22.2	20.2	20.3	29.8
		Max	34.1	28.1	28.8	26.4	27.5	34.1
Winter		Mean	19.7	18.4	19.5	17.3	19.2	20.5
		Max	25.0	24.0	25.0	23.0	21.0	24.9

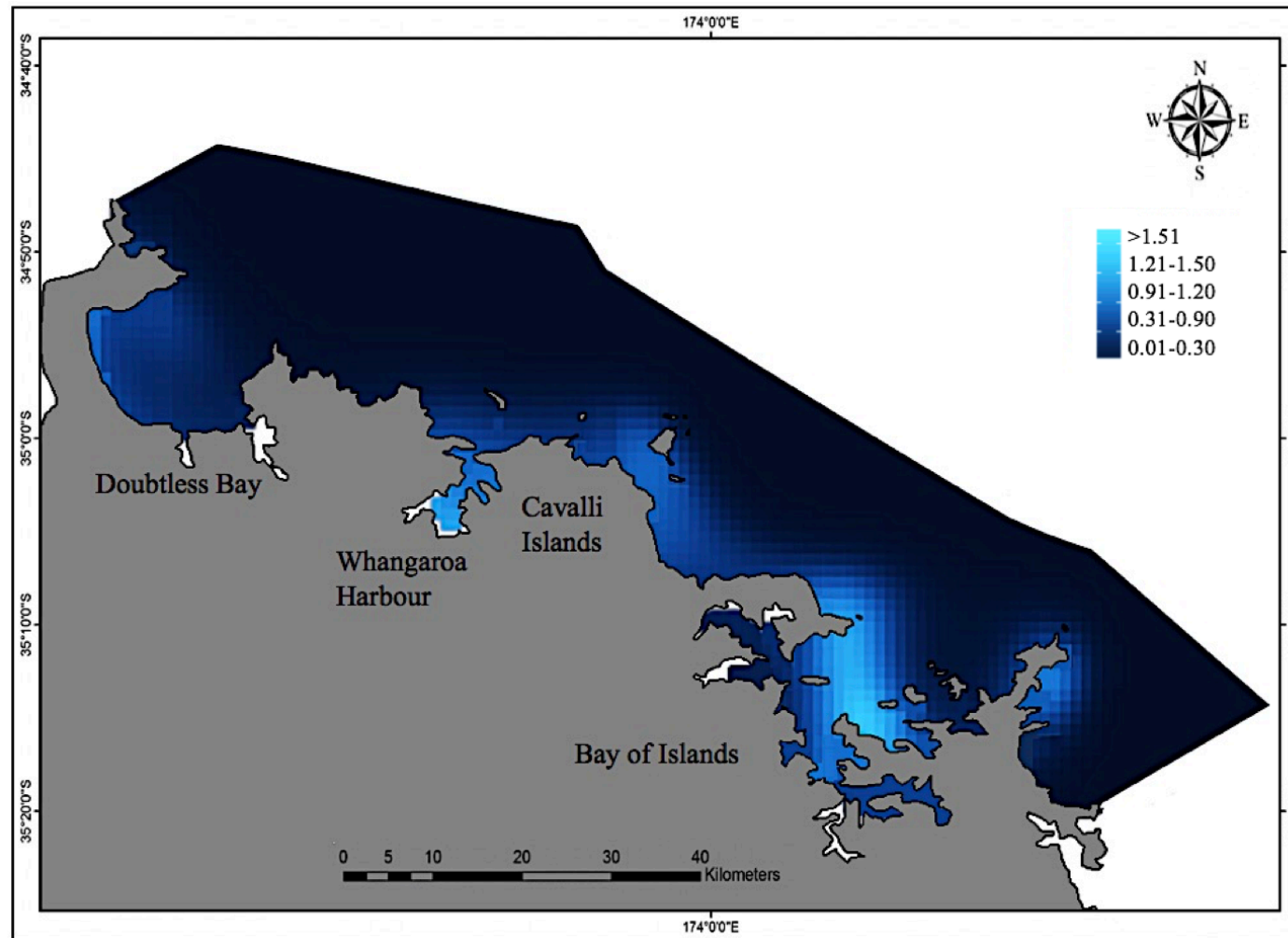


Figure 2.6: Density surface models of coastal bottlenose dolphin (*T. truncatus*) individual distribution assessed from line-transect surveys, March 2013 – September 2015, in Far North waters, New Zealand. The relative density of coastal bottlenose dolphin within 1 km × 1 km grid cells. Relative densities > 1 indicate a density larger than the overall average density in Far North Waters. White grids indicate areas with zero sightings due to no surveys.

Estimated coastal bottlenose dolphin density (individuals/km⁻²) for each *stratum* and *group size* frequencies utilised in the seasonal parametric bootstrap are given in Appendix 2.4. As dataset suggests, the density surface models indicate movement away from shore with seasonal transition from winter to summer. Winter relative densities were also decreased in open areas and wider Bay of Islands/Doubtless Bay, and an increased in relative densities in Whangaroa Harbour and the inner Bay of Islands compared to summer estimates (Table 2.12). The seasonal density surface models analysis results are given in Table 2.12. Note, spring and autumn are intermediate and not discussed in further detail. Discrete high relative density areas were found outside the Bay of Islands, particularly in Whangaroa Harbour, which has the same summer density as the Bay of Islands of 0.62 individuals km⁻².

Density surface model estimated abundance for coastal bottlenose dolphins was 391 (SE = 102) in summer and 382 (SE = 123) in winter, in concordance with non-density surface models estimates utilising the top-ranked detection function model. Overall density surface models-based *stratum*-specific estimates were more precise (i.e., the CV) than non-density surface models (Table 2.12). The CVs presented (Table 2.12) are for density estimates yet remain applicable for abundance.

Table 2.12: Comparison of density estimates of coastal bottlenose dolphins (*T. truncatus*, per 1 km⁻²) with the corresponding non-density surface models analyses, March 2013 – September 2015, in Far North waters, New Zealand. Global = all data, Stratum 1 = Bay of Islands, Stratum 2 = Cavalli Islands, Stratum 3 = Whangaroa Harbour and Stratum 4 = Doubtless Bay, DSM = Density surface model. Note: Stratum 5 is based on a global, not stratum specific, detection function.

Stratum	Non-DSM	CV %	DSM	CV %	Non-DSM	CV %	DSM	CV %
	Summer				Winter			
Global	0.61	20	0.63	15	0.63	21	0.62	16
1	0.63	25	0.64	23	0.56	31	0.57	19
2	0.52	27	0.59	22	0.54	26	0.60	23
3	0.65	46	0.64	34	0.51	42	0.53	21
4	0.36	28	0.37	25	0.28	35	0.32	30
5	-	-	0.17	56	-	-	0.13	53
Stratum	Autumn				Spring			
Global	0.62	22	0.62	18	0.62	19	0.62	16
1	0.60	23	0.61	20	0.59	29	0.62	20
2	0.53	28	0.60	25	0.53	34	0.60	21
3	0.55	49	0.61	29	0.53	47	0.58	21
4	0.34	30	0.36	24	0.30	32	0.35	32
5	-	-	0.15	48	-	-	0.15	56

2.3.4.2 Oceanic bottlenose dolphin spatial distribution

The spatial distribution analysis revealed that oceanic bottlenose dolphins did not use Far North waters uniformly and were observed in highest density in wider survey (Figure 2.7). Approximately 92 % of all sightings were recorded within this *stratum*. Some spatial overlap with coastal bottlenose dolphins was reported, with a small number of sightings occurring in Bay of Islands (3 %, $n = 1$) and Cavalli Islands (6 % $n = 2$) waters. However, the majority of detections occurred outside the 100 m depth contour (25 – 250 m (mean = 108.12, SE = 1.21)) and more than 6 km from the coast (< 1 – 49.3 km (mean = 10.01, SE = 2.13)). Bay of Islands and Cavalli Islands detections occurred near and within this contour. This suggests the ecotype is restricted to waters of greater depths with open water frequented more than shallow or enclosed waters (Table 2.13).

Table 2.13: The mean and maximum distance from shore (km) and depths (m) at which seasonal survey sightings of oceanic bottlenose dolphins (*T. truncatus*) occurred March 2013 – September 2015, in Far North waters, New Zealand.

Season	Distance from shore (km)		Depth (m)	
	Mean	Max	Mean	Max
Spring	N/A	N/A	N/A	N/A
Summer	49	42	77.8	148
Autumn	27	34	134.1	250
Winter	N/A	N/A	N/A	N/A

In Far North waters, the greatest number of oceanic bottlenose dolphin detections occurred during the autumn in all survey years, with a seasonal pattern of occurrence in nearshore waters (< 150 m depth), between December and May. Estimated dolphin density (per 1 km²) is given in Appendix 2.5, where *group size* frequencies utilised in the parametric bootstrap is detailed. The density surface models abundance estimate was 3,914 (SE = 197), in concordance with MCDS estimates of abundance (3,831, SE = 164). However, the relative precision of density surface models-based *stratum*-specific estimates were higher than non-density surface models estimates (Table 2.14).

Table 2.14: Comparison of density surface models-based estimates of oceanic bottlenose dolphin (*T. truncatus*) density (per 1 km²) each season with those obtained from the corresponding non-density surface models analyses, March 2013 – September 2015, in Far North waters, New Zealand.

	Non-density surface models	CV %	Density surface models	CV %
Overall	0.77	27	0.78	20
Summer	0.76	29	0.79	23
Autumn	0.80	32	0.83	28

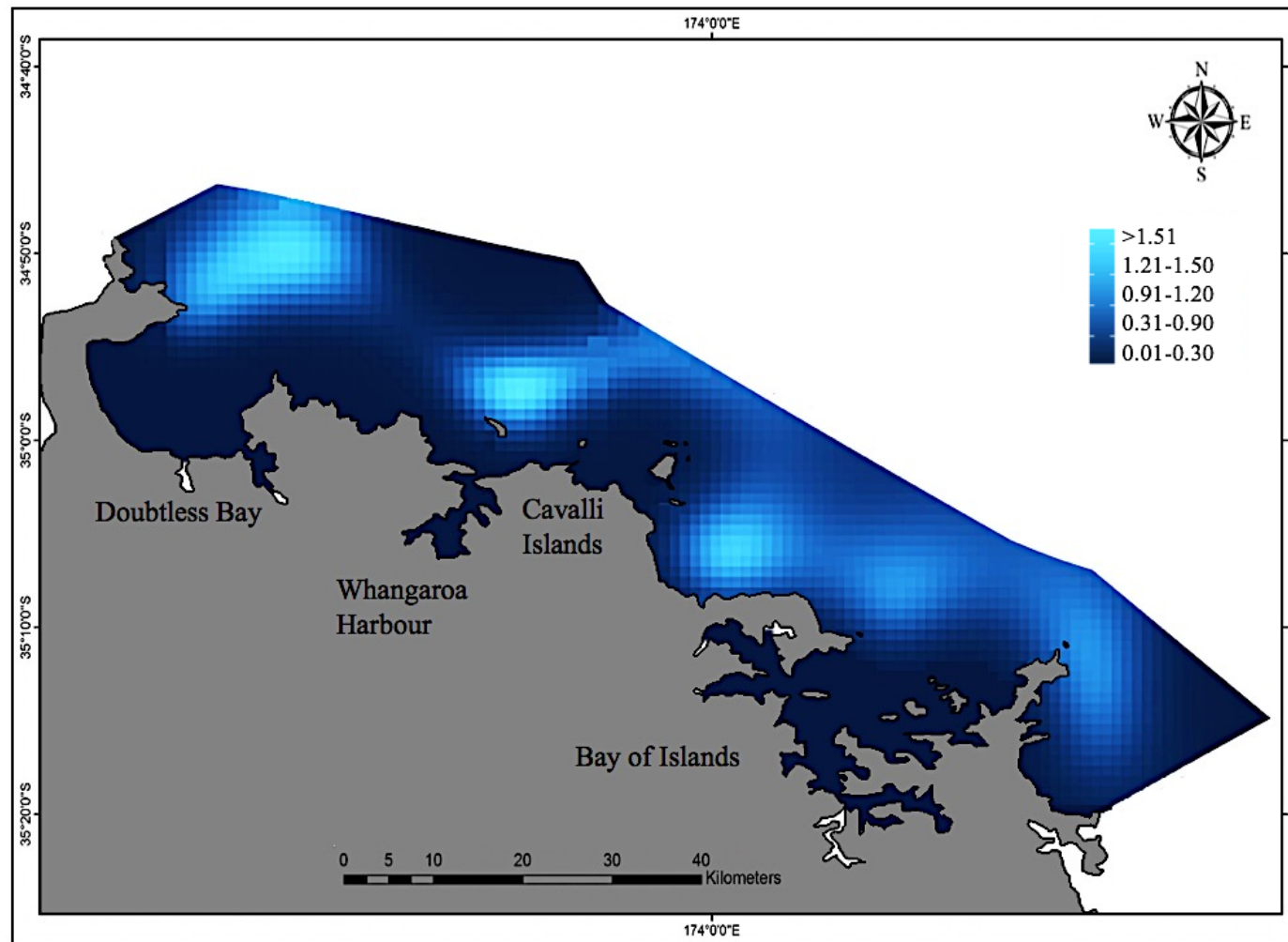


Figure 2.7: Density surface models of oceanic bottlenose dolphin (*T. truncatus*) individual distribution assessed from line-transect surveys March 2013 – September 2015, in Far North waters, New Zealand. The relative density of oceanic bottlenose dolphin within 1 km × 1 km grid cells. Relative densities > 1 indicate a density larger than the overall average density in Far North Waters. White grids indicate areas with zero sightings due to no surveys.

2.3.5 Concordance in space use

The representative range size (95 % kernel range) of coastal bottlenose dolphins was smaller than oceanic bottlenose dolphins, with a total covered area of ~794 km² and ~1,003 km², respectively (Figure 2.8). The representative range of coastal bottlenose dolphins concentrated in three areas: Bay of Islands/Cavalli Islands (including a corridor, ~557 km²), Whangaroa Harbour (~97 km²) and Doubtless Bay (~140 km²), concurring with the spatial density analysis. These areas also contained core areas (50 % kernel range): ~15 km² just outside the entrance to Whangaroa Harbour, and a larger ~234 km² area in Bay of Islands waters. oceanic bottlenose dolphin showed a continuous representative range extending from North of Doubtless Bay to South of Cape Brett, concurring with the spatial density analysis. Inside this range, two core area of approximately ~216 km² and ~86 km² were located seaward of Cavalli Islands and Doubtless Bay, respectively.

The kernel utilisation distribution analysis revealed the representative range of coastal bottlenose dolphins and oceanic bottlenose dolphins showed minimal overlap in space (Figure 2.8). The overlap area utilised by both ecotypes totalled ~196 km², which is 7.4 % of the area surveyed. An overlap of 24.7 % of coastal bottlenose dolphins representative range and 17.1 % of oceanic bottlenose dolphins representative range was observed. The core area of oceanic bottlenose dolphins overlapped with the representative range of coastal bottlenose dolphins (17km², 5.6 % of oceanic bottlenose dolphin core area, 8.7 % of total shared area) and the core area of coastal bottlenose dolphins also minimally overlapped with the representative range of oceanic bottlenose dolphins (6 km², 2.4 % of coastal bottlenose dolphin core area, 3.1 % of total shared area).

The core area of coastal bottlenose dolphins and oceanic bottlenose dolphins showed no spatial overlap (Figure 2.8). The utilisation distributions correlation of coastal bottlenose dolphins and oceanic bottlenose dolphins ($r_s = -0.89$, $n = 264$, $P < 0.05$) suggested very poor concordance in the utilisation of overlap areas. This is further supported by no sightings of the two ecotypes within the same survey zone on the same day ($n = 264$ bottlenose dolphin sightings).

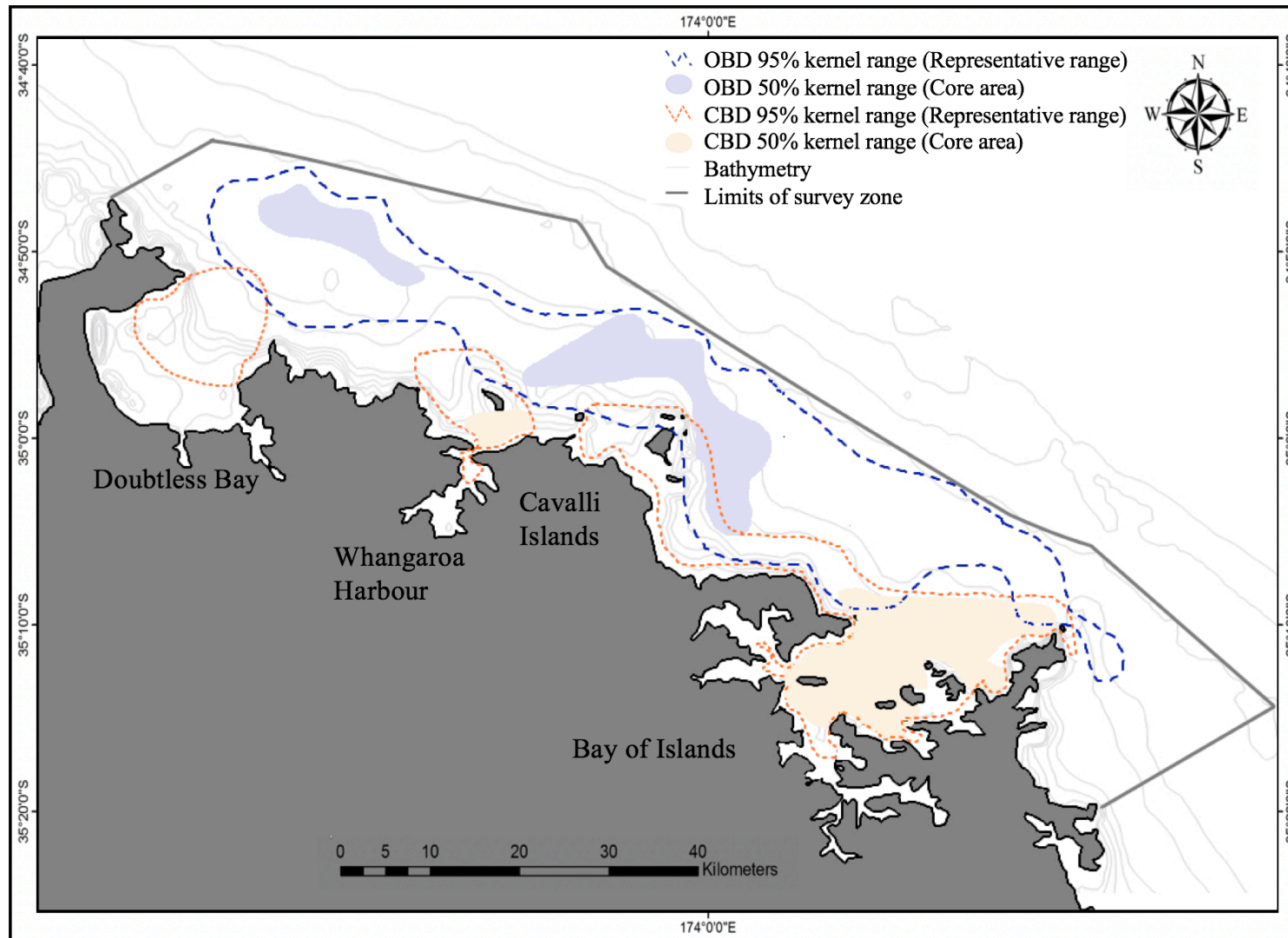


Figure 2.8: Core areas (50 % kernel range) and representative ranges (95 % kernel range) of coastal bottlenose dolphin and oceanic bottlenose dolphin (*T. truncatus*) distribution assessed from line-transect surveys March 2013 – September 2015, in Far North waters, New Zealand.

2.4 Discussion

Although it has long been recognised that coastal bottlenose dolphins are not Bay of Islands residents and are genetically part of a North-East Coast population, no studies have tried to quantify bottlenose dolphin distribution outside of the Bay of Islands in Far North waters. This study provides a comprehensive analysis of the detectability, density, distribution, and abundance of both the coastal bottlenose dolphin and oceanic bottlenose dolphin in Far North waters. Additionally, possible areas of spatial and temporal overlap in ecotype distribution is assessed for the first time. Moreover, results presented provide context to the subsequent chapters (Chapters 3 – 5), that examine the signal behaviour of both ecotypes using the region.

2.4.1 Comparison of ecotype specific density and abundance estimates with previous studies

For coastal bottlenose dolphins in Far North waters, density (0.62 individuals/km²) was higher than values reported for coastal bottlenose dolphins in other areas of the North-East coast population, such as Great Barrier Island (0.318 individuals/km², Dwyer et al., 2016). Coastal bottlenose dolphin density in Far North waters was higher during summer, which is also when the largest group sizes and number of calves occur in the area (Peters & Stockin, 2016). This is true for all *strata*, apart from Cavalli Islands and wider survey, where the coastline is exposed. In mammals, parents and offspring are vulnerable during calving (Stone & Yoshinaga, 2000; Tezanos-Pinto et al., 2015). In the Bay of Islands, winter densities were consistently lowest and group sizes smallest, coinciding with the highest number of encounters in Cavalli Islands waters. This suggests seasonal movement to exposed areas was highest outside of peak calving season (Peters & Stockin, 2016; Tezanos-Pinto et al., 2013).

Previous research indicates coastal bottlenose dolphins in the Bay of Islands have been in 7.5 % annual decline in local abundance between 1997 and 2006 using RD and POPAN models (Tezanos-Pinto et al., 2013). Additionally, the temporary emigration estimates were variable, indicating flexible temporal use of the area; a pattern also observed here. The North-East coast population of coastal bottlenose dolphins extends beyond the Bay of Islands (Baker et al., 2016). The hypothesis that local Bay of Islands abundance is not reflective of coastal bottlenose dolphin patterns of use of the wider area is supported by the 212.8 % (summer) and 196.1 % (winter) higher Far North waters estimate than that of Bay of Islands only. Additionally, whilst the current research identifies core areas for coastal bottlenose dolphins, previous research has

defined coastal bottlenose dolphins as non-resident in these areas (Tezanos-Pinto et al., 2013). It is worth noting that the current research focussed on abundance by area and not by individual (unlike Tezanos-Pinto et al., 2013), and thus an alternate categorisation of coastal bottlenose dolphins as resident in the Bay of Islands and Whangaroa Harbour (core areas) is not recommended. With no previous density or abundance estimates for oceanic bottlenose dolphins in New Zealand, no comparisons can be drawn with other studies or historic research.

2.4.2 Spatial partitioning between bottlenose dolphin ecotypes

Oceanic bottlenose dolphins and coastal bottlenose dolphins in Far North waters showed: (1) low spatial overlap; (2) no spatial concordance; and (3) behavioural divergence (as a function of space and time). Inter-ecotype groups were not observed during this study. Therefore, separation into select ranges in space and time, and behavioural variation appear to be factors of importance promoting their parapatric distribution (Bearzi, 2005; Wells & Scott, 2009). Further to this, there is a gap between the two ecotypes core range where the *Tursiops* sightings are relatively rare. This distributional and temporal dichotomy supports the existence of a coastal and an oceanic population beyond morphology.

Multiple factors (e.g., environmental conditions, prey, habitat, competition, and aggression) might act concurrently on the distribution of ecotypes (e.g., Fontaine et al., 2017; Rosenzweig, 1981). Previously it has been indicated that delphinid spatial distribution relates directly to their prey and predator's distribution (Heithaus & Dill, 2002), as well as physiographic and hydrographic factors (Parra, 2006). Those parameters might induce prey specialisations by individuals, species, or groups within species (Bräger et al., 2003; Gowans & Whitehead, 1995; Smith & Whitehead, 1999). Minimal temporal and spatial commonality among the coastal bottlenose dolphin and oceanic bottlenose dolphin could have resulted from divergence in locations with low critical resources, or where shared predation risks are highest, or both. Ecotypes with some spatial overlap but dissimilar habitat exploitation techniques could increase their reproductive isolation from one another, especially if each ecotype invests continually in the chosen technique and preferentially socialises with groups utilising the same techniques. This phenomenon has been proposed in killer whale (*Orcinus orca*) populations (e.g., Hoelzel et al., 2007). A comparable pattern has been noted in two bottlenose dolphin (*Tursiops aduncus*) populations inhabiting Moreton Bay, Australia, which appeared separated as a result of dissimilar foraging techniques (with one feeding on commercial trawling vessel

bycatch, Allen et al., 2016). However, commercial effort has dramatically reduced since research began resulting in a less defined population structure (Ansmann et al., 2012a).

2.4.3 Distribution factor: environmental conditions

The distribution of both ecotypes in Far North waters varied according to season. Coastal bottlenose dolphin groups were recorded/observed year-round. However, they were nearest to the shoreline in winter and spring and furthest in summer, concurring with prior research on the Bay of Islands local population (Constantine, 2002; Constantine & Baker, 1997; Hartel et al., 2014; Peters & Stockin, 2016). Distribution has been linked to prey distribution (Elliott et al., 2011; Scott et al., 1990), and this appears true for the North Island coastal bottlenose dolphin population. Distribution across the range is not even, with areas such as the Bay of Islands, Cavalli Islands, Whangaroa Harbour, Doubtless Bay and Great Barrier Island appearing to be frequented more often than other areas, such as the Inner Hauraki Gulf, wider survey and the East Coast Bay of Plenty (Berghan et al., 2008; Dwyer et al., 2014b; Meissner et al., 2014).

Unlike the coastal bottlenose dolphin, the oceanic bottlenose dolphins seem to be absent from the region in winter and spring. An undocumented seasonal offshore shift may help explain the lack of sightings in waters that are not fully captured due to the logistical constraints of this study (< 150 m depth). Zaeschmar et al., (2013), suggests that the species' distribution (in mixed groups with false killer whales (*Pseudorca crassidens*) and pilot whales) is also likely centred further offshore. The scars noted could offer additional evidence of bottlenose dolphins in the area, assumed to be bites from the cookie cutter shark (*Isistius brasiliensis*), a deep, tropical, and temperate water dwelling species (Jahn & Haedrich, 1988; Jones, 1971). Cookie cutter shark bites have been utilised as markers to distinguish cetacean populations (Dwyer & Visser, 2011). Consequently, oceanic bottlenose dolphins detected in Far North waters may frequent deep offshore waters in addition to the shallow continental shelf region surveyed.

2.4.4 Distribution factor: prey

In Far North waters, prey distribution has previously been considered the principal driving factor behind bottlenose dolphin distribution and reproduction (Bay of Islands, Hartel, 2010). Far North waters cross a zone of climate transition, with the margin described as more pronounced during December – May with the progression of the East Auckland Current on the

North-Eastern coast, New Zealand (Zeldis et al., 2004). Within the East Auckland Current, prey species' richness and density is higher and SST ca. 2°C warmer than on the continental shelf (Sharples, 1997). It has previously been suggested this may drive the seasonal distribution of coastal bottlenose dolphins to deeper oceanic waters and oceanic bottlenose dolphins (and associated species) to shallower waters (Baird et al., 2008; Constantine & Baker, 1997; Hartel, 2010; Zaeschmar et al., 2013).

Regions which are more affected by the East Auckland Current may provide an opportunity to maximise foraging. This may also explain the increase in summer coastal bottlenose dolphin Cavalli Islands and wider survey sightings, as the East Auckland Current only passes the seaward side of these zones (Zeldis et al., 2004). This corresponds with a higher number of coastal bottlenose dolphin sightings and more foraging activity observed in East Coast Bay of Plenty waters in summer (Meissner et al., 2014). However, the East Coast Bay of Plenty data consisted of a restricted dataset and uneven seasonal effort (57 % in summer) (Meissner et al., 2014), hindering any strong inferences but providing baseline data on trends. The consistent seasonal utilisation of Far North waters by coastal bottlenose dolphins suggests an adequate year-round prey stock to provision a larger population than the previously studied local Bay of Islands population.

Baited camera systems utilised during a study of fish stocks in the region indicates fish species diversity is highest in Far North waters between 50 – 100m, and significantly higher than over 150m, with outer Bay of Islands and Cavalli Islands (areas of highest ecotype overlap) exhibiting the greatest fish species diversity (Jones et al., 2010). Presumably, oceanic bottlenose dolphins exploit deeper areas for foraging further offshore, while coastal bottlenose dolphins prefer the shallower inshore environment. This possibly adds insight as to why oceanic bottlenose dolphins, who could move into shallow coastal waters and thus mix with coastal bottlenose dolphins, are not documented or predicted to occur in coastal regions. The stomach contents of two bottlenose dolphin morphotypes in the eastern United States were found to differ, with the inshore demersal fish species discovered in the stomachs of the coastal form totally absent in the oceanic form (Mead & Potter, 1995; Waerebeek et al., 1990). Oceanic bottlenose dolphin consumption of coastal fish species might be opportunity driven (as suggested by Klatsky et al., 2007; Zaeschmar et al., 2014). In New Zealand, false killer whales (a known associate of the oceanic bottlenose dolphin, Zaeschmar et al., 2014) were documented foraging on kingfish (*Rexea* spp.) in coastal waters and on hapuku (*Polyprion americanus*) in

deeper waters (Zaeschar et al., 2013). This is consistent with the foraging ecology described for oceanic bottlenose dolphins from other regions (Barros et al., 2000; Klatsky et al., 2007). Oceanic bottlenose dolphins and the pilot whales/false killer whales they associate with may benefit from the seasonal shoreward flooding of warm currents to acquire food that may otherwise be outside of their preferred temperature range. This may explain why some seasonal range overlap is observed between the two ecotypes but not to the extent of a sympatric distribution.

Segregation as a result of dietary needs is probable, nonetheless, it falls short of completely explaining the distribution variances between coastal bottlenose dolphins and oceanic bottlenose dolphins. Firstly, comparable prey species occur in the overlapping regions between ecotypes, allowing for an expectation of dietary commonality. Secondly, notwithstanding the variances in morphology, there is no evidence that suggests the two ecotypes cannot forage on the same species. In conjunction with environmental and prey factors, other restrictions may contribute to interspecific variations in spatial use.

2.4.5 Distribution factor: habitat

For the bottlenose dolphin, habitat heterogeneity can affect the acquisition of dissimilar habitat utilisation skills (Chilvers & Corkeron, 2001; Olin et al., 2012; Sargeant et al., 2007; Wilson et al., 2017; Wiszniewski et al., 2009). The waters around New Zealand could have created distinct *specialist* coastal and *generalised* oceanic environments, as supported by the predominantly coastal distribution of coastal bottlenose dolphins and oceanic distribution of oceanic bottlenose dolphins. For example, the stable (though seasonal) conditions in coastal environments allow for the year-round occurrence of many fish species and coastal bottlenose dolphins. Comparatively, wider survey areas are dominated by highly variable conditions and a seasonal abundance of fish and oceanic bottlenose dolphins. The seasonal distribution of oceanic bottlenose dolphins, occurring in the Far North waters in austral Summer and Autumn, support the use of highly variable areas such as wider survey seasonally. The restricted coastal distribution of coastal bottlenose dolphins, compared to the oceanic distribution of oceanic bottlenose dolphins, may result from reduced or specialised habitat utilisation skills (reviewed in Jefferson et al., 2015) of coastal bottlenose dolphins in sheltered areas, such as the core regions of the Bay of Islands and Whangaroa Harbour identified in this study. Inshore bottlenose dolphin within embayments in Australia support this theory, with fine-scale

population structure as a result of utilisation of varied habitats (Ansmann et al., 2012a, 2012b; Wiszniewski et al., 2010).

Habitat utilisation as an influence on bottlenose dolphin range, social structure, and foraging strategy has been documented. Oceanic bottlenose dolphins inhabiting colder, oceanic waters are found to transit between areas and are found in large groups (Hoelzel et al., 1998; Rossbach & Herzing, 1999; Torres et al., 2003; Wells & Scott, 2009), as noted in Far North waters with seasonal distribution and larger group sizes (mean of 55.2 vs 14.4 for coastal bottlenose dolphins). Coastal bottlenose dolphins in sheltered or protected environments usually have higher site fidelity and are found in smaller groups (Defran et al., 1999; Reeves et al., 2003; Wells & Scott, 1999, 2009). The combined factors of a species' habitat heterogeneity and biological requirements (such as body size and metabolic needs) drive distribution, habitat use and home range size (McNab, 1963). The total area required to fulfil energy requirements is determined by population size, spread, and resource availability within the habitat. There is a causal link between SST and group size in delphinids, with a higher likelihood of larger groupings at lower SST, concurring with observations of larger oceanic bottlenose dolphin groups than coastal bottlenose dolphin groups (Gygax, 2002). Food sources in cooler waters may be more abundant and/or less evenly distributed, driving the larger groups observed. The interaction of driving factors will influence the resulting home range size.

2.4.6 Distribution factor: competition and aggression

Odontocete social structure and socio-ecology is predominantly impacted by two key factors: predation and conspecific aggression (Scott et al., 2004). Encounters between coastal bottlenose dolphins and oceanic bottlenose dolphins were never observed in Far North waters, thus maintenance of social structure through aggression may be a factor promoting spatial and temporal separation. Examples are seen in other taxa, such as habitat selection and/or displacement determined through interspecific aggression among sympatric birds (Martin & Martin, 2001) and terrestrial mammals (e.g., Linnell & Strand, 2000; Loveridge & MacDonald, 2002). One example in marine mammals is the Australian humpback (*Sousa sahulensis*) and snubfin (*Orcaella heinsohni*) dolphin, where the interactions have been described as aggressive or sexual (Parra, 2006). The ultimate cause of these exchanges remains unknown (e.g., interspecific competition, mating, or infanticide) (Parra, 2006). However, no matter the function, segregation can occur as a result of aggressive exchanges among spatially overlapping populations. The group sizes of oceanic bottlenose dolphins were on average four

times larger than that of coastal bottlenose dolphins. These larger groups may dominate smaller groups, as individuals are more at risk of direct aggression due to a minimised dilution effect (Lehtonen & Jaatinen, 2016). This could act to restrict the offshore range of coastal bottlenose dolphins.

A further factor to be considered in Far North waters is the associations of oceanic bottlenose dolphins with pilot whales, which adds further risk of aggressive behaviour toward coastal bottlenose dolphins, should they interact. Habitat partitioning between parapatric coastal bottlenose dolphins and oceanic bottlenose dolphins may propagate through the aggressive rejection of coastal bottlenose dolphins by the larger oceanic bottlenose dolphins and pilot whales. Aggressive dominance has been observed in the Bahamas by the larger bottlenose dolphin over smaller spotted dolphins (Herzing & Johnson, 1997). The behaviour of coastal bottlenose dolphins in wider survey areas also supports this theory, as coastal bottlenose dolphins were predominantly observed travelling through the area and only resting, socialising, and feeding in sheltered bays. As a result, shallow waters may function as coastal bottlenose dolphin sanctuaries, areas in which interactions with larger, and possibly dominant oceanic bottlenose dolphins, would be less likely. Though it is worth noting, no physical barrier prevents the movements of either ecotype into coastal or oceanic waters.

2.4.7 Study limitations

Distance sampling necessitates some core assumptions to be met (Buckland *et al.*, 1993). The preliminary assumption being that if bottlenose dolphins were on the trackline they will be detected, i.e. $g(0)=1$ (Buckland *et al.*, 1993). Despite the low height of observers above water level, it was assumed this assumption was met (or minimally violated) due to the concurrent data collected on dive time of bottlenose dolphins in Far North waters (average 57.7 s, $n = 1200$ dive cycles for coastal bottlenose dolphin and average 137.2 s, $n = 900$ dive cycles for oceanic bottlenose dolphin; C. Peters, unpublished data). Additionally, a range of group sizes were collected across all distance bands and surveys were only undertaken in optimal sea conditions (as per Ronconi & Burger 2009). Steps were thus taken to minimise bias due to missed detections on the transect line (as per Flach *et al.*, 2008). It is worth noting, if a bias did occur the estimates (density and abundance) produced would be negatively biased. The estimates in this body of work should be viewed as conservative in light of this.

A further assumption is that no undetected movement occurred before being sighted and no groups are recorded multiple times in a single sample (Buckland *et al.*, 1993). During this study, responsive movement was detected though it was minimal (apparent observations of being attracted to or avoiding the survey vessel were rare (15 %, $n = 43$ for coastal bottlenose dolphin ($n=228$) and 0 % for oceanic bottlenose dolphin ($n = 47$); C. Peters, unpublished data). In the Bay of Islands particularly, the dolphins appeared to be habituated to vessels (Peters & Stockin 2016). Nonetheless, due to the use of closing mode the possibility of double counting the same group needed to be considered. To minimise this, focal group movement was monitored until survey was resumed. If previously detected groups crossed ahead of the vessel on the transect, the detection was removed from the dataset (as per Flach *et al.*, 2008). Additionally, to add another level of independence, all sightings from the same day in the same stratum were cross referenced from Photo-identification and removed if the same individuals were present, a benefit of closing mode.

The final key assumption is that an errorless measurement of angle, distance and group size is achieved (Buckland *et al.*, 1993). This assumption relies as much on training and/or experience of observers as it does with the equipment utilised (as per Flach *et al.*, 2008). Recording angles from a small vessel may have added operational error, due to the increased likelihood of drift compared to a larger boat (as per Flach *et al.*, 2008). To minimise this error recordings were taken as efficiently as possible and without rounding (assessed for all measurements in a scatter plot as per Flach *et al.*, 2008). The use of systematic training in sighting distance estimation reduced distance measurement errors as a good indication of sighting location allowed for the rapid recording of group distance. Additionally, no signs of ‘heaping’ were detected during initial data exploration (Buckland *et al.*, 1993). Finally, the use of distance bins in this study reduced possible bias in distance estimates, as recommended by Buckland *et al.* (1993).

Model-based deductions are singularly appropriate due to the input accuracy and the appropriate scale of application. The distance-sampling methodology is no different. While covariates considered here are not exhaustive of those that may affect dolphin distribution, coarse-scale factors have been focused on due to the intended use of the estimates produced. For density surface models, utilising a bivariate spline term, and including location of a grid where a bottlenose dolphin group was detected, offers an adaptable and comparable technique for detecting spatial variation. Note that classifying the drivers of the spatial variation was not attempted (as per MacKenzie & Clement, 2014). A wider set of factors was not included in this

study's density surface models, as the distribution modelling objective was to describe location, but not understand habitat selection of bottlenose dolphins.

Oceanic bottlenose dolphins were frequently observed in wider survey, but rarely encountered in sheltered areas of Bay of Islands and Cavalli Islands, and never in Whangaroa Harbour or Doubtless Bay. Unfortunately, seasonal occurrence resulted in a small sample size for oceanic bottlenose dolphins. This made any meaningful *stratum*-specific statistical analyses impossible, resulting in a limited discussion of oceanic bottlenose dolphin distribution. To obtain reliable estimates, it is suggested a minimum of 60 – 80 detections are required to calculate meaningful estimates from transect surveys (Buckland et al., 2001), which was not achieved in Far North waters for oceanic bottlenose dolphins. Additionally, the oceanic bottlenose dolphin groups sighted were not necessarily truly independent, as multiple sightings occurred in a single day and baseline data are not available to inform on the spread of inter- and intra-specific groupings. Applying standard group definition criteria was the only way to maintain comparability across ecotypes, though this may result in some large or very spread groups being classified as multiple detections. In fact, 34 groups were detected as a result of 30,728 km of *on survey* effort, supporting the notion that occurrence patterns were not artefacts of effort. In studies of transient or rarely occurring species, this is often a limitation. For a detection function estimate, including sightings from *off effort*, deeper water or high-density areas identified in this study might improve estimates, though these data cannot be incorporated into abundance estimates (Williams & Thomas, 2009).

Implementation of the survey design was successful. However, the detection function did decrease with increased distance as a result of covariates. Nonetheless, the CVs of this study fall within the range of comparable abundance studies (e.g., 32.0 % harbour porpoise (*Phocoena phocoena*, Williams & Thomas, 2007); 48.1 % bottlenose dolphin (Barlow, 1995) and 35.3 % Pacific white-sided dolphin (*Lagenorhynchus obliquidens*, Williams & Thomas, 2007; as summarised in Dick & Hines, 2011), rendering discussion within the body of literature appropriate. It must also be considered that in this study a complete survey of most regions was completed within days. It is thus not achievable to quantify the duration of shifts, coincidental overlap with surveys, or identify true seasonal patterns. Subsequent surveys over multiple successive timeframes would provide verification beyond occurrence. Additionally, a conclusive driver of the seasonal shift observed for both ecotypes cannot be determined as a result of a data paucity on prey movements. This topic merits additional consideration due to

possible implications on the movement of bottlenose dolphin populations and other top predators, and their management. Further to this, while all *strata* were used in all seasons, distribution and density in wider survey was not uniform along the coast for coastal bottlenose dolphins. The wider survey region of the coast between Bay of Islands, Cavalli Islands and Whangaroa Harbour appears to be important for groups. No sightings occurred between Whangaroa Harbour and Doubtless Bay. Sightings that occurred in wider survey consisted of smaller groups in a travelling behaviour state, possibly reducing detectability compared to large and socialising groups. This suggests the area could be used to transit between sheltered bays, however, the increase in abundance estimates cannot fully account for declines in all other *strata*.

Coastal bottlenose dolphin abundance estimates utilised both density surface models and non-density surface models for survey data 2013 – 2015 across seasons and Far North waters *strata*. Thus, both the historic abundance estimates achieved for the Bay of Islands (Tezanos-Pinto et al., 2013) and the methods employed there are not directly comparable to one another. Additionally, a direct comparison of density surface models and non-density surface models estimates is slightly impeded by the differences noted for some *strata*. The smooth density surface utilised likely resulted in these differences (MacKenzie and Clement, 2014a).

Chapter 3

Call differentiation of parapatric common bottlenose dolphin (*Tursiops truncatus*) ecotypes in Far North waters, New Zealand



Oceanic common bottlenose dolphin (*Tursiops truncatus*) adults and calves in Far North waters, New Zealand.

3.1 Introduction

Signal variation between populations can be a marker of divergence and even speciation. The ultimate cause of mechanical (tactile and acoustic) signal divergence varies and has been linked to hereditary, social, and environmental contexts. Such variations, particularly vocal signals and between geographically separated populations (Conner, 1982), have been linked with genetic differentiation (e.g., assortative mating Baker & Cunningham, 1985). Vocal divergence is noted and quantified in a range of taxa, notably birds (e.g., rufous-collared sparrows, *Zonotrichia capensis*, Tubaro et al., 1993), bats (e.g., horseshoe bats, *Rhinolophidae* sp., Yoshino et al., 2008), and cetaceans (e.g., blue whales, *Balaenoptera musculus*, McDonald et al., 2006; humpback whales, *Megaptera novaeangliae*, Winn et al., 1981; pilot whales, *Globicephala* sp., Van Cise et al., 2017; and striped dolphins, *Stenella coeruleoalba*, Papale et al., 2013). Hypotheses pertaining to the factors causing variation include isolation, habitat specific adaptation (e.g., Ding et al., 1995; Graycar, 1976), acoustic drift (Conner, 1982), gross morphology, genetic divergence (Janik & Slater, 2000; Slabbekoorn & Smith, 2002), socially reinforced behaviours in sympatric or parapatric populations, and/or dialects (e.g., sperm whales (*Physeter macrocephalus*, Gero et al., 2016a & b) and killer whales (*Orcinus orca*, Filatova et al., 2012; Ford, 1989, 1991)).

Accurately describing and quantifying signals, particularly of social call (whistles and burst pulse vocalisations), can be challenging. This has resulted in a suite of methodologies aimed at improving standard procedures, with both perceptual and statistical measures utilised to address the issue (for review see Deecke et al., 1999). Perceptual tool sets have indicated that dolphins can use overall frequency parameters to recognise and categorise calls by signaller, with no further signal cue available (Harley, 2008; Janik et al., 2006). Therefore, there is biological justification for the application of categories based on the frequency contour. The reliability of considering just one parameter has been questioned, with Deecke & Janik (2006) suggesting that a failure to account for supplementary fundamental features of acoustic perception may result in reduced performance in contour categorisation methods. Supplementary fundamental features include flexibility in the time domain of vocalisations, which results in altered perception of the signal frequency. For example, a greater change in absolute frequency may occur before it is detected in analysis, if it occurs in higher fundamental frequency signals (Deecke & Janik, 2006). The dynamic time warping methodology, outlined by Buck & Tyack (1993) and developed in Deecke & Janik (2006)'s programme ARTwarp,

aligns the features of two different contours through the application of a ‘time warping’ algorithm. This results in meaningful categorisation and an expression of contour similarity as a relative measure (Gridley, 2011).

Whilst advances in cetacean call categorisation have progressed, other fields of acoustic research have matched, if not exceeded, this development (Chapter 1, Section 1.2.4.1). For example, avian song categorisation is arguably the most advanced field in acoustic categorisation, particularly in relation to population comparisons (Halfwerk et al., 2016; Lachlan et al., 2016; Ranjard et al., 2017). Of particular note is the programme Luscinia (© Lachlan, 2007). This software for bioacoustics archiving, measurement, and analysis delivers an adaptable, fast, and consistent semi-automatic method to quantify bioacoustics signals. Fifteen acoustic parameters are measured from contours in addition to hierarchical information on the structure of complex signals. The application of an extensive range of analytical methods, from summary statistics to the advanced implementation of dynamic time warping, means Luscinia facilitates the comparison of distinct and complex signals. This forms the basis for subsequent bioinformatic and statistical analyses utilised to quantify divergence, including multidimensional scaling, dendrograms and geographic analysis.

The successful implementation of such tools can conceivably decrease the processing effort required for call analysis and is especially amenable for extensive datasets and multi-level repertoire comparisons (Lachlan, 2007). Thus far, Luscinia has only been utilised in avian studies, e.g., chaffinch (*Fringilla coelebs*, Riebel et al., 2015), red-backed fairy wren (*Malurus melanocephalus*, Greig & Webster, 2014; Schwabl et al., 2015), swamp sparrow (*Melospiza georgiana*, Lachlan & Nowicki, 2015), and great tit (*Parus major*, Jacobs et al., 2014). While not previously utilised in marine mammals, the methodology is applicable to the study of repertoire divergence. In marine mammals, socially maintained differences in call repertoires propagate through vertical transmission (e.g., parent – offspring, Yurk et al., 2002), or via immigrant individuals adopting the calls of a new population or group (Conner, 1982; Mundinger, 1980; Musser et al., 2014). The term ‘calls’ refers to burst pulses and whistles, which are often analysed together in the literature when calculating vocal rate. This categorisation is based on evidence that a continuous spectrum definition is appropriate (Murray et al., 1998), and the fact that cetaceans, including dolphins, exhibit a fluid transition and concurrent utilisation of whistles and burst pulses (Sayigh et al., 2013). Geographic variability in calls may produce a positive feedback loop with genetic variance, i.e., habitat-

dependent selection promotes divergence of calls among populations due to social separation (Slabbekoorn & Smith, 2002). Acoustic differentiation within a species, particularly with social species such as the common bottlenose dolphin (*T. truncatus*, referred to hereafter as bottlenose dolphin), can infer an absence of social interaction or cultural information transmission. This could be considered an implication of differentiation at the sub-species or species-level (Van Cise et al., 2017).

Little is known of the coastal bottlenose dolphin call repertoire in New Zealand (NZ). Coastal bottlenose dolphins have been shown to produce distinct, recurrent call types in other areas, such as Fiordland (Boisseau, 2005), with 77% of recordings correctly classified to a specific fiord based on call rate alone. In Far North waters, Snell (2000) provided a preliminary description of variation in the acoustic behaviour of Bay of Islands coastal bottlenose dolphins. The study primarily focussed on whistles and noted whistles with higher than expected frequencies when dolphins were socialising and resting. Whistle behaviour was also the only vocal parameter to change as a result of vessels and swimmers, with an increase in whistle rate and frequency (Snell, 2000). However, the study was restricted in sample size to 10 days and 11 dolphin groups over a single summer period (October 1999-February 2000), meaning seasonal, group, and population level variation remains unquantified.

In NZ, the oceanic bottlenose dolphin remains poorly described, as morphological and genetic samples are rare and difficult to collect (Chapter 2, Tezanos-Pinto, 2009; Tezanos-Pinto et al., 2013; Zaeschmar et al., 2013; Zaeschmar et al., 2014). Geographic range and distribution are also lesser known than with the coastal bottlenose dolphin. In contrast to the coastal bottlenose dolphin, nothing is known about the oceanic bottlenose dolphin call repertoire. Geographic variability in social behaviour, particularly call repertoire, could aid differentiation between ecotypes, thus improving current understanding of their distribution, behaviour and social associations and ultimately their conservation management.

This chapter examines geographic and ecotype variability in bottlenose dolphin call composition with the overarching goal of clarifying whether social differentiation is likely in Far North waters where limited genetic, morphological, or survey information exists. Specific questions include:

- 1) Is semi-automated categorisation and comparison of call contours using the software Luscinia applicable for bottlenose dolphins?

- 2) Are coastal bottlenose dolphin and oceanic bottlenose dolphin calls acoustically distinct and do they differ in call rate?
- 3) Can calls from Far North waters be acoustically categorised as the coastal- or oceanic-type?

As it is problematic to ascertain if call composition or call contours exhibit more ecological plasticity (Slabbekoorn & Smith, 2002; as per Van Cise et al., 2017), the inclusion of both facets within this study offers a comprehensive examination of social call divergence, through whistle and burst pulse vocalisations of bottlenose dolphin in Far North waters.

3.2 Materials and methods

3.2.1 Data collection

To acquire a representative sample of calls from the study area, efforts were made to record a good proportion of groups and sub-groups from each study site. In addition, calls were recorded across multiple levels of behavioural state (travelling, resting, milling, socialising, and diving), group size (three categories: the absolute *minimum* number of dolphins counted, the absolute *maximum* number of individuals believed to be in the group and the *best estimate* for the group size; Dwyer et al., 2016), group composition (i.e. adult only, adults with juveniles, adults and/or juveniles with calf/neonate groups), and location within each study area (as per Chapter 2). Trained observers identified any additional detectable species or groups during encounters and noted any mixed-species associations. When dealing with groups larger than 40 individuals, focal-sub groups were sampled (as per group size recording in Chapter 2, Section 2.2.1, data is summarised in Appendix 1.1). The group size collected for each sub-group was preferentially used to calculate total encounter group size if required. To standardise field techniques, acoustic data from all regions were collected using one recording system deployed in a similar manner and monitored using a standardised data input system (version 3.296+ © CyberTracker Conservation 2013). All encounters were also documented via Dictaphone recordings, time-synched to hydrophone recordings for any supplementary information.

Call recordings were obtained from March 2013 – September 2015 during systematic surveys in Far North waters (Chapter 2). A Cetacean Research Technology Inc. C75 omnidirectional hydrophone with built-in pre-amplifier (flat frequency response of 1 Hz – 85 kHz; sensitivity -209.52 dB re 1 V/μPa) was utilised, attached to a Tascam DR-680 digital multitrack recorder

sampling at 96 kHz, 24-bit. The hydrophone was calibrated prior to utilisation with a 1 kHz pistonphone. The hydrophone was deployed with approximately 15 m of cable behind a stationary (engine off) 5.8 m research vessel within 30 – 200 m of focal animals.

3.2.2 Data filtering

Recordings were taken for this study if bottlenose dolphin focal group were observed within 300 m of the observing vessel. To minimise the effect of sound from the surface and reduce the likelihood of individuals transiting through the recording zone undetected, recordings were taken in < 3 Beaufort Sea State. Acoustic recordings were separated into geographic regions consistent with the survey design: Bay of Islands, Cavalli Islands, Whangaroa Harbour, Doubtless Bay, and wider survey. Ecotype presence was confirmed based primarily on morphology (Chapter 1, Visser et al., 2010; Zaeschmar, 2014) and further supported by location (Chapter 2). Acoustic recordings ceased if the focal group moved more than 300m from the observing vessel or data collection on the focal group was complete.

3.2.2.1 Terminology

To avoid misperception and aid links with other whistle/call literature, the subsequent terminology is applied throughout. A ‘contour’ describes the basic unit of analysis. Any narrow-band tonal signal ≥ 0.1 s in length with a fundamental frequency above 3 kHz is termed a ‘contour’ (Figure 3.1; Kriesell et al., 2014). Contours with breaks < 0.03 s are labelled continuous (Gridley et al., 2014). The term ‘call’ is presented as a contour or loop (≥ 2 repeated contours) disconnected by a silence 0.03 – 0.25 s long (referred to as a disconnected multi-loop call in the literature, Kriesell et al., 2014).

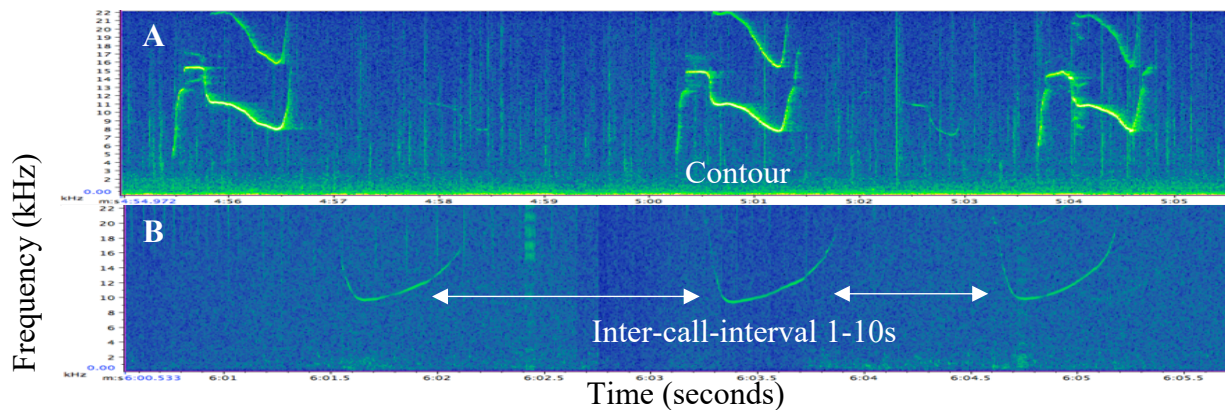


Figure 3.1: Call contours measured from call recordings of bottlenose dolphins September 2013 – September 2015, in Far North waters, NZ with A) coastal bottlenose dolphin and B) oceanic bottlenose dolphin (*T. truncatus*).

3.2.3 Data preparation

3.2.3.1 Call extraction

Visual examination of spectrograms was performed in Raven 1.5 (Beta version, ©2002 – 2013 Cornell Lab of Ornithology) utilising a discrete Fourier transform plus Hamming window and 50 % frame advance. Discrete Fourier transform frame lengths were fixed to ensure comparable temporal and spectral resolution between recordings. These were separated into 1-minute (min) samples with a hierarchical naming system. The presence of calls was visually and audibly confirmed.

Once obtained from Raven, samples were added to Luscinia (version 1.11.12, Lachlan, 2007). Spectrograms were set at a: frame length – 5 ms; time step – 1 ms; maximum frequency – 22 kHz; dynamic range – 40 – 50 dB; dereverberation parameter – 100 % (as per Lachlan et al., 2013; 2016). A high-pass filter with a threshold of 1.0 kHz was added before spectrograms were created. The measurement procedure of each recording was two-fold: 1) identify contour parameters and 2) classify contours into single contour or repeated loops (contour loops). The methodology is detailed by Lachlan et al. (2013).

The fundamental frequency contour was defined as the lowest frequency band associated with a call and its harmonics were traced in a subsequent step once all fundamental frequencies in the file were traced. For Pulsed calls the lowest frequency band that spans the entire call was traced (as per Van Cise et al., 2017). This band was deemed to best correlated with the pulse repetition rate and most power, in line with the fundamental frequency of whistle calls (Watkins 1967). A maximum of 100 randomly chosen calls were traced per recording (Figure 3.2).

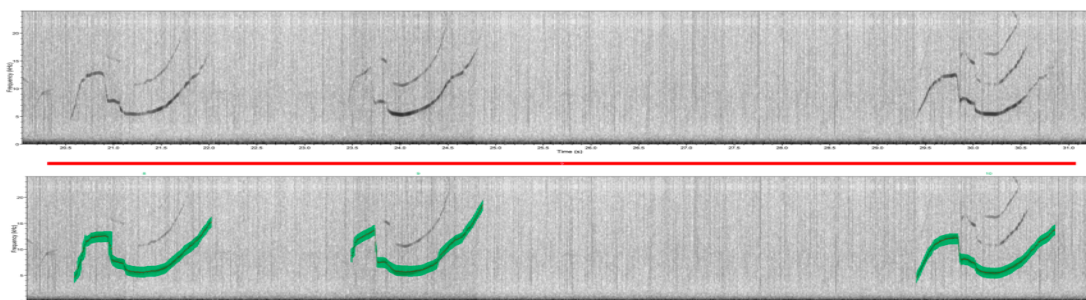


Figure 3.2: Example of manual call contour traces of fundamental frequency for a call with original spectrogram shown on top; the traced contour shown on bottom. Red line indicates loop range.

Calls made by several individuals vocalising simultaneously could potentially be incorrectly

identified as a multi-component call. To circumvent this bias, the multi-component label was only applied if it was detected > 3 times with equal component order and timing.

3.2.4 Data analysis

A multi-scale approach was applied to all analyses. The latest tools, techniques, and analytical approaches utilised three distinctive approaches. Geographic, intra- and inter-ecotype acoustic variations in Far North waters were identified. Analyses were performed at the encounter, recording, loop, and contour level for each geographic area (Bay of Islands, Cavalli Islands, Whangaroa Harbour, Doubtless Bay and wider survey) and ecotype (see Figure 3.3 for details).

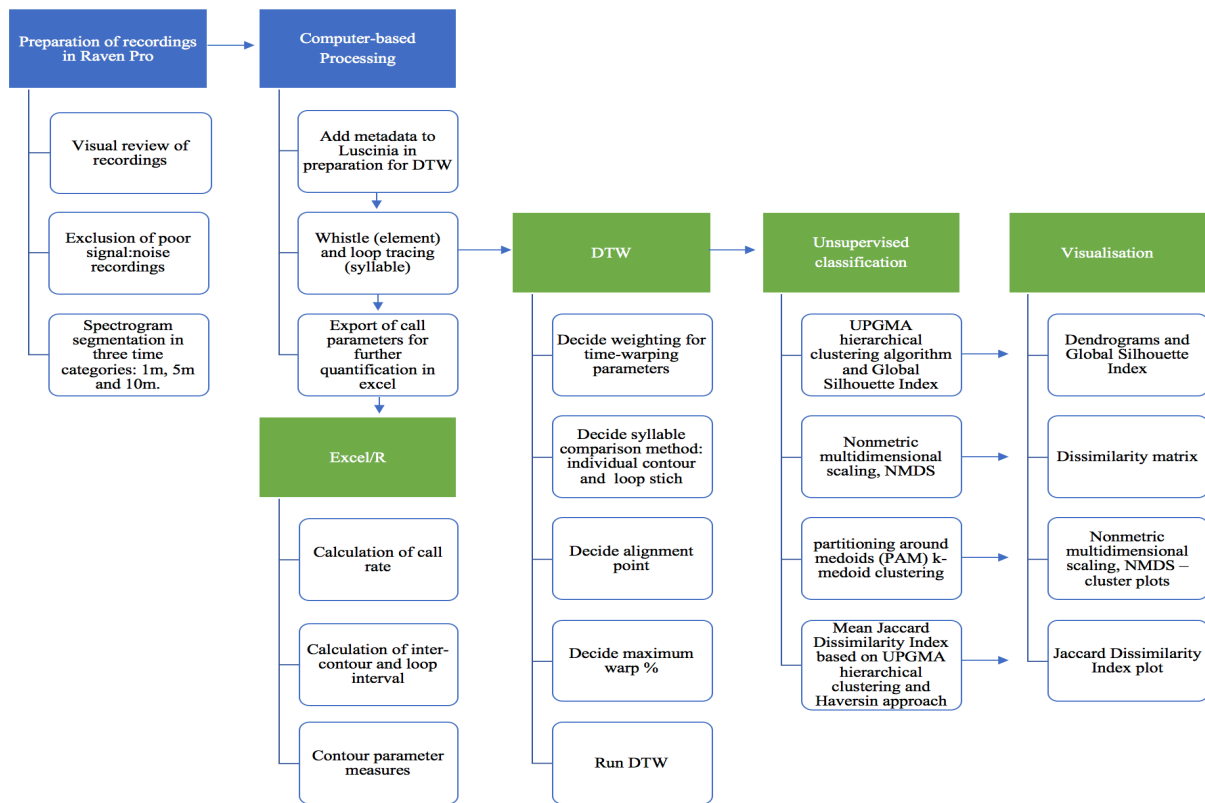


Figure 3.3: Illustration of key call data analysis steps and the order in which they were utilised. Blue background: data preparation and green background: data analysis.

Statistical analyses were conducted using free statistical software R (R Core Development Team, 2014, RStudio for Mac version 1.0.136) and the internal Luscinia tool set with the significance threshold set at 0.05, unless stated otherwise. Call rate and frequency parameter data were initially tested for normality and heterogeneity of variance, and subsequently analysed using the Shapiro-Wilk and Bartlett tests, respectively, to test if assumptions were violated. All data were also tested for significant variation at a seasonal and annual level. If significant variation was not detected, data were combined for subsequent analysis. If

significance was indicated, results were analysed independently. Results of assumptions tests determined whether parametric or non-parametric statistics applied, as appropriate. If non-parametric tests were required, Wilcoxon's rank sum or Kruskal-Wallis tests were utilised. To avoid pseudo-replication, only mutually exclusive data (not overlapping temporally) were used in the analysis (randomly selected).

To ensure the comparisons of calls across ecotypes were meaningful, a Chi-square test was utilised to ascertain whether the number of recordings made in each location and behaviour state were even for both ecotypes.











3.2.4.1 Test of the validity of the semi-automated call comparison method

The manual human comparison method was tested to ascertain the validity of the semi-automated method in detecting fine- and broad-scale variations in/between repertoires. Bottlenose dolphins are known to share call-types within a population, thus the algorithm was tested first regarding whether it could detect natural call-type categories, as obtained by visual categorisation of spectrograms. For that purpose, recordings containing a total of 200 good signal-noise ratio contours were tested, with 100 contours from each ecotype assessed independently, a sub-sample of overall data. The criteria for incorporating calls was high signal-to-noise ratio (2 and 3) and un-masked calls; otherwise call selection was random.

3.2.4.1.1 Visual categorisation of spectrograms

Human categorisation utilising a visual grouping task from spectrograms was performed in Raven 1.5 (Beta version, ©2002 – 2013 Cornell Lab of Ornithology, Bioacoustics Research Program) as outlined in section 3.2.4.1. Calls were manually categorised by five independent human judges. Each judge created, reviewed and edited slides in Microsoft PowerPoint, with each slide consisting of a single call group (pre-existing based on Table 3.1 or a new call type if no match was found) with the top example in the centre. The judges added any matches to the template around it, effectively clustering the data. One PowerPoint per ecotype was created, resulting in 12 files in total (five independent reviewers and lead researcher). The lead researcher (CHP) was also responsible for the creation of the template catalogue (based on the categories listed in Table 3.1) and randomly selecting the sample to be tested by all other judges.

Table 3.1: Base template for manual matching of bottlenose dolphin (*T. truncatus*) whistle contours (based on categorisations previously used for bottlenose dolphin in New Zealand, Boisseau, 2005; Guerra, 2013).

Call code	Start frequency	End frequency	Number of inflections	Call shape
1	low	high	0	
2	high	low	0	
3	low	high	1	
4	high	low	1	
5	low	high	1	
6	high	low	1	
7	low	high	2	
8	high	low	2	
9	low	high	>2	
10	high	low	>2	

Initially, the judges compared each call spectrogram in chronological order. Then the judges rated the similarity of each of the 100 call samples on a scale from 1 (call and template dissimilar) to 5 (call and template similar; as per Kriesell et al., 2014). All judges, apart from CHP, had no previous bioacoustics experience. Fleiss' Kappa statistic (k ; Gravetter & Wallnau, 2016) was used to compare the judges' ratings. This approach determined inter-observer call categorisation agreement and category consistency (calculated both with and without CHP's results). If all judges rated the samples identically, then $k = 1$ (Landis & Koch, 1977), alternatively k would equal 0 if agreement was as would be expected. Finally, an all-inclusive categorisation was completed based on the consistency test, which was then compared to an Unweighted Pair Group Method with Arithmetic Mean. An Unweighted Pair Group Method with Arithmetic Mean is an agglomerative (bottom-up) hierarchical clustering method (Sokal & Michener, 1958), which builds a dendrogram based on the pairwise similarity matrix structure.

3.2.4.1.2 Categorisation within Luscinia and method comparison

To detect natural clusters in the data, 100 calls for each ecotype were clustered using the Unweighted Pair Group Method with Arithmetic Mean hierarchical clustering algorithm and a Global Silhouette Index (Lachlan et al., 2013; Lifjeld et al., 2016). The Global Silhouette Index is created using a distance matrix (with Euclidean distance) generated during clustering to quantify how alike a call is to its own cluster (cohesion) vs other clusters (separation) (Rosenzweig, 1981). The visual representation displays the k -value (from k -medoid clustering) against the Global Silhouette Index. A peak in the Global Silhouette Index value (-1 – 1)

indicates the best clustering tendency for k . The resulting dendrograms were annotated with the categorisation given to each call during visual inspection to test for method alignment.

3.2.4.2 Geographic and ecotype variation in call production rate

The rates of production of calls were compared to assess specific call use as a function of area and ecotype. For all acoustic recordings containing calls, the rate of production of calls was standardised and calculated as calls per minute per dolphin in the following manner:

$$\text{call rate} = \frac{x_i * 60}{nt} \quad (1)$$

Where: i = recording

x_i = the number of individual calls heard in i th recording

n = the number of dolphins in the group (focal or sub)

t = the time elapsed from the first audible call to the last audible call

The number of dolphins in each focal group was estimated in the field using minimum, maximum, and best estimate, and was subsequently validated with photo-identification (details of methodology in Chapter 2). To avoid ‘call inflation’ on recordings, where dolphins were only audible for short periods, the value for t was set to a minimum of 60 s. Thus, if only two calls were heard 10 s apart during the entire recording, the call rate would be 2/min rather than 12/min. Although arbitrary, this approach was more appropriate than ignoring recordings with small t values, as significantly quiet recordings would be over represented (Boisseau, 2005). Oceanic bottlenose dolphin call rate was calculated from focal sub-groups size in order to minimise group size bias in estimates.

Given that call production is influenced by behavioural state (Boisseau, 2005), recordings were made from all behavioural states (Chapter 2). To ensure comparisons between the ecotypes and areas were meaningful, a chi-square test was utilised to ascertain if the numbers of recordings made during each behavioural state were comparable for the profile of each ecotype and area.

Further investigation of density dependence within ecotypes was achieved through comparison of Pearson correlation coefficients. Linear regression was additionally utilised to plot the call rate (measured as both calls per minute and calls per dolphin per minute) occurring within each group size interval for both ecotypes.

3.2.4.3 Comparison of call parameters

Seventeen time-frequency call parameters were measured from each call contour using Luscinia's measurement functions and visual assessment. Spectrograms of 50 randomly selected calls (independent of ecotype and geographic location) were analysed with successive measurements of 21, 41, 61, and 81 points and visually examined to determine the optimal peak frequency point number. Via this process, it was determined that 61 points provided the best call contour representation, because this value afforded the precision to detect subtle changes in frequency for longer duration calls without introducing excessive measurement repetition in shorter duration calls. Calls often have a harmonic structure which may be important in quantifying them individually (Lammers et al., 2003). However, in this study, the distance to signalling animals was unknown, hence harmonic information was unreliable due to the variable attenuation of higher frequencies over distance. As such, whilst it is included, it must be interpreted with caution. The 61 points were used in dynamic time warping analysis (see section 3.2.5.4.) and to measure parameters listed in Table 3.2. Additional measurements were assessed visually (lower section of Table 3.2).

Table 3.2: Contour parameters measured through the preparatory stage of 61-point dynamic time-warp analysis and additional visual assessment.

Parameter	Definition
Measurements were assessed using a 61-point contour trace in Luscinia:	
Peak frequency	Frequency at which the highest amplitude occurs
Peak time	Time at which the highest amplitude occurs
Centre time	Amplitude-weighted central time (i.e. the time at which half of the call's cumulative energy has been produced)
Mean frequency	Mean frequency throughout the entire call
Start frequency	Frequency at the start of the call
End frequency	Frequency at the end of the call
Minimum frequency	Lowest frequency throughout the entire call (also referred to as fundamental frequency)
Maximum frequency	Highest frequency throughout the entire call
Frequency range	Disparity between minimum and maximum frequency
Time of minimum frequency	Measured as a proportion of call length
Time of maximum frequency	Measured as a proportion of call length
Length (s)	Total duration of call
Additionally, the following measurements were added visually (not using 61-point assessment) building from the contour traced in Luscinia:	
Number of Harmonics	Number of harmonics visible on the spectrogram
Number of inflections (+ to -)	Changes in contour gradient from upsweep – downsweep
Number of inflections (- to +)	Changes in contour gradient from downsweep – upsweep
Inflection timing	All inflection times (measured as proportion of call length)
Inflection frequencies	Frequency values at inflection points

All parameters, except mean and peak frequency, were found to possess homogenous variances between areas and ecotypes. As a result, for mean and peak frequency, the Welch statistic was used in lieu of the F statistic, as it represents a robust proxy when group variances are unequal. Non-parametric testing was utilised when parameters were not normally distributed.

3.2.4.4 Ecotype variation in call repertoire

Luscinia's dynamic time warping algorithm was utilised to compare whistle and burst pulse contours from recordings of repertoires grouped across ecotype, encounter, recording, and geographic location (Lifjeld et al., 2016). The algorithm seeks the optimal alignment of contours/loops and facilitates the comparison of pairs of loops through the measurement of Euclidean distances along contours/loops. The dynamic time warping technique considers the frequency modulation of all variables inside loops. This results in a more holistic comparison of loop and contours than comparisons of single parameters (maximum frequency, loop length, etc.; e.g., Gridley et al., 2014; Lifjeld et al., 2016; Figure 3.4). Implementation steps are detailed in section 3.2.4.4.1. and followed Lifjeld et al. (2016). The dynamic time warping process in Luscinia has several advantages for this study, namely (Lachlan, 2007):

1. Interpolation between points, optimising scoring for rapidly modulated contours.
2. Includes time as an acoustic feature, which accommodates the comparison of signals that have a varied length to be flexibly compared.
3. Allows 'break-points' between loops, allowing for the reliable comparison of multi-loop calls with different numbers of contours.
4. Permits flexible normalisation. The sample standard deviation and weighting determined by analysis of acoustic features is combined.

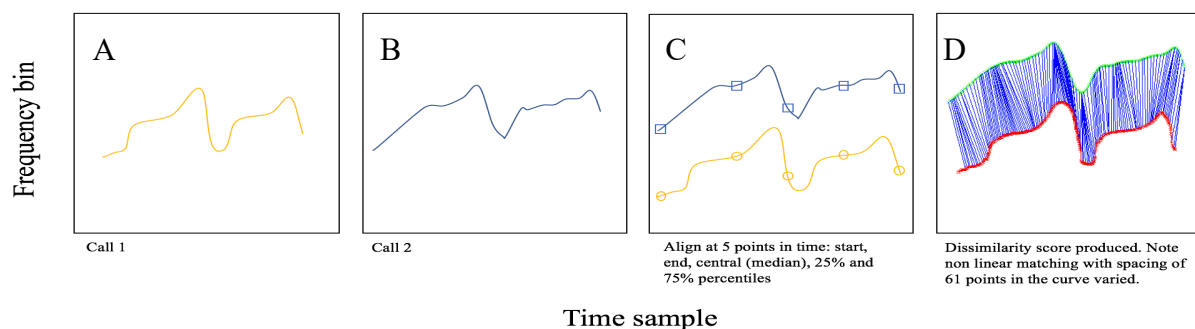


Figure 3.4: Illustration of the dynamic time warping process. The A) and B) frame display the unmodified traced contours, C) contours with transformation alignment to achieve the minimum least-squares distance between the two, and D) shows a dynamic time warping measurement cross-comparison following warping.

3.2.4.4.1 Call repertoire analyses - preparing contours

A fundamental step in this analysis is to normalise contour features relative to each other. Every 1 ms four acoustic features were measured, namely: time, fundamental frequency, fundamental frequency change, and vibrato amplitude. The parameter weightings utilised in this analysis were: *Time* – 10.0; *Fundamental Frequency* – 7.386; *Fundamental Frequency Change* – 7.203; *Vibrato Amplitude* – 0.009; *all others* – 0. The chosen values were dictated by the bottlenose dolphin database using the inverse of standard deviations of each parameter. This includes all parameters except time, where the mechanism of normalisation differs (refer to Lachlan et al. (2013) and Lifjeld et al. (2016), for further explanation). The inclusion of time facilitates the quantitative assessment of contours of differing lengths. The rationale behind including fundamental frequency change was that delphinids (including bottlenose dolphins) are cable of perceiving both relative and absolute frequency change (Thompson & Herman, 1975).

Finally, the occurrence of periodic oscillation in frequency (perceived as a buzz) is measured through *vibrato amplitude*. Weber's Law is a good estimate of animal perception (Akre et al., 2011), including for some of the features examined (Jacobs, 1972; Yunker & Herman, 1974). Weber's law suggests the difference in size (i.e., delta I) is continually proportional to the original stimulus (Formankiewicz & Mollon, 2009; Pienkowski & Hagerman, 2009). As such, measurements were transformed to reflect this principal. Log transformation achieved this for *fundamental frequency* and *vibrato amplitude*. The resulting log-transformed frequency was used to calculate *fundamental frequency change*. The acoustic parameters were normalised by (Lachlan et al., 2013):

$$X'_{i,j,k} = X_{i,j,k}(W_k/S_k) \quad (2)$$

Where $X_{i,j,k}$ is the value of i (contour/loop) at j (time point) for feature k (segment), and w and s are normalisation parameters. For the above three parameters, s was the mean of ecotype/location standard deviations (*fundamental frequency*: 0.363; *fundamental frequency change*: 0.113; *vibrato amplitude*: 2.96). Time was treated differently, with s calculated as the duration of the longer contour/loop in each pairwise contour/loop comparison. With this approach, an 8 ms contour would be as different from a 4 ms contour as a 0.8 ms contour would be from a 4 ms contour, if all other parameters are equal (Lachlan et al., 2013). w was set to 1 for all parameters apart from time (fixed to 10), which decided using test datasets. *Compression* = 0.2 (min length of 10), *time standard deviation* = 1, *loop repetition weighting* = 0.2, and a

maximum warp = 100 % (Lifjeld et al., 2016). This meant that these measurements were averaged over 5 ms non-overlapping windows for elements longer than 50 ms, and that, for shorter elements, windows were made of a length to generate 10 measurements per element. This averaging procedure reduced measurement error. Additionally, the *weight by relative amplitude*, *log transform frequencies*, *interpolate in time warping* and *dynamic warping* preferences were chosen (Lifjeld et al., 2016, p. 6). All comparisons utilised a stitch loops method with 5 alignment points (Lachlan, 2007).

3.2.4.4.2 Vocalisation comparison - measuring contours, loops and repertoires

The steps of contour and loop (two separate assessments) comparison were as follows (modified from Lachlan et al., 2013):

- 1) Generate a dissimilarity matrix of normalised measurements of contour pairs (A & B, of lengths n & m). Each point in A was compared to each point-to-point segment in B.
- 2) Measure distances between segments (to generate accurate distance measures for modulated signals). The distance between point i in A and segment jk in B was calculated as (Lachlan et al., 2013):

$$d_{i,j}^2 = \begin{cases} \partial_{ij}, \partial_{ij} < \partial_{ik} - \partial_{jk} \\ \partial_{ik}, \partial_{ik} < \partial_{ij} - \partial_{jk} \\ \partial_{ij} - (\partial_{ij} + \partial_{jk} - \partial_{ik})^2 / 4\partial_{jk}, \text{ otherwise} \end{cases} \quad (3)$$

Where $\partial_{ij} = \sum_h^4 (X'_{A,i,h} - X'_{B,j,h})^2$ is the squared Euclidean distance between the normalised measurements at point i and j .

- 3) The optimal dissimilarity matrix path was calculated through the Luscinia dynamic programming algorithm (Lachlan, 2007), with the calculation of recurrence (Lachlan et al., 2013):

$$\gamma_{i,j} = d_{i,j} + \min(\gamma_{i-1,j}, \gamma_{i,j-1}, \gamma_{i-1}, \gamma_{j-1}) \quad (4)$$

- 4) The analysis steps culminated in an overall dynamic time warping distance (D_{AB}) between A and B (contours or loops). D_{AB} was then given by $\gamma_{n,m-1}/l$, where l is the path length of the trajectory followed from $\gamma_{1,1}$ to $\gamma_{n,m-1}$ by the dynamic time warping algorithm (Lachlan et al., 2013). Due to the point-to-segment measurements, D_{AB} was

not symmetric, thus the larger distance (D_{AB} and D_{BA}) of each pair-wise comparison was chosen (Lachlan et al., 2013).

- 5) A final feature was included to represent the repetitions of contours/loops within their 1-min recording. Log transformation was also utilised; s was calculated as the mean standard deviation across ecotypes/locations, and w was 0.2. The result gave an overall measure of contour/loop dissimilarity within recording.

The steps of repertoire comparison follow on from the above (modified from Lachlan et al., 2013). Contour/loop dissimilarities were joined to quantity repertoire dissimilarities using a subsequent dynamic time warping algorithm. The key difference in this analysis was the comparison between recordings. The initial dissimilarity matrix, D , in this analysis comprises the contour/loop dissimilarity measures and the dynamic time warping algorithm searched for the optimal alignment of contours/loops between recordings. Normalisation was achieved using the recording with the highest number of contours/loops (Lachlan et al., 2013):

$$\begin{aligned}\Gamma_{i,j} &= D_{ij} + \min(\Gamma_{i-1,j}, \Gamma_{i,j-1}, \Gamma_{i-1,j-1}) \\ X &= \Gamma_{n,m} / \max(n, m)\end{aligned}\tag{5}$$

Here, the first line portrays the recurrence used to calculate the dynamic time warping. The normalisation for two recordings of lengths n and m (both 1 min) and number of traced contours/loops, respectively, is shown in line two. The result was the recording dissimilarity, X . The dissimilarities identified were the basis of subsequent analysis.

3.2.4.4.3 Vocalisation comparison – grouping across ecotypes

A Unweighted Pair Group Method with Arithmetic Mean clustering analysis of recordings and encounters was utilised initially, followed by a partitioning around medoids k-medoid clustering algorithm to additionally cluster repertoires. Subsequently, the Global Silhouette Index for each k-value was calculated to search for natural clusters in the dataset. Differences repertoire and loop variability between ecotypes/locations were tested next using Anderson's test of multivariate dispersion (Anderson, 2008). Once a principal coordinates ordination of the dissimilarity matrix was completed, the distance between each datapoint and the spatial median of the corresponding ecotype was calculated. This was founded on a nonmetric multidimensional scaling ordination of the data, using 2 dimensions – x,y (Lachlan et al., 2013). Different repertoires within an encounter were not statistically independent, so the

distances to the spatial median of each repertoire or loop were averaged to generate encounter scores of variability. The level to which repertoires were more similar to their own ecotypes spatial median than to the other ecotypes spatial median needed to be quantified (as per Lifjeld et al., 2016). In order to quantify this divergence, d_{AB} , between ecotypes, A and B , was assessed as (Lachlan et al., 2016; Lifjeld et al., 2016):

$$d_{AB} = \frac{\sum_{i=1}^{n_A} d_{i,SB} - d_{i,SA}}{n_A} + \frac{\sum_{j=1}^{n_B} d_{j,SA} - d_{j,SB}}{n_B} \quad (6)$$

with a sample size of n_A and n_B . The divergence between a data point (i) and the spatial median of ecotype A and B , respectively, is represented by $d_{i,SA}$ and $d_{i,SB}$ (Lachlan et al., 2013; Lifjeld et al., 2016). The resulting scores were subsequently compared between ecotypes/locations using an F-test dissimilarity score. Distance distribution frequency plots draw the dissimilarity scores at varying levels: 1) over the whole dissimilarity matrix (overall); 2) within individual recordings (individual); 3) within areas (area); and 4) within ecotype (ecotype).

3.2.4.5 Micro-geographic variation in call repertoire

The geographic distance between encounters (with research vessel utilised as a proxy) was calculated using the Haversine approach distance (for summary refer to Brummelen, 2013). Each pair (of recordings) was ranked by their corresponding encounter's geographical distance and then categorised into 20 evenly-sized distance bins. The Jaccard Index calculated repertoire similarity, which is the proportion of common contours (categorised from hierarchical clustering) produced during the two recordings. The hierarchical clustering solution with the highest Silhouette Index was applied to provide the overall number of categories. A Jaccard Index between samples was calculated based on this categorisation. The mean Jaccard Index for each of the distance categories was plotted (with 95 % mean confidence intervals). This was calculated by a delete-half jackknife method, with 10,000 bootstrap repetitions. Each repetition removed half of the recordings (selected randomly).

3.3 Results

3.3.1 Study effort

Acoustic data were collected in Far North waters from September 2013 – September 2015. Prior to analysis, a total of 118 recordings were categorised as containing no identifiable

bottlenose dolphin calls. These were excluded from the subsequent analysis, leaving 1,017 valid recordings. A total of 31 coastal bottlenose dolphin encounters resulted in 827 1-min long recordings yielding a total sample of 12,661 calls. In addition, a total of 36 encounters (4 with oceanic bottlenose dolphin only and 32 sub-groups from 6 oceanic bottlenose dolphin mixed encounters), resulted in 190 1-min long recordings, generating a total sample of 18,972 calls. Examples of acoustic data are shown in Figure 3.5 and a summary of acoustical field research efforts are provided in Appendix 1.1.

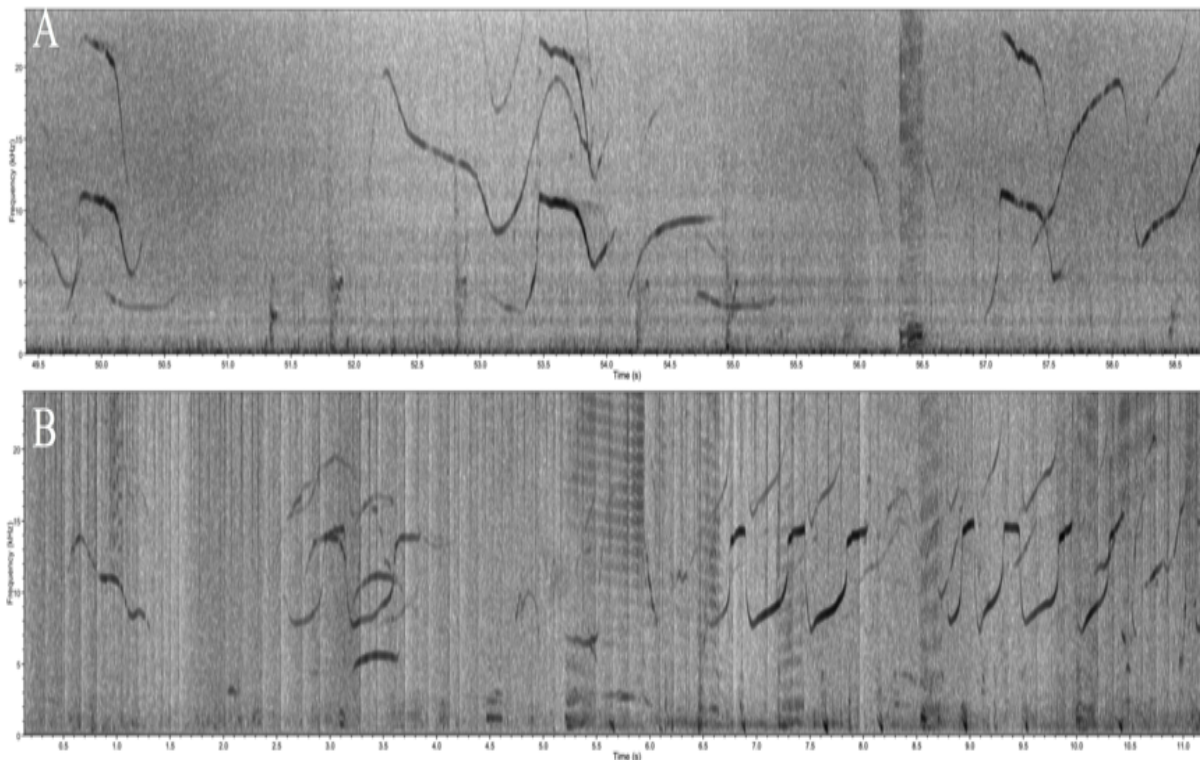


Figure 3.5: Example spectrograms from a range of vocalisations, including calls with A) coastal bottlenose dolphin and B) oceanic bottlenose dolphin (*T. truncatus*).

The number of recordings made for each of the four locations were compared and found to be significantly different in coastal bottlenose dolphins ($X^2 = 2.38$; $df = 3$; $P = 0.261$). However, when grouped into Bay of Islands and non-Bay of Islands (Cavalli Islands, Whangaroa Harbour and Doubtless Bay), no evidence of a difference was found between recordings ($X^2 = 7.03$; $df = 1$; $P = 0.282$; Table 3.3). This grouping was therefore used in analysis first, before analysing only by region, where appropriate. No significant difference was detected in the number of recordings made in each behavioural state at each location for coastal bottlenose dolphins (Table 3.3). As oceanic bottlenose dolphins mainly used wider survey areas (Chapter 2), no differentiation between areas could be determined.

Significant evidence of a difference was found for the number of recordings made for each ecotype ($P = 0.042$; Table 3.3). This was considered for ecotype comparisons in all analyses. Recordings were taken during all six behavioural states. The number of recordings made during behavioural states were not equal between ecotypes ($P = 0.081$; Table 3.3), though were comparable within ecotype proportions.

Table 3.3: Number of recordings made in each comparison category for all behavioural states of common bottlenose dolphin (*T. truncatus*) ecotypes. Note, CBD = coastal bottlenose dolphin, OBD = oceanic bottlenose dolphin, BOI = Bay of Islands.

Predominant surface behaviour	CBD	% of total	OBD	% of total	Total	<i>P</i> value	CBD		<i>P</i> value
							BOI	non-BOI	
Socialising	203	23.3	62	32.6	265	0.011	113	90	0.391
Travelling	146	16.7	40	21.1	186	0.042	79	67	0.386
Diving	133	15.3	35	18.4	168	0.037	73	60	0.222
Milling	103	11.8	19	10.0	122	0.040	48	55	0.319
Foraging	192	22.0	22	11.6	214	0.024	102	90	0.213
Resting	95	10.9	12	6.3	107	0.041	46	49	0.201
Total	872	-	190	-	1,062	0.042	461	411	0.282

3.3.2 Tests of the validity of the semi-automated call comparison method

A high inter-observer categorisation agreement was detected amongst judges (Fleiss' kappa statistic excluding CHP: $k = 0.839$, number of judges = 5, $Z = 56.2$, $P = 0.002$). Additionally, 83 % of categorisations matched CHP's assessment. The majority of difference between CHP and other judges (76 % differences in categorisation) were a result of ambiguity in one call type. Overall, the presence of clearly distinct call types was detected in the repertoire of bottlenose dolphins, as demonstrated by visual categorisation results. This supports the use of visual categorisation prior to comparison using a semi-automated methodology.

The visual and computational categorisation of coastal bottlenose dolphin call contours clustered the same call-types together. Additionally, the highest Global Silhouette Index was 0.29, indicating a moderate clustering tendency, with 28 clusters. The estimate of the number of call-types in the dataset based on visual categorisation was 22 clusters. Comparable concordance was also found for oceanic bottlenose dolphins, indicating that ecotype did not affect methodology success. All visually identified call-types clustered together, except in a single case (for group 14, see Appendix 3.1). Additionally, a Global Silhouette Index high of 0.26 suggested a moderate clustering tendency, with a total of 24 clusters. Visual categorisation estimated 20.8 % less clusters with 19 identified call types. In conclusion, both methods resulted in comparable categorisation of clusters, thus validating the computational method.

3.3.3 Geographic and ecotype variation in call production rate

As call rates were not normally distributed, comparisons between areas and ecotypes were made using a Kruskal-Wallis test (Table 3.4). The rates of all calls varied significantly between the two ecotypes, even in comparable locations (Table 3.4). As a result, the total rate of call production (per minute per dolphin) also varied between ecotypes, being higher in oceanic bottlenose dolphins than coastal bottlenose dolphins ($X^2 = 85.90$, $P < 0.0001$). The total number of calls recorded from dolphin groups regardless of group size (measured as calls per minute), was also higher in oceanic bottlenose dolphins (mean per group 10.01 ± 2.38 coastal bottlenose dolphin vs 51.00 ± 13.21 oceanic bottlenose dolphin).

Table 3.4: Comparison of call rates (per minute per dolphin) between common bottlenose dolphin ecotypes (*T. truncatus*) and area (in coastal bottlenose dolphin only) using Kruskal-Wallis. Values in bold are significant at the 95 % level. SE is illustrated in brackets.

Call	Median values		X^2	P
	coastal ecotype	oceanic ecotype		
Total/min	10.01 (1.31)	51.00 (17.82)	203.18	< 0.0001
Total/min/dolphin	0.31 (0.01)	0.62 (0.02)	85.90	< 0.0001
	Bay of Islands	Non-Bay of Islands		
Total/min	11.30 (2.35)	3.12 (0.08)	18.28	< 0.0001
Total/min/dolphin	0.61 (0.0.3)	1.50 (0.04)	15.44	< 0.0001

Further evidence of density dependence within ecotypes was provided by comparison of Pearson correlation coefficients. Significant positive correlations existed between group size and total call rate ($r = 0.289$, $P < 0.0001$ oceanic bottlenose dolphin; $r = 0.158$, $P < 0.0001$ coastal bottlenose dolphin). Conversely, there was a significant negative correlation between group size and total call rate/dolphin for coastal bottlenose dolphins ($r = -0.372$, $P < 0.0001$) and oceanic bottlenose dolphins ($r = -0.280$, $P = 0.871$, Figure 3.7). Thus, it appears that as group size increased, overall call rate increased but individual dolphins tended to call proportionally less for both ecotypes. Group size of coastal bottlenose dolphins (median = 21 animals, range = 1 – 48, $n = 31$) was not significantly smaller than for oceanic bottlenose dolphins (median = 48 animals, range = 5 – 70, $n = 36$; Mann-Whitney test, $W = 402$, $P = 0.28$).

Similar trends were evident in the Bay of Islands for the coastal bottlenose dolphin ecotype. Significant positive correlations existed between group size and total call rate per minute ($r = 0.120$, $P = 0.0017$). Conversely, significant negative correlation was found when comparing group size with total call rate ($r = -0.349$, $P < 0.0001$; Figure 3.7). Thus, it also appears that in

Bay of Islands waters, as group size increased, overall call rate increased but not in proportion with the number of individual dolphins, which indicates individuals may call proportionally less. In all other areas, no significant correlation was found. This suggests that density dependence in coastal bottlenose dolphins is most prevalent in the Bay of Islands. As all recordings were taken in only two areas for oceanic bottlenose dolphins, it was not possible to assess the correlation between areas and call rates.

In non-Bay of Islands waters, grouping variation was additionally assessed for each area. The total rate of call production varied between areas in coastal bottlenose dolphins, being higher in Doubtless Bay than all other areas ($X^2 = 103.24$, $P < 0.001$). When comparing areas, the total number of calls recorded from dolphin groups, regardless of group size, was higher in the Bay of Islands and comparatively lower in Doubtless Bay ($X^2 = 32.01$, $P > 0.001$) and Whangaroa Harbour ($X^2 = 30.72$, $P < 0.001$), and lowest in Cavalli Islands ($X^2 = 85.90$, $P < 0.001$). However, within each area, no significant variation was detected, suggesting a density dependent element to call production.

Further evidence of density dependence within ecotypes was provided by comparison of Pearson correlation coefficients. Results from cross-validated testing suggested up to 89.4 % of all recordings, and 63.2 % of all coastal bottlenose dolphin recordings, may be assigned correctly to ecotype and location (Bay of Islands, non-Bay of Islands), respectively, based solely on production rate during each recording (Table 3.5). Most false categorisations were the result of attributing recordings from Whangaroa Harbour to the Bay of Islands (21.3 %) and the Bay of Islands to Whangaroa Harbour (6.0 %). Cavalli Islands and Doubtless Bay were correctly assigned on 100.0 % and 99.2 % of occasions, respectively.

Table 3.5: Cross-validated categorisation of recordings to ecotype (coastal bottlenose dolphin or oceanic bottlenose dolphin, *T. truncatus*) and area (in coastal bottlenose dolphin only) based solely on call rates. The mean correct categorisation rate is 89.4 % (50.0 % expected by chance) for ecotype and 63.2 % by area for coastal bottlenose dolphin.

Observed	Predicted	
	Oceanic bottlenose dolphin	Coastal bottlenose dolphin
Oceanic bottlenose dolphin	88	12
Coastal bottlenose dolphin	21	79
	Bay of Islands	non-Bay of Islands
Bay of Islands	52	48
non-Bay of Islands	19	81

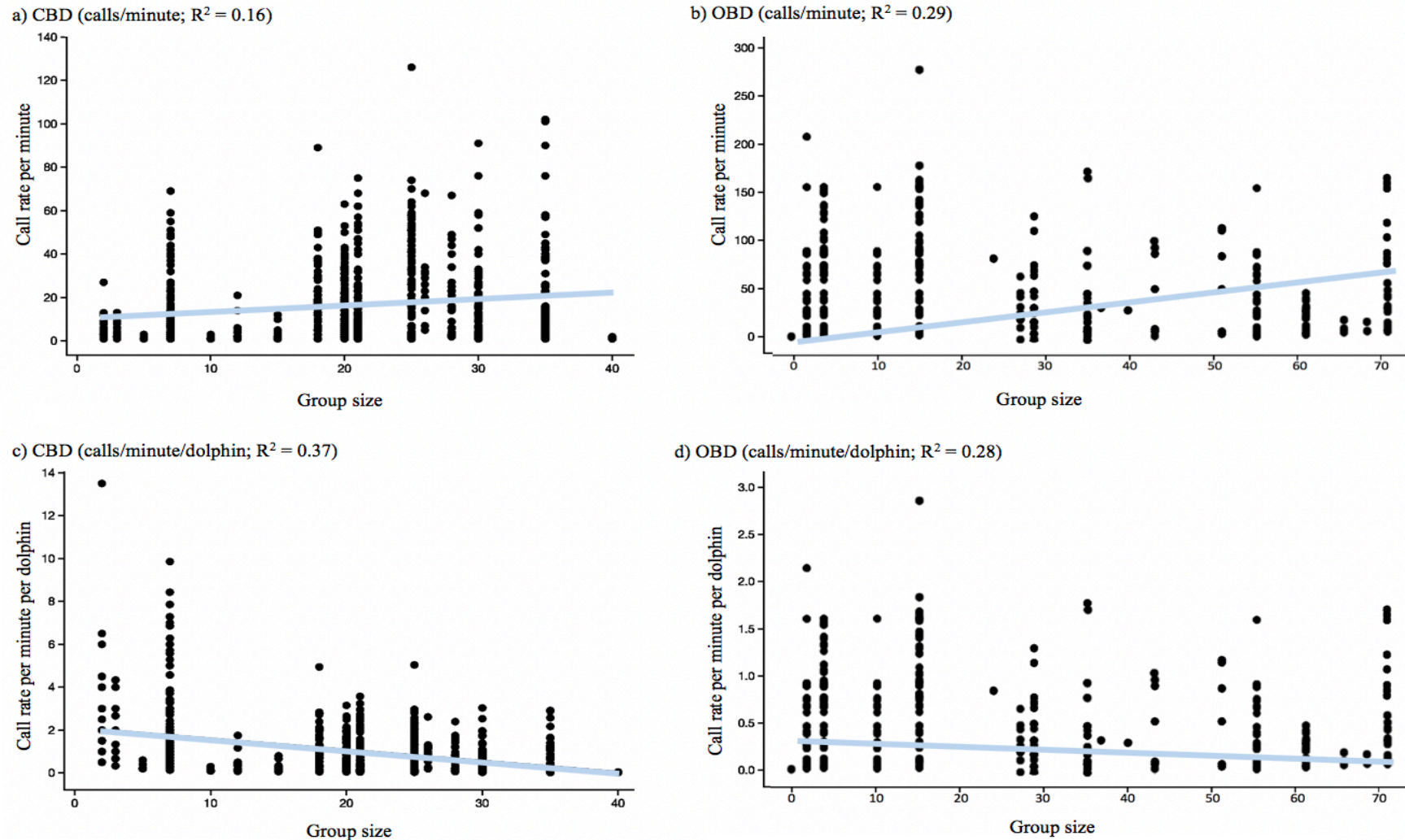


Figure 3.7: Linear regression of call rate (measured as both calls per minute and calls per dolphin per minute) against group size in bottlenose dolphins (*T. truncatus*). Note, CBD = coastal bottlenose dolphin and OBD = oceanic bottlenose dolphin.

3.3.4 Comparison of call parameters

Broadband recordings suggested the fundamental frequencies of calls very rarely rose beyond 25 kHz, therefore it is assumed that the omission of calls reaching higher fundamental frequencies will not overly bias the dataset. Consequently, from an original dataset of 31,633 calls, 201 were excluded due to the contour of the fundamental frequency exceeding 22 kHz (the upper limit of analysis used in this thesis due to the focus on social acoustics with fundamental energy in the 0 – 22 kHz range). These exclusions represented 0.14 % of all coastal bottlenose dolphin samples ($n = 18$) and 0.97 % of oceanic bottlenose dolphin samples ($n = 183$). Contours thought to represent repeated calls (either by the same individual or a ‘call mimic’) were further excluded from the analysis.

Call repeats of this kind were common within recordings. Of the 31,432 calls considered to have high signal to noise ratio (i.e., recording quality 3), 9,128 appeared to be repeats (approximately 29.1 %). However, due to the problems associated with identifying calling dolphins, it is not clear if these represented individual repetition or call mimicry. Some idiosyncratic calls were recorded days, weeks, months, and even years apart (Appendix 3.2). As signaller identity was undefinable in this study, assessment of the signature-call hypothesis was not feasible for these ecotypes. Recordings made from dolphins in small groups may allow further insight into call signatures, however small groups were rare in the present study so repeats were not excluded.

Mean call parameter measures are given in Table 3.6, and results of one-way analysis of variance for each ecotype to investigate differences between call parameters recorded for coastal bottlenose dolphin and oceanic bottlenose dolphin are summarised in Table 3.7. Note, true independence cannot be achieved here due to repeated contour types. The calls recorded from oceanic bottlenose dolphins were found to have significantly ($P > 0.05$) higher measures for 71.4 % of call parameters (Table 3.6 – 3.8). Coastal bottlenose dolphin call duration was significantly longer ($X^2 = 21.13$, $P < 0.010$, Table 3.8). Oceanic bottlenose dolphin calls had significantly more visible harmonics and contour inflections (both positive to negative and *vice versa*, Table 3.8). Results suggest the calls recorded in oceanic bottlenose dolphins contained more information than those of coastal bottlenose dolphins, as reflected by their more complicated contours, even though the duration of calls was shorter.

Table 3.6: Summary of means (and standard deviations, SD) for parametric parameters measured from calls recorded in both ecotypes of common bottlenose dolphin (*T. truncatus*).

Parameter (kHz)	coastal ecotype (n = 12,643)		oceanic ecotype (n = 18,789)	
	Mean	SD	Mean	SD
Mean frequency	10.38	3.03	11.22	3.02
Start frequency	9.74	3.85	10.67	3.87
End frequency	11.21	4.55	10.79	4.25
Minimum frequency	7.43	2.82	8.31	2.92
Maximum frequency	13.90	3.94	14.12	3.70
Frequency range	8.07	3.45	9.32	3.70
Peak frequency	10.36	3.03	11.23	3.02

Table 3.7: Summary of one-way analysis of variance (ANOVA) for frequency parameters measured from whistles recorded in both ecotypes of common bottlenose dolphin (*T. truncatus*). Values in bold are significant at the 95 % level. * represents square root transformed data; ** represents the use of the Welch test in lieu of the *F* statistic if variances were not homogenous (i.e. for significant Levene tests). Note, parameters are measured between and within groups. Ecotype (coastal or oceanic) is a factor.

Parameter		Levene Statistic	Levene <i>P</i>	Mean sum of squares	<i>F</i>	<i>P</i>
Mean frequency	Between	10.76	0.001	57.21	118.05**	< 0.0001**
	Within			12.66		
Start frequency*	Between	1.48	0.224	0.09	33.17	< 0.0001
	Within			0.91		
End frequency*	Between	0.01	0.922	0.87	4.33	0.042
	Within			0.92		
Minimum frequency	Between	1.30	0.255	0.15	63.31	< 0.0001
	Within			4.71		
Maximum frequency	Between	0.55	0.457	79.47	47.93	< 0.0001
	Within			23.01		
Frequency range	Between	0.03	0.947	103.03	42.15	0.020
	Within			17.89		
Peak frequency	Between	11.46	0.001	53.24	86.48**	< 0.0001**
	Within			11.16		

Table 3.8: Summary of Kruskal-Wallis test for non-parametric call parameters measured from both coastal bottlenose dolphin and oceanic bottlenose dolphin (*T. truncatus*) ecotypes. Values in bold are significant at the 95 % level. Note, rel = relative, freq = frequency.

Parameter	coastal ecotype (n = 12,643)		oceanic ecotype (n = 18,789)		<i>X</i> ²	<i>P</i>
	Median	I-Q range	Median	I-Q range		
Duration (s)	0.75	0.52-0.83	0.63	0.57-0.70	21.13	< 0.010
Prop time of min freq	0.52	0.31-0.64	0.54	0.46-0.59	1.86	0.172
Prop time of max freq	0.57	0.39-0.65	0.52	0.41-0.61	1.18	0.291
Harmonics #	0.69	0.51-0.70	3.72	3.12-4.01	24.85	< 0.010
Major inflections +to-	1.51	1.39-1.72	1.83	0.95-1.24	24.01	< 0.010
Major inflections -to+	0.87	0.12-0.93	1.25	1.13-1.57	16.72	< 0.010
Rel time of peak freq	0.49	0.35-0.56	0.54	0.10-0.71	2.74	0.087
Rel centre time	0.46	0.32-0.58	0.53	0.28-0.78	3.01	0.062

Additional analysis at various locations for coastal bottlenose dolphins is provided in Table 3.9-3.11. In coastal bottlenose dolphins, the calls recorded in the Bay of Islands were found to have higher measures for all parameters, except minimum frequency, and significantly ($P > 0.05$) higher measures for 42.9 % of call parameters (Table 3.9 – 3.11). Call duration varied between locations, being significantly ($X^2 = 35.04$, $P = 0.033$) longer in the Bay of Islands (Table 3.11). Bay of Islands calls also had significantly more contour inflections (particularly positive to negative), whilst non-Bay of Islands calls had significantly more visible harmonics (Table 3.11). These results suggest the Bay of Islands calls contained more information than those in non-Bay of Islands areas, as reflected by their longer durations and more complicated contours.

Table 3.9: Summary of means (and standard deviations, SD) for parametric parameters measured from calls recorded from Bay of Islands and non-Bay of Islands coastal bottlenose dolphins (*T. truncatus*).

Parameter	non-Bay of Islands (n = 7,089)		Bay of Islands (n = 5,554)	
	Mean	SD	Mean	SD
Mean frequency (kHz)	10.36	3.02	11.54	3.56
Start frequency (kHz)	9.73	3.85	10.27	3.87
End frequency (kHz)	11.19	4.53	12.84	5.30
Minimum frequency (kHz)	7.70	2.79	6.49	3.44
Maximum frequency (kHz)	14.82	3.95	15.71	4.59
Frequency range (kHz)	8.12	3.04	9.42	3.11
Peak frequency (kHz)	9.70	3.40	11.18	4.17

Table 3.10: Summary of frequency parameters measured from whistles recorded from the common bottlenose dolphin (*T. truncatus*) coastal ecotype. Values in bold are significant at the 95 % level. * represents square root transformed data; ** represents the use of the Welch test in lieu of the F statistic if variances were not homogenous (i.e. for significant Levene tests). Note, parameters are measured between and within groups. Location (Bay of Islands and non-Bay of Islands) is a factor.

Parameter		Levene Statistic	Levene P	Mean sum of squares	F	P
Mean frequency	Between Within	13.21	< 0.0001	40.21 6.85	79.79**	< 0.0001**
Start frequency*	Between Within	0.35	0.554	0.05 0.47	5.66	0.721
End frequency*	Between Within	1.80	0.053	0.64 0.72	4.18	0.375
Minimum frequency	Between Within	13.48	< 0.0001	0.10 3.22	6.30**	0.814**
Maximum frequency	Between Within	14.33	< 0.0001	94.35 20.90	41.99**	< 0.0001**
Frequency range	Between Within	0.05	0.835	105.42 14.63	42.15	0.024
Peak frequency	Between Within	18.52	< 0.0001	54.71 11.15	5.69**	0.911**

Table 3.11: Summary of Kruskal-Wallis test for non-parametric call parameters measured from Bay of Islands and non-Bay of Islands coastal bottlenose dolphins (*T. truncatus*). Bold values are significant at the 95 % level. Note, rel = relative, freq = frequency.

Parameter	Bay of Islands median	I-Q range	non-Bay of Islands median	I-Q range	X^2	<i>P</i>
Duration (s)	0.75	0.51-0.80	0.61	0.46-0.81	35.04	0.033
Prop time of min freq	0.42	0.29-0.65	0.48	0.27-0.69	3.72	0.260
Prop time of max freq	0.49	0.28-0.57	0.50	0.31-0.62	4.38	0.745
Harmonics #	0.61	0.54-0.72	0.83	0.51-0.70	27.35	< 0.010
Major inflections +to-	1.56	1.36-1.78	1.41	1.30-1.56	19.06	0.021
Major inflections -to+	0.76	0.37-0.94	0.75	0.52-0.87	1.81	0.051
Rel time of peak freq	0.43	0.35-0.56	0.49	0.37-0.53	2.01	0.068
Rel centre time	0.47	0.30-0.53	0.49	0.34-0.52	2.71	0.063

3.3.5 Ecotype variation in call repertoire

For the coastal bottlenose dolphin, recordings came from an estimated population of 358 (CV: 18 %; 95 % confidence interval (CI): 251 – 437) with varying spatial use of the Far North waters (as defined in Chapter 2). As for the oceanic bottlenose dolphin, recordings originated from groups where social structure data were not available. This is likely a result of the large Far North waters population size (3,914, SE = 197, Chapter 2) and the spatial/temporal distance between encounters, thus variation in the social group at each encounter may be represented in the results.

Call repertoires were compared to assess frequency distribution at varying levels (individual, location, ecotype (coastal bottlenose dolphin or oceanic bottlenose dolphin)). The distance distribution analysis indicated that intra-ecotype frequency distribution had lower dissimilarities than the overall (intra-ecotype) distribution. When moving along the x-axis, the intra-ecotype frequency distribution has lower dissimilarities (peaking at 0.35) than the overall (inter-ecotype) distribution (peaks ~0.37, Figure 3.10). Individual recordings have the lowest dissimilarity of 0.31, with some possible correlation from repeated loops (Figure 3.8). Area dissimilarity (peaks at ~0.38) is very similar to overall dissimilarity (Figure 3.8).

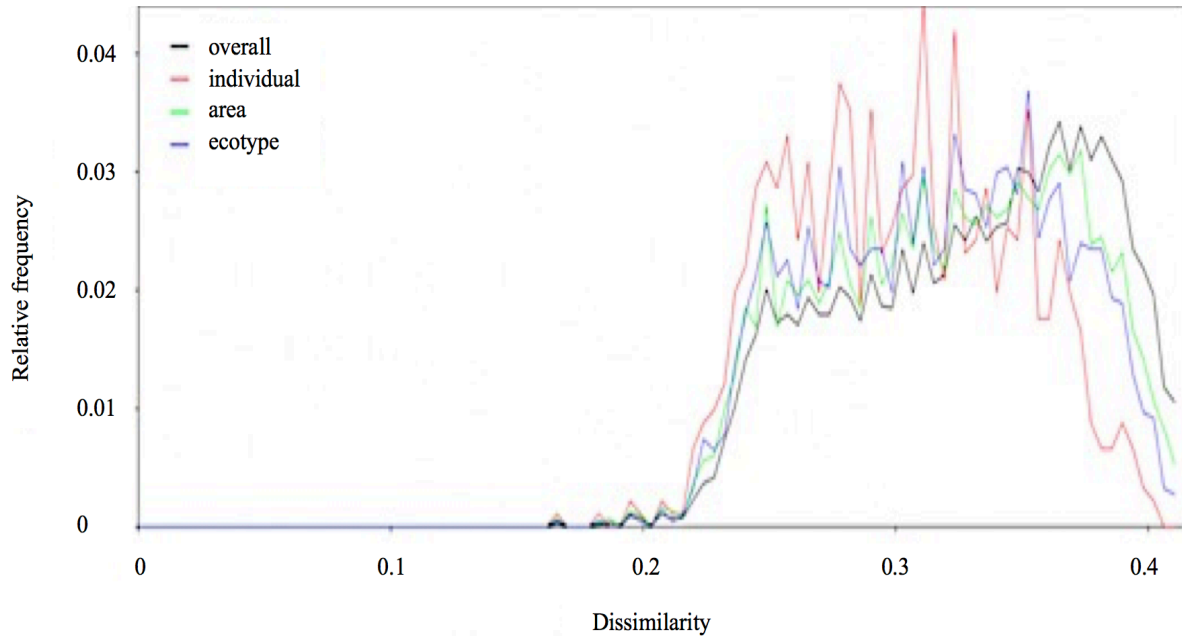


Figure 3.8: Distance distribution analysis of call repertoire as a function of common contour for coastal and oceanic bottlenose dolphins (*T. truncatus*).

When encounter repertoires were clustered (Figure 3.9) using the Unweighted Pair Group Method with Arithmetic Mean algorithm, ecotype separation occurred with no exceptions. Likewise, k-medoid clusterings of encounters and recordings organised ecotype to their own grouping with 100% success rate and $k = 2$ or $k = 3$, respectively. Note both analysis types represented unsupervised clustering, contrasting methods such as discriminant function analysis. This signifies a well-defined divergence of ecotypes. Moreover, Global Silhouette Index indicated a well-defined peak at $k = 2$ (Appendix 3.3) for encounters and $k = 3$ for recordings. A natural clustering of the dataset is therefore two and three main clusters, respectively.

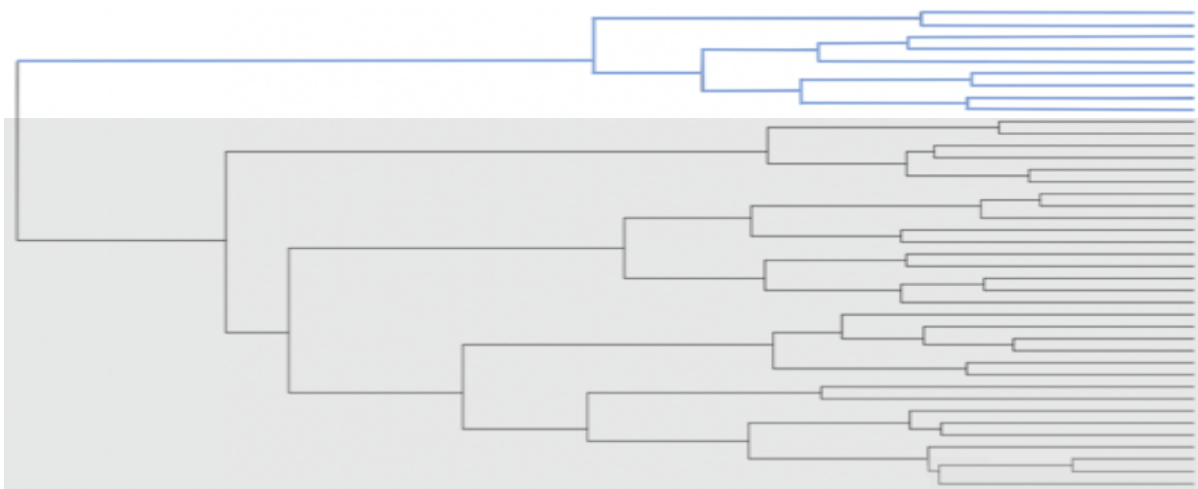


Figure 3.9: Dendrogram of encounter repertoires from coastal bottlenose dolphins and oceanic bottlenose dolphins (*T. truncatus*). Dendrogram was created from 61-point contour traces. Note, coastal bottlenose dolphins = grey line with a grey background and oceanic bottlenose dolphins = blue line.

Geographic dissimilarity (area) within ecotypes was also considered. In coastal bottlenose dolphins, when encounter repertoires were clustered using the Unweighted Pair Group Method with Arithmetic Mean algorithm (Figure 3.10), the two main area groups (Bay of Islands and non-Bay of Islands) were separated, with some exceptions. To investigate the exceptions, analysis was rerun with each area considered independently (Bay of Islands, Whangaroa Harbour, Cavalli Islands, and Doubtless Bay). Using the Unweighted Pair Group Method with Arithmetic Mean algorithm, two of the three area groups (Cavalli Islands and Doubtless Bay) were separated with no exceptions, whereas Bay of Islands and Whangaroa Harbour were interspersed with no clear division (Figure 3.10A). K-medoid clusterings (here $k = 2$) with recordings and encounters, classified Cavalli Islands and Doubtless Bay according to their location with 65.3 % and 78.0 % accuracy, respectively. Again, a clear divergence between the Cavalli Islands and Doubtless Bay was suggested, with a clear Global Silhouette Index peak for recordings and encounters with $k = 2$, indicating a natural separation into two clusters.

For Whangaroa Harbour and the Bay of Islands, k-medoid clusterings of recordings and encounters classified these areas by location with 19.2 % accuracy and $k = 2$, indicating no natural partition was identified. This is further supported by the lack of a clear peak for recordings and encounters when using the Global Silhouette Index for recordings. When considering all areas (Bay of Islands, Whangaroa Harbour, Cavalli Islands, and Doubtless Bay), a clear peak, with $k = 3$ for recordings and encounters, was apparent with the Global Silhouette Index for recordings, implying three natural partitions in the dataset. Following k-medoid clusterings ($k = 3$), recordings and encounters were classified according to their location (Cavalli Islands, Doubtless Bay, and Bay of Islands/Whangaroa Harbour) with 100 % accuracy.

In oceanic bottlenose dolphins, when recording and encounter repertoires were clustered using the Unweighted Pair Group Method with Arithmetic Mean algorithm, the two area groups (wider survey and Cavalli Islands) were separated with exceptions (Figure 3.10B). This was supported by k-medoid clusterings, with recordings and encounters classifying wider survey and Cavalli Islands according to their area with only 21.1 % accuracy with $k = 2$. No significant divergence between Cavalli Islands and wider survey was indicated by unsupervised clustering. Additionally, the Global Silhouette Index for recordings indicated the two clusters were not a natural partition of the data given that there was no clear peak with $k = 2$ for recordings or encounters (as evident in nonmetric multidimensional scaling, Appendix 3.4).

The pairwise inter-ecotype divergence score was greater than any intra-ecotype comparisons (Table 3.12). In addition, both ecotypes had lower divergence scores within the same area than they did with each other (Table 3.12), suggesting divergence did not only occur as a result of location.

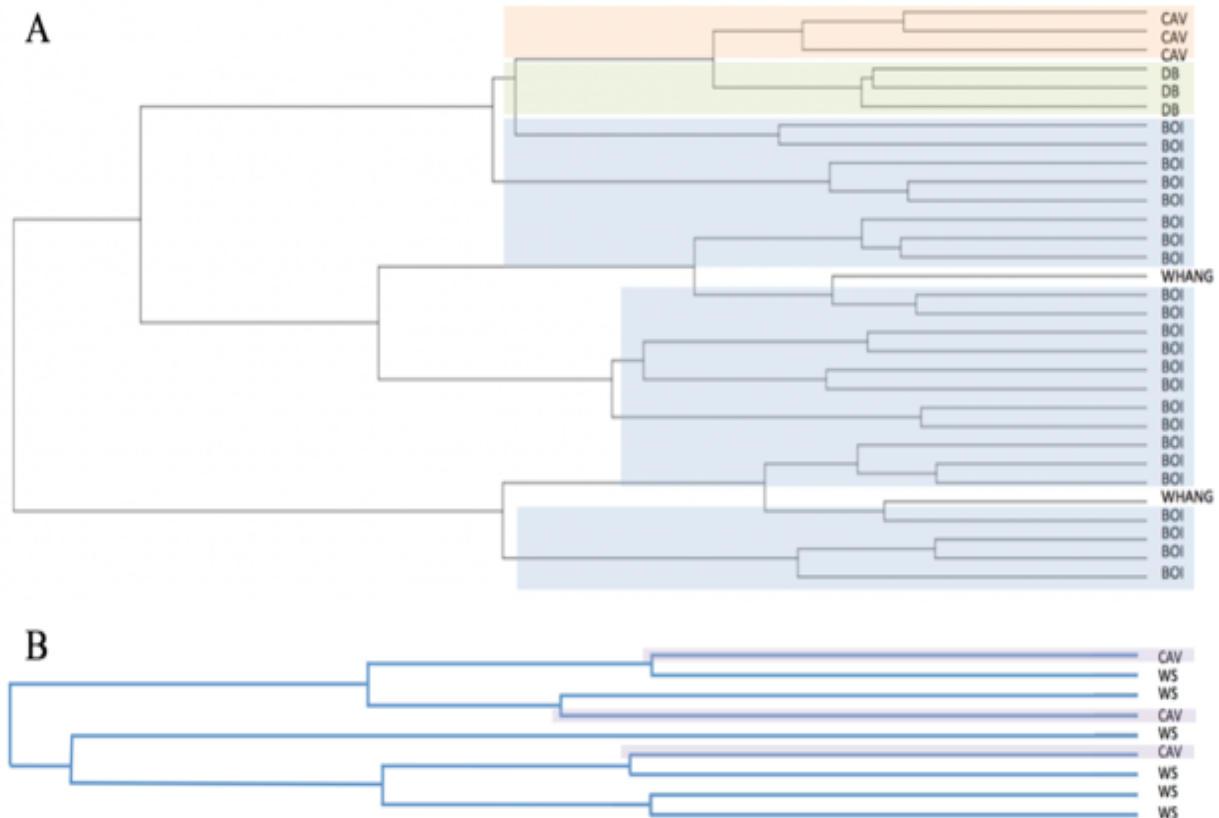


Figure 3.10: Dendrograms of encounter by area repertoires from A) coastal bottlenose dolphins and B) oceanic bottlenose dolphins (*T. truncatus*). The dendrograms were calculated from 61-point contour traces using the Unweighted Pair Group Method with Arithmetic Mean clustering algorithm based on the dissimilarity matrix produced by a dynamic time warp analysis. Note, CAV = Cavalli Islands, WS = wider survey, BOI = Bay of Islands and DB = Doubtless Bay.

Table 3.12: Estimates of pairwise divergence in repertoire structure (per recording) between coastal bottlenose dolphins and oceanic bottlenose dolphins (*T. truncatus*). Note, CAV = Cavalli Islands, WS = wider survey, BOI = Bay of Islands, WHANG = Whangaroa harbour and DB = Doubtless Bay, enc = enclosed waters of BOI, WHANG and DB.

Scenario A	Scenario B	Recordings	Encounters
coastal ecotype	oceanic ecotype	0.1872	0.1943
coastal ecotype - CAV	oceanic ecotype - CAV	0.1124	0.1253
coastal ecotype - enc	coastal ecotype - open (CAV)	0.0892	0.0915
coastal ecotype - BOI	coastal ecotype - non-BOI	0.0824	0.0825
coastal ecotype - BOI	coastal ecotype - DB	0.0677	0.0691
coastal ecotype - WHANG	coastal ecotype - DB	0.0580	0.0593
coastal ecotype - CAV	coastal ecotype - WS	0.0035	0.0036
oceanic ecotype - CAV	oceanic ecotype - WS	0.0008	0.0006
coastal ecotype - BOI	coastal ecotype - WHANG	0.0002	0.0003

3.3.6 Micro-geographic variation in call repertoire

To investigate the effect of geographic variability in repertoire at a finer scale than *stratum*, a geographic analysis was applied. Ecotype comparison resulted in two cluster categories (from a hierarchical clustering solution with the highest Silhouette Index) and coastal bottlenose dolphin comparison between areas into three cluster categories.

The Jaccard Dissimilarity Index indicated that in coastal bottlenose dolphins, 55.5 % of variation in repertoire was explained within a 5 km radius (Figure 3.11A). A peak of 56.3 % dissimilarity was observed at 35 km apart. This distance approximately corresponds to the distance between the Bay of Islands and Cavalli Islands and Whangaroa Harbour and Doubtless Bay. More variation was described between ecotypes within a shorter distance (Figure 3.11A). This result indicates variation between ecotypes was less dependent on distance than within ecotype variation. The Jaccard dissimilarity index further indicated that the difference between ecotypes was stable at approximately 80.0 % within 20 km. Beyond 20 km, variation oscillated, with a peak of 87.2 % dissimilarity at 85 km apart (Figure 3.11b).

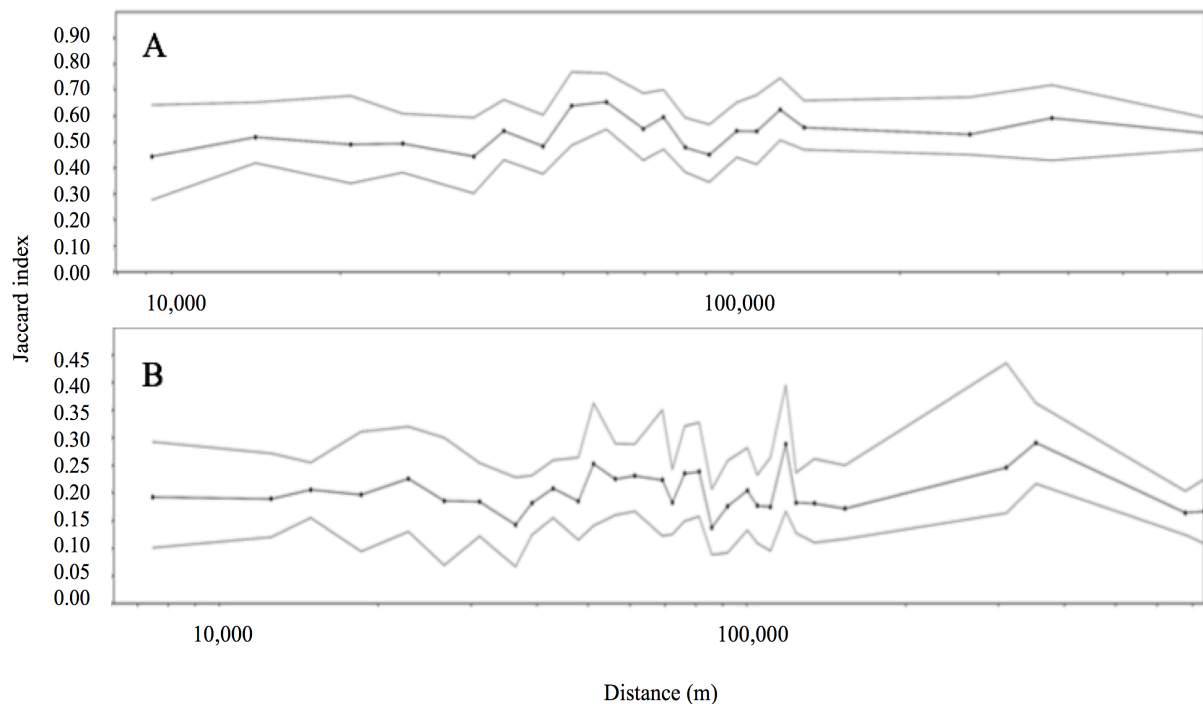


Figure 3.11: Geographic comparisons of common pool contours of common bottlenose dolphins (*T. truncatus*). Hierarchical clustering and Jaccard Index of call comparisons: A) coastal bottlenose dolphin only and (B) All recordings from both ecotypes (oceanic bottlenose dolphin and coastal bottlenose dolphin). Plot represents the mean Jaccard Dissimilarity Index for distance (in metres), plus an estimate of the 95 % confidence interval around the mean.

Call repertoires were also compared between the subclasses of group size, behavioural state,

season, and year (Appendix 3.5). Values were averaged across subclasses to allow comparison of Spearman's correlations within and between ecotypes. For all four variables, call repertoire was more analogous within each ecotype than between ecotypes (see section 3.3.4, Table 3.7). Notably, in nonmetric multidimensional scaling of calls, no clustering was evident for either season or year (see section 3.3.6, Table 3.12).

3.4 Discussion

The comparison of social acoustics between odontocete populations is rare, due to the problems associated with defining the signals for comparison and how to compare them. This study shows that naturally occurring calls have structural variables that can be used to differentiate between *Tursiops* ecotypes, and from proximate regions within ecotype. Statistical characterisations of call variables suggest that while ecotype-specific call characteristics are evident, some degree of within-region variability in call structures also exists. The call structure analyses described here provide an additional tool for monitoring and assessing dolphin stocks.

3.4.1 Ecotype variation in calls

The consistent differences between call repertoire and contour characteristics of oceanic and coastal bottlenose dolphin ecotypes demonstrates that acoustic categorisation between these ecotypes is possible. Coastal bottlenose dolphins and oceanic bottlenose dolphins share minimal overlapping distributions and, therefore, inter-ecotypic reproduction is possible (Chapter 2). Nevertheless, sympatric groups have shown reproductive isolation (Yang et al., 2005), implying that selection can prevent inter-ecotype breeding, which has occurred in captivity (e.g., Sea World, South Africa, as discussed by Best (2007)). Call frequency variation may be efficient for discriminating heterospecifics and conspecifics, fostering intra-specific communication and assuring mating with genetically similar associates is successful (Wilczynski et al., 1999). Thus, the two ecotypes may be effectively exploiting divergent acoustic niches, as proposed in other spatially overlapping cetaceans (Gridley, 2011; Mossbridge & Thomas, 1999; Rendell et al., 1999). Contrary to this, if a small level of undetected mixing outside this region is possible, there might be an area of “acoustic mixing” between ecotypes, thus reducing acoustic drift through horizontal learning (Van Cise et al., 2017, p. 746). Given the level of divergence between the coastal bottlenose dolphin and oceanic bottlenose dolphin this is unlikely, yet possible.

Alternatively, acoustic structure may maintain genetic structure in this area, i.e., preferential mate choice of individuals which sound alike to the perceiver versus prospective mates with dissimilar call repertoires. A positive feedback loop where individuals preferentially procreate with those that sound alike may occur, thus inducing accumulative differentiation between the two ecotypes. This has occurred in some avian playback experiments (Slabbekoorn & Smith, 2002), and might similarly be applied to dolphins.

The possible rationalisations for the ecotype variation observed is discussed in Chapter 4. It should be noted the two morphotypes differ in body size, with the oceanic being larger. Other studies have indicated that when body size is larger, the skull morphology also varies, including aspects related to the production of vocalisations, such as calls, resulting in lower mean frequencies utilised (Kurihara & Oda, 2007; Perrin et al., 2011). However, in this study, the larger oceanic bottlenose dolphin was recorded utilising significantly higher frequencies, contrary to what would be expected based on morphology only. This is not a unique observation, as Gridley (2011) previously reported the larger *T. truncatus* exploiting higher frequencies than the smaller *T. aduncus*. Other factors are therefore likely to affect the variation noted. Social variation (e.g., isolation or affiliation) would be a more plausible explanation. May-Collado et al. (2007a & b) suggest that in scenarios where long-range communication is necessary, such as small and variable social group structure, increased duration and decreased frequency calls are produced more often. Alternatively, shorter and higher frequency calls are more common in larger or more stable social groups. However, the need for communication over longer distances has been supported for oceanic bottlenose dolphin, particularly with their wider ranging and open ocean habitat (Chapter 2). Further examination is, therefore, necessary to understand the connection between group dynamics and call parameters (Chapter 4).

In environments with numerous surfaces that reflect sound, the intermission amid repeated contours could be longer to decrease signal loss through reverberation (Naguib, 2003). Call rate in shallow areas of Far North waters might result from the probable reverberation off solid substrates (e.g., rocks) and surface and bottom reflections. The evidence for geographical variation in the repertoire of coastal bottlenose dolphin was by no means unique to NZ's bottlenose dolphin. Indeed, similar trends have been documented in Portugal (e.g., Dos Santos et al., 1995), Scotland (e.g., Janik, 2000c), and Australia (e.g., Ward et al., 2016). These populations represent both species and/or ecotypes of *Tursiops* in a variety of habitats. Thus, it is possible that call repertoires exhibit geographical variation between groupings or

populations. Further acoustic data from supplementary data collection might aid in the understanding of distributional boundaries between the two ecotypes in other regions, when the collection of genetic/morphological data remains limited and/or problematic (e.g., Van Cise et al., 2016). Other species' population boundaries have been described based on acoustic data, e.g., blue whales (*Balaenoptera musculus*; Balcazar et al., 2015; McDonald et al., 2006) and humpback whales (*Megaptera novaeangliae*; Garland et al., 2015). In this study, combining acoustic data with the distribution of the two morphologically distinct types is important for the successful management and conservation of bottlenose dolphins in Far North waters.

The complexity of individual contours is also worth considering. Oceanic bottlenose dolphin contours had more gradient changes and harmonics. Calls are used by many *delphinid* species and appear to maintain group cohesion (Caldwell & Caldwell, 1965; Janik et al., 2006; Tyack, 1986). The social complexity hypothesis proposes that increased communication complexity is required with increasingly complex social structure (Freeberg et al., 2012). Calls seem to be important in group cohesion (Janik & Slater, 1998) and may encode individual information (Caldwell et al., 1990; Sayigh et al., 1990).

It has further been suggested that calls are not only contact calls, but that they also form a phatic system (Brownlee & Norris, 1994). A phatic system is an open communication channel in which the modulation and/or temporal sequencing of calls may encode context-specific information. Thus, calls with more complex structures have the potential to confer more information to conspecifics. The higher complexity in the oceanic bottlenose dolphin call repertoire could indicate social structure with higher complexity, as communication has been shown to be increasingly complex in frameworks that necessitate better information transfer (Connor, 2007). Additionally, there is evidence of oceanic bottlenose dolphin groups mixing with both false killer whales (*Pseudorca crassidens*) and pilot whales in NZ (Zaeschmar et al., 2014). The greater complexity may, therefore, reflect social complexity. An alternative explanation is that differences observed are a result of sampling bias only. This may occur if encounters with groups are more frequent during episodes of foraging or socialising in oceanic bottlenose dolphins than in coastal bottlenose dolphins, meaning differences identified could reflect behavioural state or social context during an encounter. Additional data collection would allow this level of comparison.

Overall, the call differences observed between ecotypes appear to fulfil the criterion of dialects, i.e., consistent differences in vocalisations between neighbouring groupings or populations of potentially interbreeding individuals (Crance et al., 2014). It is not clear, however, what process would drive the development of dialects within bottlenose dolphins. Several mechanisms have been proposed within birds and humans, including cultural drift (e.g., Lemon, 1975), innovation (e.g., Potvin & Clegg, 2015), and cultural diffusion (e.g., Slabbekoorn & Smith, 2002; Slater, 1989). It is also suggested that cetacean call repertoire variation can be both driven by social group and behaviour. This is illustrated by the existence of socially motivated killer whales (*Orcinus orca*; Crance et al., 2014; Deecke et al., 2010; Filatova et al., 2012; Musser et al., 2014; Riesch et al., 2006; Yurk et al., 2002) and behaviourally motivated killer whales (Filatova et al., 2013; Holt et al., 2013). Bottlenose dolphins are described as a very social species, identified as forming stable social groupings and fusion-fission associations (e.g., Mahaffy et al., 2015). The variability in social groupings is highlighted in this study with the group recorded having a significant effect on results. All these possibilities should be considered in future research.

3.4.2 Micro-geographic variation in calls within ecotype

The intra-specific variation observed was lower than between ecotypes for both ecotypes, especially when whole call repertoires were compared. However, micro-geographic distinction in call features was still evident within the coastal bottlenose dolphin ecotype. Non-Bay of Islands areas were acoustically distinct from the Bay of Islands, although the difference was less distinct between Bay of Islands and Whangaroa Harbour than among all other areas. Coastal areas of Bay of Islands/Whangaroa Harbour are characterised by the frequent use of single elements and mixing in dendrogram analysis. Call duration was significantly longer in the Bay of Islands. Calls from the Bay of Islands also had significantly more contour inflections (particularly positive to negative), whilst Non-Bay of Islands calls had significantly more visible harmonics. These results suggest the calls recorded in the Bay of Islands contained more information than those recorded in non-Bay of Islands areas. Further investigation is therefore necessary (Chapter 4) to establish if similar forces are acting on the calls in the Bay of Islands and non-Bay of Islands areas, resulting in comparable features within repertoires.

Signals may be adapted or adjusted through vocal learning, which could result in the production of calls which are like or unlike one another (Janik & Slater, 2000). In birds, acoustic

convergence has been demonstrated in multiple species (Clement et al., 2000). Birds can learn and adapt their vocalisations like dolphins (Clement et al., 2000). In this study, possible convergence and exchange of similar call contours and features in coastal bottlenose dolphins are presented, despite some geographic variability. Connected multi-looped contours were rare or non-existent across all coastal bottlenose dolphin locations analysed, in contrast with results from oceanic bottlenose dolphins (Chapter 4). The pattern of call likeness may be the result of mitochondrial DNA relatedness. The areas within this study all form part of a large related population of coastal bottlenose dolphins (Tezanos-Pinto et al., 2009). If genetics alone underlie acoustic similarity, a greater similarity between the areas would be expected, which was not the case.

The significant differentiation between encounters (social group proxy) in the dendrogram for coastal bottlenose dolphins indicates that divergence between the two regions (Bay of Islands and non-Bay of Islands) could be affected as a result of differences amongst social groups. Call contours (particularly signature calls) are transferred through social learning, thus it is possible shared acoustic habitats have resulted in comparable call types in different areas (Janik & Slater, 1997). Yet, the habitat features of the areas are dissimilar. The Bay of Islands and Whangaroa Harbour are characterised by sheltered bays and reef, whereas Cavalli Islands and Doubtless Bay are characterised by sloping sea beds, sandy bottoms, and rocky shores (personal obs.). It is therefore clear that independent acoustic modification to specific habitat characteristics should not be dismissed. These two theories are not mutually exclusive. In this overlapping environment, social learning of call characteristics optimised for acoustic transmission may ensue, even if the adaptation does not persist for a long period (Wiszniewski et al., 2009). Additional research into call propagation in different habitats would aid in clarifying the likelihood of this possibility. Furthermore, consideration of social dynamics between areas could aid in the assessment of call convergence, i.e., is convergence universal across groups or socially motivated, e.g., male alliances (Connor et al., 2001; Cook et al., 2004; Watwood et al., 2005).

As in oceanic bottlenose dolphins, the call differences observed in coastal bottlenose dolphins between areas appear to fulfil the criterion of dialects, i.e., consistent differences in calls between neighbouring groupings or populations of potentially inter-breeding individuals (Conner, 1982; Marler & Tamura, 1962; Nottebohm, 1969). Evidence suggests dolphins in the different areas overlap to a degree, are part of a larger population, and are not genetically

distinct (Tezanos-Pinto et al., 2009). According to field efforts conducted on the local Bay of Islands population since 1993, transient bottlenose dolphins have periodically appeared and individual use of the area has altered (e.g., Constantine, 2000; Tezanos-Pinto et al., 2013). Outside of the Bay of Islands, in Far North waters, individuals have only been the focus of dedicated photo-identification for three years. This means it is currently not possible to confirm whether the transients individuals were from other parts of the survey area. Clearly marked individuals have been observed leaving the local Bay of Islands population for periods ranging from several months to indefinitely, with a consistent local Bay of Islands population decline (Tezanos-Pinto et al., 2013).

3.4.3 Study limitations

There was high temporal co-occurrence of contours, resulting in temporal patterning of calls. Biologically this might enhance information propagation by decreasing the chance of environmental conditions altering the signal between subsequent transmissions of that call type (Catchpole & Slater, 2008). Due to the fact calls may preserve group cohesion over extended distances (Janik, 2000b), the repetitive production observed in this study likely helps preserve contact of individuals in association (Quick, 2006; Smolker et al., 1993). Lengthier intervals result in a greater chance of the following call being missed. This could be due to the individual moving out of hydrophone range or a close noise masking the subsequent call. Utilising calls with longer inter-call intervals could, therefore, remain biologically useful for upholding group cohesion. Although this might be under represented by the methodology used herein.

The variations measured for call rate and repertoire may be partially explained by differences in the acoustic environments of recordings. Oceanic bottlenose dolphins were found in waters much less protected from the swell and wave action. Within coastal bottlenose dolphin locations, the Bay of Islands had a much greater degree of boat traffic, with four operational wharves for both tourist and fishing vessels (Peters & Stockin, 2016). In addition, the Bay of Islands and Whangaroa Harbour have many shallow and protected water areas. These factors may combine to produce higher ambient noise levels in the Bay of Islands and Whangaroa Harbour than Cavalli Islands, Doubtless Bay, and wider survey. Higher background noise levels may have affected some of the measurements made from individual calls. For example, spectrographic sidebands at higher frequencies may have become less apparent and peak frequency measurements more biased towards lower frequencies. Whilst only a careful

selection of calls with good signal-to-noise ratios were utilised, further exploration of this effect is required. Additionally, whilst attempts were made to randomise the selection of sample calls based on group size, behavioural state, season, and year, it is unlikely the capricious nature of these sounds were captured to their full extent. At present, the functional nature of the sequenced calls is unclear. However, clear differences existed between each ecotype in terms of their structure.

The use of loops by bottlenose dolphins was demonstrated, however, they were hard to identify and may have been under-represented due to less stereotyped contours within loops being missed (Buck & Tyack, 1993; Janik & Slater, 1998). The application of technologies such as acoustic tags (e.g., Johnson & Tyack, 2003) or array localisation (e.g., Quick et al., 2008) could aid in ascribing calls to a particular signaller and thus improve reliability.

Calls might be amplitude modulated, resulting in environmental prejudice dependent on the location in which the recording was taken (Esch et al., 2009b; Watwood et al., 2004). Call quality, in conjunction with equipment settings and analysis protocols (i.e., spectrogram dynamic range), would have influenced the perception of weaker calls (Watwood et al., 2004). Moreover, the frequency of a call may influence masking (e.g., low frequency masked by boat noise or attenuation of low amplitude high frequency calls). Subsequently, a greater proportion of calls may be missed than in a captive setting.

Chapter 4

Signal exchange of the oceanic common bottlenose dolphin (*Tursiops truncatus*) during intra- and inter-species associations in Far North waters, New Zealand



Oceanic common bottlenose dolphins (*Tursiops truncatus*) in inter-species association with pilot whales (*Globicephala* sp.) in Far North waters, New Zealand.

4.1 Introduction

Animals rely on signal exchange for biologically vital functions, such as predator avoidance, reproduction (i.e., mate acquisition), foraging (i.e., to increase potential energetic gain), or young viability (i.e., collective young rearing experience) (Dudzinski, 1996; Fischer et al., 2015, 2016; Plowes et al., 2014; Suzuki, 2014). Whatever the ultimate and/or proximate causes, group establishment necessitates social communication among individuals (e.g., Brudzynski, 2013).

Studies of social communication necessitate accurate identification of the range of signals utilised (see for review: Snijders & Naguib, 2017). Social organisation can be reduced to patterns of synchronised behaviour (Oosterom et al., 2016; Philips & Austad, 1990). Coordination is mediated through the exchange of information about the environment and participants (Dudzinski & Ribic, 2017; Smith, 1981). A variety of pathways exists for the dissemination of information: acoustic-, visual-, chemical-, and mechano-reception are the most common. Acoustic-, visual-, and mechano- pathways are observable by researchers (Kremers et al., 2016 for review). Signal production has evolved to concurrently utilise multiple paths, referred to as ‘multimodal’ signals, to enhance detection rather than increase the range of information transmitted (Kremers et al., 2016; Leavens et al., 2010; Micheletta et al., 2012). Examples of multimodal signals have been observed in birds (e.g., Starling, *Sturnus vulgaris*, Henry et al., 2015), primates (e.g., Chimpanzee, *Pan troglodytes*, Hobaiter et al., 2017), and teleost fishes (e.g., Butler & Maruska, 2016; Keller-Costa et al., 2015). Further to the use of different signal types, it is also necessary to make the distinction that multimodal communication can occur even in a single signal type (Hobaiter et al., 2017). An applicable example is call vocalisation in cetaceans, which involves auditory and visual (bubble emission) cues in both the production by the signaller and perception by the receiver (see for review: Mann, 2000).

Dolphin vocal behaviour is their primary mode of social communication (as discussed by Janik & Slater, 1998). As such a wealth of data on how dolphin vocal behaviour relates to general behavioural activity exists (e.g., Esch et al., 2009a & b; King et al., 2016; May-Collado & Quiñones-Lebrón, 2014). Bottlenose dolphins (*Tursiops* spp.) exhibit extensive and complex behavioural systems, including vocal communication (Sayigh et al., 2013; Taruski, 1979). Current consensus in the literature indicates the production rate and variation of vocalisations (e.g., whistle, screams, barks, etc.) is highest during socialising and lowest during resting (e.g.,

Gridley et al., 2016; Norris et al., 1994; Weilgart & Whitehead, 1990). It is intuitive to assume that other forms of communication, as well as the environment and behaviours that dictate their use, drive (at least in part) fluctuations in vocal activity (Dudzinski et al., 2010).

Oceanic common bottlenose dolphins (*Tursiops truncatus*, referred to hereafter as oceanic bottlenose dolphin) forming inter-specific groups with pilot whales (*Globicephala* sp.) add additional complexity to the assessment of communication context. Description of complex interactions is improved with higher rates and types of communication. Hidden Markov models are popular in speech recognition applications (which they were originally designed for, see Zucchini et al., 2009 for review). This is a result of their flexibility in classifying sounds from observation series (Ren et al., 2009). A hidden Markov model incorporates the “stationary spectral configuration” (state), “transitions between states” (“spectral changes over time”) (Putland et al., 2018, p. 480), and the effect of underlying motivational states (Ren et al., 2009). Hidden Markov models have described the acoustic behaviour of birds (Somervuo et al., 2006; Ranjard et al., 2017), fish (Vieira et al., 2015), and mammals (Scheifele et al., 2015; Popov et al., 2017; Putland et al., 2018). In many cases hidden Markov models are deemed to outperform alternate approaches (Weisburn et al., 1993; Kogan and Margoliash, 1998; Brown & Smaragdis, 2009), due to the inclusion of spectral changes along a time sequence (Ren et al., 2009). Hidden Markov models also account and allow for variation in call frequency (Ren et al., 2009) and are thus appropriate in the varied environment of mixed species grouping. Additionally, the behavioural states and other communication forms of the individual dolphins are usually not directly observed. This renders hidden Markov models suitable for modelling contexts that could influence call use, including inferring use of multimodal signalling.

The simultaneous call- (hydrophone) and mechano- (video recording) assessment with surface behavioural observations in this study facilitates an in-depth examination of dolphin social communication and behaviour. The primary aim is to examine signal use, including call behaviour (whistle and burst pulse vocalisations) and the use of multimodal communication of bottlenose dolphins. This study aims to quantify the effects of inter-species groupings on the social communication of oceanic bottlenose dolphin in Far North waters, New Zealand (NZ), using call parameters as the dependent variable. In line with the groupings and call variation observed in Far North waters (Chapter 2 and 3), the following questions are posed:

- 1) Does the formation of interspecific groupings with pilot whales affect the call behaviour of oceanic bottlenose dolphins?

- 2) How do vocal parameters change in relation to biotic and abiotic factors in intra- and inter-specific groupings?
- 3) Is multimodal signal exchange utilised in intra- and inter-specific groupings?

4.2 Materials and methods

4.2.1 Data collection

Data collection consisted of concurrent surface and sub-surface observations on focal groups of oceanic bottlenose dolphins, consistent with methods described previously (refer to Chapters 2-3). In summary, for this chapter line transect surveys were utilised year-round between September 2013 – September 2015 (a subset of total data), between sunrise and sunset from Research vessel *Te Epiwhania*, a 5.5 m Stabicraft vessel powered by a 100 hp four-stroke engine (Chapter 2, Appendix 1.1 – 2.1).

4.2.1.1 Surface observations

Observational and environmental data were recorded on a HTC Touch Pro2 Windows Mobile device or Acer Iconia B1 tablet computer with associated Garmin GLO GPS device. CyberTracker (CyberTracker, Conservation, Version 3.296+) software was programmed to record continuous GPS tracks (with GPS recordings every 30s and additionally with every data input) (as per Chapter 2). Surface observations were taken every minute (data collected is detailed in section 4.2.1.1.1. and 4.2.1.1.2.).

4.2.1.1.1 Group composition and size

All data were analysed at the focal sub-group level; however, data were recorded the same way at the focal and whole group level to provide context and comparison. Every minute, the whole *group size*, focal *group size*, *group type* (mixed or single species), direction of travel, and proximity of single and mixed species focal groups within whole group were recorded (as per Chapter 2). Dolphins were considered to be in focal groups when “any number of individuals were observed in apparent association, moving in the same direction and often, but not always, engaged in the same activity” (Dwyer, 2014, p. 37) < 5 body length apart (Constantine, 2002; Constantine et al., 2004; Shane, 1990b; full definition in Chapter 2, Section 2.2.1). Additionally, the elliptical spread area was included ([focal group size/spread area of focal group]*100) in the estimation of focal group density (number of dolphins per 100m²), and

could be interpreted as group cohesion, or a measure of proximity among dolphins. *Surfacing synchrony* was additionally assessed. The instantaneous point at which any part of the individual's body breaks the water surface was termed *surfacing* (Hastie et al., 2003). *Surfacing synchrony* was quantified by scanning (left to right) and recording the number of animals within the focal group surfacing in sequential 3-second intervals for a 30-second period directly after each 1-minute behavioural observation. A 3-second interval was selected to minimise bias due to multiple surfacings within one interval by the same individual. The decision was made based on bottlenose dolphin dive behaviour literature, which demonstrates dive durations of < 3 seconds are rare (following methodology of Hastie et al., 2003).

Whole and focal group sizes were logged according to three categories: the absolute *minimum* number of dolphins counted, the absolute *maximum* number of individuals believed to be in the cluster, and the *best estimate* for the most likely number of dolphins in the cluster (Dwyer et al., 2016). For analytical purposes, group composition was also recorded in three categories (i.e., adults only, adults with juveniles, and adults and/or juveniles with calf/neonate groups). Group composition was confirmed as per Chapter 2, and as demonstrated in Figure 4.1.

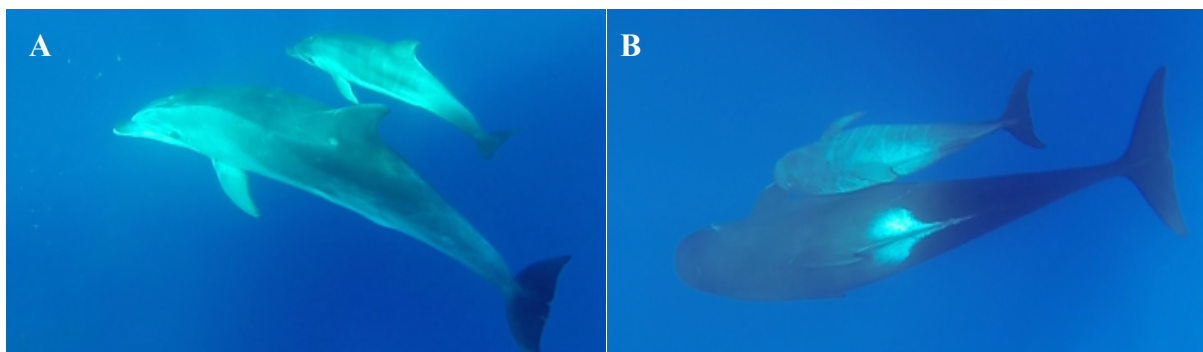


Figure 4.1: Example of a neonates/calves in oceanic common bottlenose dolphins (*T. truncatus*) and pilot whales (*Globicephala* sp.) displaying foetal folds and flanked by adults of their own species.

4.2.1.1.2 Surface behaviour

To determine the predominant behavioural state of the focal sub-group was scanned from left-to-right (as per Dwyer 2014). Eliminating bias that may occur as a result of individuals, behaviour or missing part of the group (Mann, 1999). Behavioural states are defined as recognisable subcategories of behaviour consisting of multiple behavioural events (Lusseau, 2003). Focal group *behavioural state* (travelling, milling, socialising, diving, foraging, and resting, as per Chapter 2) was recorded every minute. The same process was followed for whole group estimates concurrently to focal group observations.

4.2.1.2 Subsurface mechanical (tactile and call) and photic observations

Mechanical (call) signal recordings from both oceanic bottlenose dolphins and pilot whales were obtained with a calibrated Cetacean Research Technology Inc. C75 omnidirectional hydrophone. The hydrophone included a built-in pre-amplifier (flat frequency response of 1 Hz to 85 kHz; sensitivity -209.52 dB re 1 V/ μ Pa), fitted to a Tascam DR-680 digital multitrack recorder. Sampling occurred at 96 kHz, 24-bit, consistent with the methodology described in Chapter 3. Recordings included both oceanic bottlenose dolphin only, pilot whale only, and oceanic bottlenose dolphin mixed (oceanic bottlenose dolphin and pilot whale) groups, which were distinguished in processing.

Additional subsurface behavioural event data, collected and analysed in this Chapter, result from the concurrent (time-synced) collection of subsurface videos of dolphin behaviour with surface and call data (See Chapter 2 – 3). Videos were recorded opportunistically from the bow of the research vessel *Te Epiwhania* (Appendix 2.1). Prior to filming, water clarity was measured (using a Secchi disk, for results see Appendix 4.1) and the distance of the closest group to the vessel was recorded. Recordings were only taken if a group was within 10 m of the vessel and visibility was at least 2 m to standardise recording protocol. A bespoke video recording rig, with simultaneously recording Go-pro 3+ (© GoPro. Inc., 2013) video cameras in underwater housings (1080 p, 60 fps, and 180° field of view), was utilised to record subsurface behaviours (Appendix 4.2). All recordings were monitored via a live feed on-board the vessel using a Wi-Fi extension cable (© CamDo solutions Inc., 2013) attached to a Samsung SM-T110 tablet computer running GoPro Studio software (© GoPro. Inc., 2013, Appendix 4.2). All recordings were calibrated with a shallow water filter during filming (BackScatter Inc., 2013, Appendix 4.2). Subsurface behavioural data collection utilised focal group and all-occurrence sampling (Altmann, 1974, as per Chapter 2). Recording and follows ceased when no individuals were in the field of view in excess of 3 minutes.

4.2.2 Mechanical (tactile) and photic data processing, definition and ethogram

Subsurface video preparation followed methods utilised in Cusick and Herzing (2014). For recording selection and analysis criteria refer to Appendix 4.3 – 4.6. The software Final Cut Pro 10.1 (© Apple Inc, 2016) was used to analyse videos frame-by-frame.

Subsurface behaviour was defined using a population specific ethogram applicable to both bottlenose dolphin and pilot whales, which was used at the individual level and assessed behavioural events (contacts and body postures) within a focal group follow (Table 4.1). Group level behavioural states were concurrently collected using surface observations (see section 4.2.1.1.2). The ethogram was developed using a sample set of data prior to full analysis (based on Dudzinski, 1996; Dudzinski et al., 2010, 2012; Frohoff, 1993; Östman, 1994). Researcher bias in development, and thereafter in analysis, was controlled by two independent reviews of videotapes.

Behavioural events were defined as recognisable instantaneous (single point in time) behaviours (see Appendix 2.2 for full definitions, Altmann, 1974). This includes both contact events and posture events. The term *contact* denoted any physical contact with any part of either animals' body (with body parts detailed in Appendix 4.3). Published literature definitions of *contact* between the body of one individual and the body of another vary extensively (See for summary: Sakai et al., 2006). In the current study, the most observed contact behaviours were: *rub*, *pet*, *melon-to-genital*, *circle chase/dive*, *bite*, and *touch*. The term *posture* denoted any recognisable change in shape/orientation of an individuals' body. Dolphin posture was categorised as follows: *horizontal*, *side-down left* and *right*, *upside down*, *head down* and *head up* (Dudzinski et al., 2009). Key terms for this chapter are summarised for contact and posture events (Table 4.1) and all terms feature in Appendix 4.4.

4.2.3 Data analysis

All statistical analyses were conducted using free statistical software R (R Core Development Team, 2014, R Studio for Mac version 1.0.136) with the significance set at 0.05, unless otherwise stated. Data were initially tested for normality and heterogeneity. All data were also tested for significant variation on a seasonal, annual, and group (composition and size) level. If significant variation was not detected, data were combined for subsequent analysis.

4.2.3.1 Comparison of call parameters and group type variation in encounter call repertoire

Evidence from broadband recordings suggests fundamental frequencies of oceanic bottlenose dolphin calls rarely rise beyond 24 kHz. Thus, it is assumed the omission of calls reaching higher fundamental frequencies will not overly bias the dataset. Consequently, from an original

19,155 calls dataset, 183 were excluded due to the fundamental frequency exceeding 24 kHz (the upper limit of reliable recording for the equipment used). These exclusions represented 0.96 % of oceanic bottlenose dolphin samples (n = 183), leaving 18,972 calls.

Table 4.1: Definitions of most observed behavioural events of oceanic common bottlenose dolphins (*T. truncatus*) and pilot whales (*Globicephala* sp., adapted from Dudzinski et al., 2009).

Definitions	
Contact (mechanical tactile)	
Rub	Active movement between one individuals' pectoral fin and another individuals body
Pet	Pectoral-fin-to-pectoral-fin contact, where active movement of at least one of the pectoral fins is observed
Touch	Physical contact between the pectoral fin of one individual and another individual's body without active movement of either
Melon to genital	One individual positioned with rostrum near genital region (including mammary slit). Not always implying milk transfer
Circle chase/dive	One individual circling another individual while swimming and/or diving
Bite	One individual making contact with another individual with rostrum (mouth open)
Posture (photic)	
Horizontal	Ventral side parallel to the sea floor
Left-down	Right pectoral fin toward water surface and left is toward sea floor
Right-down	Left pectoral fin toward water surface and right is toward sea floor
Upside down	Individual is horizontal with ventral side toward water surface and the dorsal side toward the sea floor
Head down	Individual in a vertical position in the water column with its head toward the sea floor
Head up	Individual in a vertical position in the water column with its head toward water surface
Turn towards	One individual changes direction of travel in the water column with its new direction towards another individual
Turn away	One individual changes direction of travel in the water column with its new direction away from another individual

The omnidirectional recording systems meant recognise the 'calling' individuals within the interspecific groups was not feasible. Thus, questions posed were restricted to quantify differences in contours and call repertoire between intra- and interspecific groups (May-Collado, 2010). A one-way analysis of variance (ANOVA) was utilised to investigate differences between calls parameters recorded for oceanic bottlenose dolphin only and oceanic bottlenose dolphin in mixed species groupings with pilot whale (oceanic bottlenose dolphin mixed). All parameters, except mean and peak frequency, were found to possess homogenous variances between groupings. As a result, for mean and peak frequency, the Welch statistic was used in lieu of the *F* statistic, as it represents a robust proxy when population variances are

unequal (Welch, 1951). Parameters that were not normally distributed were subjected to non-parametric testing. Call repertoires were also compared between the subclasses of *group size*, *behavioural state*, *season*, and *year*. Values were averaged across subclasses to allow comparison of Spearman's correlations within- and between-group types.

Discriminant analyses were performed to investigate whether whistles recorded from inter-specific encounters have more overlap than recordings of intra-specific groups during key behavioural states (social and travel, May-Collado, 2010). If the contour and/or repertoire structure is being modified toward contour 'similarity', a reduction in correct species assignment test power would be expected. First data (frequency and duration) were distribution normalised through Box-Cox transformation (Sokal & Rohlf, 1995). The normalised data were subsequently utilised for discriminant analysis. This was done for intra- and inter-specific groups and in both behavioural states (as per May-Collado, 2010). The Kappa Index test assessed the performance of the discriminant function vs. chance. Statistical significance was set at 0.05 (as per May-Collado, 2010).

One hundred randomly selected calls were clustered using the Unweighted Pair Group Method with Arithmetic Mean hierarchical clustering algorithm (as per Chapter 3). Subsequently, analyses using a Global Silhouette Index at different depths within the tree, to detect natural categories in the data, were utilised based on a dissimilarity matrix generated by a dynamic time warp analysis (Lachlan et al., 2013, as per Chapter 3). The resulting dendrograms were annotated with the classification given to each call during visual inspection to test for method alignment (all methods followed chapter 3). Luscinia's dynamic time warping algorithm was utilised to compare whistle and burst pulse contours from recordings of repertoires grouped across encounter, group type (oceanic bottlenose dolphin mixed and oceanic bottlenose dolphin only), and surface behavioural state (travelling and socialising) (Lifjeld et al., 2016). Implementation steps followed Lifjeld et al. (2016) and are detailed in full in Chapter 3 Section 3.2. Following initial comparison, two approaches were taken to further explore call parameters and multimodal communication: hidden Markov model of single covariates (Section 5.2.2.1), and multiple covariates considered concurrently using an information-theoretic approach (Section 5.2.2.2). Both approaches utilise both surface and subsurface variables.

The overlap of calls from oceanic bottlenose dolphins and pilot whales was additionally investigated. Misidentification could result in data biased towards greater complexity in

contours of oceanic bottlenose dolphin. To test for possible overlap, 10 recordings of pilot whales only were tested for commonality with 10 recordings of oceanic bottlenose dolphin only. Discriminant analyses were performed as per behavioural assessment above (May-Collado, 2010). Commonality was low (significant difference in 80% of contour types (n = 10 contours)) with pilot whales producing longer and more modulated calls. Significant difference was not identified for upsweep or downsweep contours (Chapter 3, Table 3.1, call code 1 & 2), thus any bias in the dataset would result in complexity being underestimated. The ability for observers to distinguish between species was therefore deemed acceptable for the questions posed in this study.

4.2.3.2 Multivariate mixed hidden Markov models (hidden Markov model) of subsurface responses

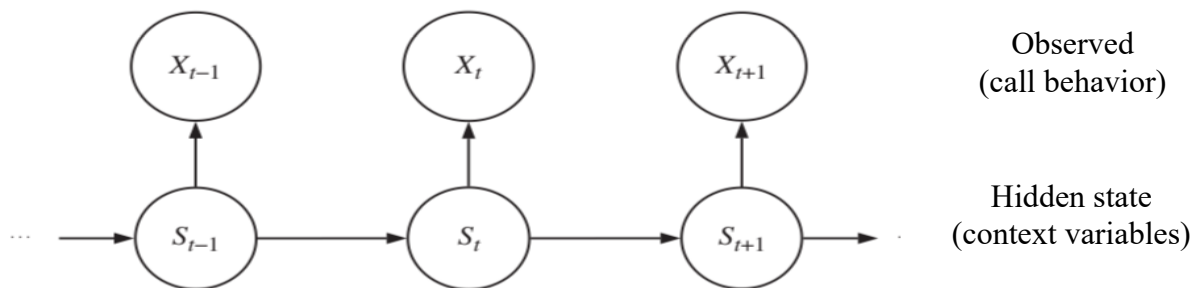
To investigate the inter-active process acting on communication, the call data from Chapter 3 were re-analysed using a time series method (Stifter & Rovine, 2015). As summarised in Chapter 3, recordings were separated into 1-minute samples for analysis. These samples have cycles of high and low call rates and mean frequency, which has previously been linked to changes in behaviour (Taruski, 1979). As 1-minute samples do not necessarily reflect biological persistence in a state, serial time correlation between 1-minute sample recordings may occur. When recording the calls in the field, the contours are heard/observed and the context recorded infers the presence of latent ‘hidden’ contexts that are the underlying causal source of the call patterns. Considering all the above, hidden Markov models (for review see Eddy, 1998) which account for the fact that different latent contexts lead to different patterns in the observed call data, were deemed the appropriate approach to modelling the dataset. The latent (or hidden) states permit the subtleties of call parameters to be described and infrequent or variable events to be detected (Chan et al., 2004; Stifter & Rovine, 2015; Popov et al., 2017).

A Markov chain selects the currently active distribution at a point in time, thus inducing observation-level dependence, allowing for the tendency of calling behaviour to be clustered (Popov et al., 2017). For call rate or mean frequency, each state is defined based on the probability of it occurring in relation to additional ‘hidden’ variables (i.e., species ratio, surface behaviour, tactile/posture rate). The transition probability is defined by transitioning each state to any other states, quantified by the hidden Markov model (Chan et al., 2004; Stifter & Rovine, 2015; Popov et al., 2017). The different distributions within the hidden Markov model can translate as representing the different calling states of a group of oceanic bottlenose dolphins.

4.2.3.2.1 Model formulation and statistical inference

All methods of hidden Markov model were comparable with Popov et al. (2017) and Quick et al. (2017). In this study the observable time series are a count of call rate (calls/minute/dolphin) or mean frequency (mean frequency/minute/dolphin). A realisation of one of the N distributions is assumed for each observation. The N state-dependent distributions are assumed to be negative binomial distributions, which can handle over-dispersion in the state-dependent distribution (Popov et al., 2017). N was chosen following AIC assessment (see section 4.2.3.2.4 for AIC details), careful consideration of the dataset considerations, or a combination thereof (Popov et al., 2017).

Visualisation of the dependence structure of a basic hidden Markov model used on oceanic bottlenose dolphin data is presented below. Dependences are represented as arrows. Here, the state process S_t is the context of the dolphins (it cannot be observed) at time t , and the observations X are calls/mean frequency/time interval, with t indicating the time period (modified from Popov et al., 2017). S_t is modelled by a first-order N-state Markov chain, in particular assuming the S_t distribution is singularly a result of the preceding context state variable S_{t-1} (Popov et al., 2017).



The analysis steps for hidden Markov models in this chapter were:

- 1) Formulate a baseline model;
- 2) Develop covariates;
- 3) Incorporate covariate information to produce covariate models;
- 4) Select covariate models which display best improvement on baseline model (AIC and Joint log-likelihood);
- 5) Include constituent algorithms: likelihood of observed time series computation using the forward algorithm;
- 6) Include constituent algorithms: State sequence underlying the observations decoded using the Viterbi algorithm;

- 7) Present the stationary (or equilibrium) distribution of observed variables (fixed hidden values, Patterson et al., 2009). I.e., the influence of hidden states on observed call variables;
- 8) Calculate transition probabilities for observed sequence with fixed hidden values - how likely oceanic bottlenose dolphins were to switch observed call states under the condition of those hidden states; and
- 9) Evaluate persistence in each state sequence with set covariate values - how likely the dolphins were to persist in observed call states under the condition of those hidden states.

4.2.3.2.2 Baseline model

To fit a hidden Markov model in this study, a strong simplifying assumption was applied and the data from all recordings were combined and a single model fitted. The observed data sequences (same stochastic process) were assumed to be stable and identical (same stochastic process). This was deemed appropriate in this case due to its application in other similar datasets and the identical recording protocols across the dataset (DeRuiter et al., 2016; Zucchini et al., 2016; Popov et al., 2017).

For the baseline model, homogenous (time constant) state transition probabilities we assumed, $\gamma_{ij} = Pr(S_t = j | S_{t-1} = i)$ (summarised in equation 3 in Table 4.2). In this homogeneous state process, based on call data, *steady state* (in equilibrium) is assumed at the beginning of the observation period. This is because the actual call behaviour will have been active already for a period of time, not the result of the recording starting (as per other acoustic studies, i.e., Popov et al., 2017). Equilibrium in the initial distribution is then assumed (stationary distribution). Here, d was calculated via $\delta(I_N - \Gamma + U) = 1'$, where I_N is an $N \times N$ identity matrix and U is an $N \times N$ matrix of ones (as per Popov et al., 2017; Zucchini et al., 2016). The homogeneity assumption was, however, relaxed, requiring δ to be estimated.

It can be problematic to directly interpret Markov chain parameters, thus both the stationary distributions and the transition probabilities matrix (t.p.m) were examined for fixed ratio values (as suggested in Patterson et al., 2009). Consequently, the behaviour of the stationary distribution and t.p.m. for all model levels were examined (Popov et al., 2017).

Table 4.2: Components of hidden Markov models used in this study (modified from Popov et al., 2017; Jurafsky & Martin 2018):

#	Equation	Description
1	$S_t, t = 1, \dots, n,$	State process for a single dataset. Here a series from 1 to N is considered and the N distribution that X_t (see equation 2) is derived from.
2	$X_t, t = 1, \dots, n$	Observable time series for a single dataset
3	$\Gamma = \begin{pmatrix} \gamma_{11} & \dots & \gamma_{1N} \\ \vdots & \ddots & \vdots \\ \gamma_{N1} & \dots & \gamma_{NN} \end{pmatrix}.$	A $N \times N$ transition probability matrix (t.p.m.). Γ^t would indicate the transition probability matrix at time t .
4	$P_i(x) = \frac{\Gamma(x + n_i)}{\Gamma(n_i)\Gamma(x + 1)} \left(\frac{n_i}{n_i + u_i} \right)^{n_i} \left(\frac{u_i}{n_i + u_i} \right)^x.$	A negative binomial distribution probability mass function with $q = 2$ parameters. Note, n_i = state-specific size, u_i = mean and $\Gamma(\cdot)$ = the gamma function.
5	$\Gamma = \begin{pmatrix} 1 - \gamma_{12} & \gamma_{12} \\ \gamma_{21} & 1 - \gamma_{21} \end{pmatrix}.$	A two-state hidden Markov model with t.p.m. to illustrate how the likelihood function was constructed
6	X_1, \dots, X_n	Likelihood of an observed time series. Each expresses the probability of an observation X_t being generated from a state. Under the assumption of independence of the recording time-series, the joint log-likelihood was the sum of the log-likelihoods of individual recording. This joint log-likelihood was maximised numerically, using Newton-Raphson-type optimisation in free statistical software R, using the routine NLM() (R Core Development Team, 2014, RStudio for Mac version 1.0.136)
7	$\delta = 1/(\gamma_{12} + \gamma_{21})(\gamma_{21}, \gamma_{12})$	The stationary distribution, when the Markov chain was in equilibrium at the start of the time series
8	$\begin{aligned} &\ell(\theta 19, 0, \dots, 0) \\ &= \frac{1}{\gamma_{12} + \gamma_{21}} (\gamma_{21}, \gamma_{12}) \begin{pmatrix} P_1(19) & 0 \\ 0 & P_2(19) \end{pmatrix} \\ &\times \begin{pmatrix} 1 - \gamma_{12} & \gamma_{12} \\ \gamma_{21} & 1 - \gamma_{21} \end{pmatrix} \begin{pmatrix} P_1(0) & 0 \\ 0 & P_2(0) \end{pmatrix} \dots \begin{pmatrix} 1 - \gamma_{12} & \gamma_{12} \\ \gamma_{21} & 1 - \gamma_{21} \end{pmatrix} \\ &\times \begin{pmatrix} P_1(0) & 0 \\ 0 & P_2(0) \end{pmatrix} \begin{pmatrix} 1 \\ 1 \end{pmatrix}, \end{aligned}$	The corresponding likelihood of the initial datasets, where $\theta = (\gamma_{12}, \gamma_{21}, \mu_1, n_1, \mu_2, n_2)'$. In the first dataset, the call rates or mean call frequencies were given by (1.3, 0, ..., 0 and the ellipsis do not indicate zeros, but general observations.

4.2.3.2.3 ‘Hidden’ state covariates in hidden Markov model

4.2.3.2.3.1 Development of covariates

Subsurface and surface influences on call behaviour were considered by including these variables as ‘hidden’ states (covariates) on the probability of transitions between states of call behaviour. The assumption was made that the covariates provided explanatory information about oceanic bottlenose dolphins’ likelihood of transitioning between call states. All the covariates considered in this analysis originated from instantaneous focal follow data, both surface and subsurface. Independent covariates were unlikely, so an all-encompassing analysis was not a good compromise between the number parameters, improved model fit, and

biological inference (Popov et al., 2017).

Each model was considered with one covariate (listed in Table 4.3). The only disparity between models of mean frequency and call rate was *group size*, which was also added as a covariate for mean frequency. Since call rate was calculated based on the number of individuals, *group size* was not included in the base comparison. Model formulation included only a single covariate at any time to avoid numerical instability for the hidden Markov model analysis performed. Additional covariates were considered separately in subsequent analyses, if required, to maintain numerical stability.

Table 4.3: Potential covariates for hidden Markov models from the original dataset of oceanic common bottlenose dolphins (*T. truncatus*) and pilot whales (*Globicephala* sp.). * only included in mean frequency models, ** variable combined with only top models.

Covariate	Variable definition
Year	1 st September 2013 – 31 st August 2014 and 1 st September 2014 – 31 st August 2015
Month	Defined as lunar month
Water depth	Water depth (m) at time of recording
Substrate	Predominant substrate type – rocky, sandy, vegetation
BSS	Beaufort sea state; 1, 2, 3 or 4
Wind speed	0 – 5, 6 – 10, 11 – 15, 16 – 20 (knts)
Surface behaviour	Travelling, milling, resting, foraging, socialising, and diving
Calf presence (y/n)	Refer to Appendix 2.2, for calf definition
Species ratio	Group size of each species present and whole group were logged according to the same categories as group size.
Mixed species (y/n)	Yes/no, indicates if group is oceanic bottlenose dolphin only or pilot whale only (pilot whale only) if no, and mixed oceanic bottlenose dolphin with pilot whale (oceanic bottlenose dolphin mixed) if yes
Tactile type	Predominant tactile per minute (Section 4.2.2.)
Posture type	Predominant posture per minute (Section 4.2.2.)
Tactile/posture rate	Mean number of tactile/posture per minute
Detection range	Secchi disk measurements of visibility (m)
Surface cohesion	The elliptical spread area was included ([group size/spread area]*100) in the estimation of group density (number of dolphins per 100 m ²)
Synchrony	The number of animals surfacing in sequential 3-second intervals for a 30-second period
Group size*	Collective group size was logged according to three categories; minimum, maximum and the best estimate (Dwyer et al., 2016; Peters & Stockin, 2016; section 4.2.1.1.1.). Best estimate was modelled.
time to change (TTCh)**	Additionally, time to change (TTCh) was included in analysis for the top covariates indicated (as per Popov et al., 2017). The time (minutes) to the nearest (before or after the current time bin) change in group call behaviour is measured. This was included as oceanic bottlenose dolphin coordinate their behaviour (with calls) before, during, and after a change in context.

4.2.3.2.3.2 Covariates in the t.p.m.

Covariates in the hidden Markov model were assumed to influenced the transition between states, not the state-dependent distributions (fixed for a given state, Zucchini et al., 2016). The t.p.m. row constraints, i.e., $\gamma_{ij} \in [0,1]$, $\sum_{i=1}^N \gamma_{ij} = 1$, for $i = 1, \dots, N$, were handled with a multinomial logistic link function (Popov et al., 2017):

$$\gamma_{ij} = \frac{\exp(\beta'_{ij} y_t)}{\sum_{l=1}^N \exp(\beta'_{il} y_t)}, \quad (9)$$

Where the vector $y'_t = (1, y_{1,t}, \dots, y_{k,t})$ included k covariates at time t . Additionally, b_{ij} is a $k + 1$ column vector with estimated coefficients (Popov et al., 2017). This analysis set $b_{ii} = 0$ for $i = 1, \dots, N$; this is standard practice in multinomial logit modelling (McFadden, 1984; as used in Popov et al., 2017). With the addition of covariates in the t.p.m., the number of parameters increased from the baseline model, represented by $N(N - 1)$ to $N(N - 1)(k + 1)$ (Popov et al., 2017).

In the baseline model all covariate coefficients were treated as zero. The addition of covariates influenced the transition probabilities and the Markov chain was no longer homogeneous. The state process could no longer be described as stationary, thus the initial state distribution was estimated alongside the other model parameters.

4.2.3.2.3.3 Model selection and checking - AIC protocol

In order to choose between different candidate models, the model selection criteria of Akaike's Information Criterion with correction for small samples (AICc) was applied (Akaike, 1973). AICc scores are a version of AIC created to deal with small sample sizes, which is advised to be used as a default (Symonds & Moussalli, 2011). Each base and covariate model were assessed with AICc scores which include the data fit and complexity of the model. This approach results in the simpler model being favoured if two models had similar fit. The calculation of AICc scores was as follows (Akaike, 1973):

$$AIC = -2\ln(l) + 2k + \frac{2k(k + 1)}{n - k - 1} \quad (10)$$

$$AIC_c = AIC + \frac{2k^2 + 2k}{n - k - 1}$$

Where l is the maximum likelihood estimate and k is the number of parameters (including the intercept). Joint log-likelihood for all encounter datasets was used, with p the number of

parameters estimated (i.e., the length of the vector h) and n_{tot} the total number of observations. Finally, evidence ratios (ER; calculated as the ratio of two model likelihoods) quantified the relative empirical support for any two models in the set. The process of model selection provided evidence as to which factors were better predictors of the response variable (i.e., which factors had stronger effects). An additional model selection criterion was applied. Ordinary pseudo-residual plots were produced to quantify the goodness-of-fit of the hidden Markov model (following Popov et al., 2017 and Zucchini et al., 2016). The resulting plots allowed any outliers or inadequacy of fit to be identified (following Popov et al., 2017).

4.2.3.2.3.4 Interpretation of the t.p.m parameters.

For t.p.m. covariate models, their effect on the t.p.m was described using the stationary (or equilibrium) distribution. This assumed a fixed level covariate (Patterson et al., 2009; Popov et al., 2017). The covariate value and the estimated coefficients provided information on the model's marginal behaviour. The influence of the covariate can be assessed by comparing fixed level results. Confidence intervals for the stationary distributions were calculated using the delta method (Oehlert, 1992). Set covariate values were also used to calculate the probability of transition for those set values. This allowed interpretation of how likely the oceanic bottlenose dolphins were to switch states under the conditions of those variables.

4.2.3.2.3.5 Likelihood estimation

Models were fitted via a numerical maximum likelihood estimation approach, utilising the *nlm* optimiser in R, primarily due to the associated low computational cost (see Altman, 2007 for implementation details). For an observed time series (Table 4.1, equation 6), the likelihood was calculated, by considering all possible hidden state sequences that may have influenced call observations. The models were run 100 times to achieve maximisation and check numerical stability (Quick et al., 2017). The two state-dependent distributions are negative binomials with $p_i(x)$ given in Table 4.1, equation 8, with the parameters (l_1, n_1) and (l_2, n_2) , respectively (corresponding likelihood is detailed in Table 4.1, equation 8; Popov et al., 2017).

4.2.3.2.3.6 Viterbi algorithm - sequence of hidden states

For a model, “the most likely sequence of hidden states, given the likelihood of observations under the state-dependent distributions and the transition probabilities between states” (Quick

et al., 2017, p. 10), was estimated using the Viterbi algorithm (Forney, 1973). The Viterbi hidden Markov model package in R was utilised (R Core Development Team, 2014). This approach produced the most likely sequence of the ‘hidden’ states based on the data available (Quick et al., 2017). Specifically, the aim was to produce the sequence s_1, s_2, \dots, s_n that maximises the conditional probability (Popov et al., 2017):

$$\Pr(S_1 = s_1, \dots, S_n = s_n, X_1 = x_1, \dots, X_n = x_n) \quad (11)$$

The state sequences for each encounter were decoded separately, due to the independence assumption (introduced in Table 4.1, equation 6).

4.3 Results

4.3.1 Mechanical and photic effort

Call data and corresponding subsurface video were collected in Far North waters between September 2013 and September 2015. A total of 10 encounters, 4 from oceanic bottlenose dolphin only and 6 from oceanic bottlenose dolphin mixed were recorded. Due to the large group sizes of oceanic bottlenose dolphin mixed encounters, focal sub-groups were preferentially sampled, resulting in 32 sub-groups (referred to as oceanic bottlenose dolphin mixed throughout). From the 36 focal groups 190 acoustic recordings were taken, yielding a total sample of 18,972 calls (oceanic bottlenose dolphin only $n = 8,031$ and oceanic bottlenose dolphin mixed $n = 10,941$). The call data summary is shown in Chapter 3, details on acoustic field research efforts are provided in Appendix 1.1, and an example spectrogram is provided in Appendix 4.7. Call rate results are also provided in Appendix 4.8.

Video effort return in oceanic bottlenose dolphins was 75.1 % ($n = 60$, Appendix 4.9). A total of 589 events were recorded from oceanic bottlenose dolphins ($n = 139$ oceanic bottlenose dolphins only, $n = 450$ oceanic bottlenose dolphins mixed). Mean rates of contact for behavioural events across the entire sample period are shown in Appendix 4.10 – 4.11. Of the 589 events recorded, 392 were contact and 197 postures. Two predominant contact interaction types could be attributed to the broad categorisation of mother-calf (melon to genital, 19.13 %, $n = 75$) and aggression (circle chase/dive and bite, 59.4 %, $n = 233$). The number of concurrent mechanical and photic counts were sufficient and the assumptions met to conduct analysis of the effects of factors on call behaviour, including mechanical and photic behaviour.

4.3.2 Comparison of call parameters

The calls recorded from oceanic bottlenose dolphin mixed were found to have significantly (KW or ANOVA: $P < 0.05$) higher measures for 66.7 % ($n = 18,972$) of call parameters than oceanic bottlenose dolphin only (Table 4.4 and Appendix 4.12). Call duration was significantly longer ($X^2 = 17.53$, $P < 0.010$) in oceanic bottlenose dolphin mixed (Table 4.4). Oceanic bottlenose dolphin mixed calls had significantly more visible harmonics and more contour inflections (both positive to negative and *vice versa*) (Table 4.4). Note, true independence cannot be achieved here due to repeated contour types. These results suggest the calls recorded of oceanic bottlenose dolphin mixed contained more information than oceanic bottlenose dolphin only, as reflected by the longer duration of calls.

Table 4.4: Summary of Kruskal-Wallis test for non-parametric call parameters measured from oceanic common bottlenose dolphins (*T. truncatus*). Values in bold are significant at the 95 % level. Note, oceanic only = oceanic bottlenose dolphin only and oceanic mixed = oceanic bottlenose dolphins in mixed species groups with pilot whales (*Globicephala* sp.), rel = relative, freq = frequency.

Parameter	oceanic only Median	I-Q range	oceanic mixed Median	I-Q range	Chi-square	<i>P</i>
Duration (s)	0.59	0.57 – 0.61	0.70	0.62 – 0.70	17.53	< 0.010
Prop time of min freq	0.54	0.47 – 0.56	0.54	0.46 – 0.59	2.04	0.991
Prop time of max freq	0.53	0.46 – 0.57	0.51	0.41 – 0.61	3.47	0.463
Number of harmonics	3.18	3.12 – 3.52	3.99	3.52 – 4.01	23.17	< 0.010
Major inflections (+to-)	0.97	0.95 – 1.00	1.21	1.04 – 1.24	20.91	0.042
Major inflections (-to+)	1.17	1.13 – 1.25	1.49	1.28 – 1.57	19.42	0.019
Rel time of peak freq	0.52	0.21 – 0.71	0.55	0.10 – 0.63	1.98	0.084
Rel centre time	0.50	0.34 – 0.69	0.59	0.28 – 0.78	4.62	0.099

Frequency and temporal variables produced in inter-specific groups were intermediate to those of intra-specific groups (Figure 4.2). Behaviour state also significantly affected frequency and temporal variables. Groups in a travelling state did not utilise significantly different calls as a result of group structure. Conversely, in a socialising state, calls emitted by inter-specific and intra-specific groups were significantly different (Appendix 4.12, Figure 4.2).

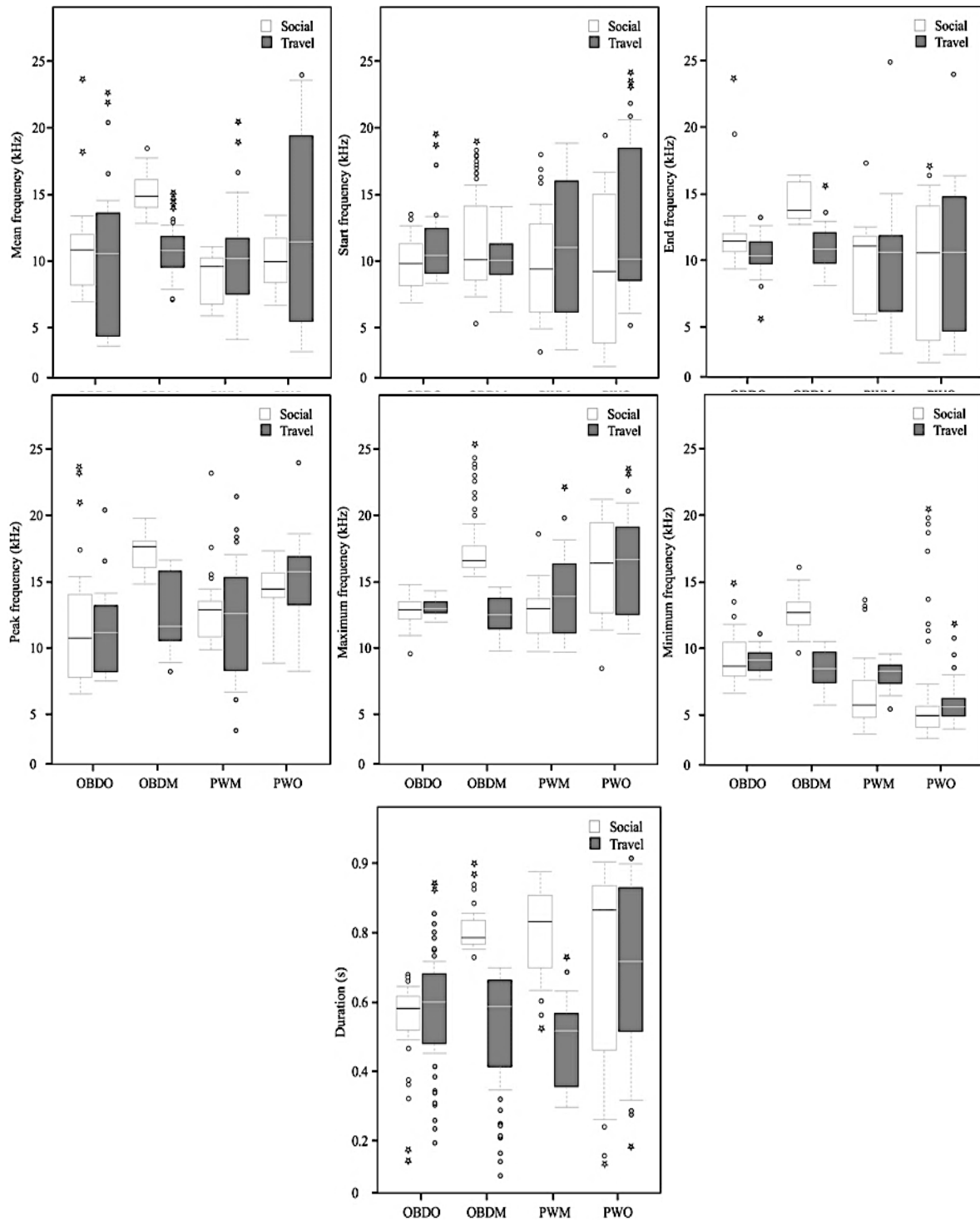


Figure 4.2: Call variation of intraspecific groups based on behavioural context in oceanic common bottlenose dolphins (*T. truncatus*) and pilot whales (*Globicephala* sp.). single species and mixed groups. Note, OBDO = oceanic bottlenose dolphins only and OBDM = oceanic bottlenose dolphins in mixed species groups with pilot whales with measurements from oceanic ecotype, PWO = pilot whales only and PWM = oceanic bottlenose dolphin in mixed species groups with pilot whales, measurements from pilot whales.

4.3.3 Group type variation in encounter call repertoire

Call repertoire was more analogous within each *group type* than between *group type*, apart from when *behaviour state* was included as a factor (See Appendix 4.13 for average Spearman's correlations of call repertoire with *group size*, *behaviour state*, *year* and *season* variables). Notably, in nonmetric multidimensional scaling of calls, clustering was found as a result of *behaviour state* and *group size* but not *season* or *year* (Appendix 4.13 – 4.16). When encounter repertoires were clustered (Figure 4.3) using a Unweighted Pair Group Method with Arithmetic Mean hierarchical algorithm, mixed and oceanic bottlenose dolphin encounters were distinct with some omissions. Correspondingly, k-medoid clusters of recordings and encounters, classified group type correctly for 68 % of comparisons with $k = 2$ (Appendix 4.14 – 15).

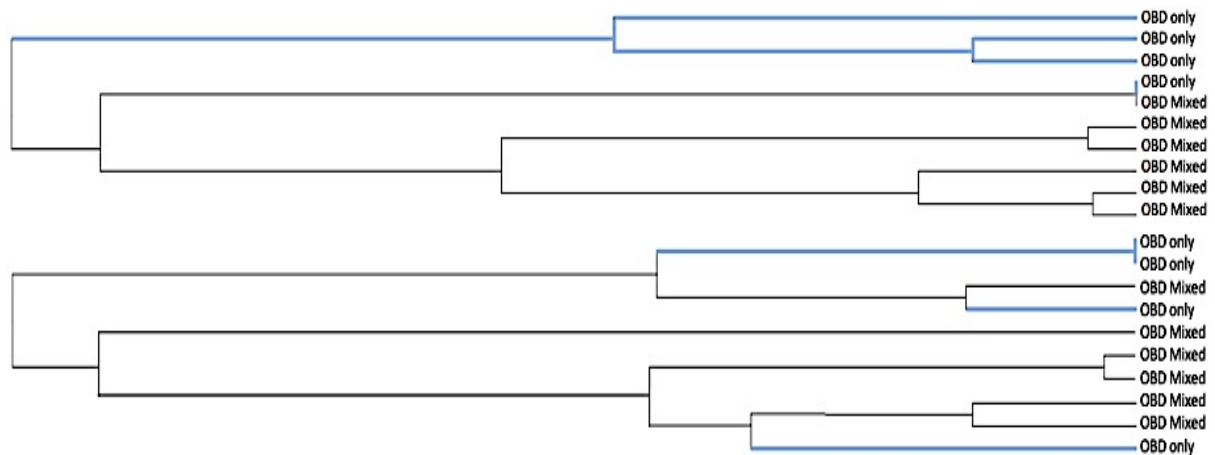


Figure 4.3: Dendrograms of encounter call repertoires of oceanic common bottlenose dolphins (*T. truncatus*) recorded during socialising (top) and travelling (bottom). Note, OBD only = oceanic bottlenose dolphin only and OBD mixed = oceanic bottlenose dolphin in mixed species groups with pilot whale (*Globicephala* sp.).

Note, clustering was unsupervised (unlike, e.g., discriminant function analysis), indicating a true divergence between oceanic bottlenose dolphin in intra- and inter-specific group types. Additionally, the Global Silhouette Index of recordings indicated $k = 2$ (Appendix 4.14, see Chapter 3 for further details) for recordings and encounters. This suggested two clusters in the dataset. For further clarity in clustering success, see dendrogram of recordings (Appendix 4.16). The divergence score between oceanic bottlenose dolphin only and oceanic bottlenose dolphin mixed groups was greater than within group comparisons (Table 4.5). In addition, both groupings had lower divergence scores within the same *season* than with each other (Table 4.5), suggesting divergence observed occurred not only as a consequence of seasonal variation.

Table 4.5: Estimates of pairwise population divergence in call repertoire structure (per recording and encounter) in oceanic common bottlenose dolphins (*T. truncatus*). Note, oceanic only = oceanic bottlenose dolphins only and oceanic mixed = oceanic bottlenose dolphins in mixed species groups with pilot whales (*Globicephala* sp.).

Scenario A	Scenario B	Recordings	Encounters
oceanic only	oceanic mixed	0.1327	0.1027
oceanic only-socialising	oceanic mixed-socialising	0.1293	0.0934
oceanic only-group size	oceanic mixed-group size	0.1204	0.0877
oceanic only-milling	oceanic mixed-milling	0.1195	0.0853
oceanic only-travelling	oceanic mixed-travelling	0.1022	0.0816
oceanic only-summer	oceanic mixed-autumn	0.0981	0.0743
oceanic only-autumn	oceanic mixed-summer	0.0092	0.0057
oceanic only-foraging	oceanic mixed-foraging	0.0079	0.0020
oceanic only-resting	oceanic mixed-resting	0.0063	0.0012
oceanic only-summer	oceanic mixed-summer	0.0011	0.0009
oceanic only-autumn	oceanic mixed-autumn	0.0008	0.0006

4.3.4 Multivariate mixed hidden Markov models of subsurface responses

4.3.4.1 ‘Hidden’ state covariates in hidden Markov model

Six negative binomial models were fitted with three- and five-states for call rate and mean frequency, respectively (as a result of baseline model selection detailed in Appendix 4.17). Both model selection criteria (AIC_c and cross-validation) chose the negative binomial model, with *species ratio TTCh* as the best-performing one-covariate model for both call rate and mean frequency. It also outperformed the baseline three- and five-state model (cf. Appendix 4.17).

Comparing *species ratio* with *mixed species (y/n)* indicated that including information relating to the ratio of species within a group improved the fit, as opposed to considering presence only. Further to this, according to both model selection criteria, *tactile/posture rate* and *surface behaviour* variables also resulted in a considerable improvement in the fit compared to other variables and the baseline three- and five-state models.

The inclusion of time to change improved the fit of all top performing models. This underlined the potential importance of the above additional variables in subsequent analysis (Table 4.6). Before considering model results, the fit of data was assessed using pseudo-residuals (Appendix 4.18). A lack of fit was not identified. There were no (call rate) or very few outliers (0.5 %, n = 2, mean frequency, Appendix 4.18), as well as no apparent temporal pattern for either dataset.

Table 4.6: Model selection criteria of negative binomial hidden Markov models for call rate and mean frequency with 1 covariate in oceanic common bottlenose dolphin only (*T. truncatus*). Note: AIC_c = Akaike's Information Criterion for small sample size, llk = maximum log likelihood, CV = mean cross-validated (log) likelihood. Key: pale grey highlight = top negative binomial model, blue highlight = best performing negative binomial model.

	Model	AIC _c	llk	CV
Call rate (3-state)	wind speed	5,272.15	-4328.112	-501.219
	year	5,271.46	-4327.573	-501.217
	BSS	5,265.32	-4326.434	-501.210
	month	5,244.25	-4328.547	-501.135
	surface cohesion	5,242.03	-4,327.002	-501.132
	synchrony	5,240.12	-4,321.783	-501.132
	substrate	5,226.84	-4,300.561	-501.131
	detection range	5,216.47	-4,264.718	-499.957
	water depth	5,209.91	-4,217.483	-499.901
	calf presence (y/n)	5,201.56	-4,202.435	-499.857
	surface behaviour	3,862.15	-2,920.351	-361.527
	posture type	3,847.05	-2,918.003	-360.114
	tactile type	3,799.32	-2,903.122	-358.335
	mixed species (y/n)	3,739.02	-2,576.704	-347.959
	mixed species (y/n) TTCh	3,614.11	-2,501.292	-331.280
	tactile/posture rate	3,534.61	-1,911.279	-329.336
	tactile/posture rate TTCh	3,528.73	-1,873.155	-325.831
	species ratio	3,525.24	-1,809.573	-323.815
	species ratio TTCh	3,523.76	-1,800.254	-322.702
Mean frequency (5-state)	BSS	5,291.96	-9,643.102	-669.747
	detection range	5,291.73	-9,601.393	-669.745
	water depth	5,291.45	-9,571.348	-669.745
	wind speed	5,283.27	-9,425.672	-669.744
	synchrony	5,281.53	-9,406.235	-669.743
	surface cohesion	5,280.02	-9,392.487	-669.742
	Month	5,280.02	-9,562.049	-669.742
	Year	5,279.84	-9,571.141	-669.741
	posture type	5,278.63	-9,662.358	-669.740
	Substrate	5,278.27	-9,591.125	-669.740
	group size	5,278.19	-9,500.824	-669.739
	tactile type	5,278.05	-9,488.203	-669.738
	calf presence (y/n)	5,277.51	-9,400.513	-669.731
	tactile/posture rate	4,345.92	-7,126.231	-492.108
	surface behaviour	4,271.63	-7,108.174	-478.523
	surface behaviour TTCh	4,270.52	-7,108.002	-472.826
	tactile/posture rate TTCh	4,264.08	-7,091.273	-441.040
	mixed species (y/n)	4,252.57	-7,067.565	-425.395
	mixed species (y/n) TTCh	4,133.01	-7,015.914	-416.813
	species ratio	4,019.33	-7,002.193	-407.784
	species ratio TTCh	4,019.01	-7,001.371	-407.121

4.3.4.2 The effect of species ratio on call parameters

The estimated mean negative binomial distribution for each state of hidden Markov model, including *species ratio TTCh* as a covariate, are presented in Appendix 4.19. For call rate, judging by the mean values, states 1 to 3 were labelled as *low*, *medium* and *high* call rate, respectively. Two additional states were added for mean frequency, with states 1 to 5 labelled as *very low*, *low*, *medium*, *high*, and *very high*, respectively.

Species ratio TTCh was categorised as *low ratio* (≤ 33 % oceanic bottlenose dolphin), state 2 as *medium ratio* ($\geq 34 - \leq 67$ % oceanic bottlenose dolphin), and state 3 as *high ratio* (≥ 68 % oceanic bottlenose dolphin), based on the ratio of animals in the frame. The stationary distribution of call rate (Figure 4.4A) and mean frequency (Figure 4.4B) were then considered. For call rate, moving from *oceanic bottlenose dolphin only* to *low ratio* groupings, the probability of being in the fewest calls state decreased steadily.

The use of states with a moderate or high number of calls, respectively, gradually increased (Figure 4.4A). Indeed, the probability of being in state 1 (lowest call rate) was 37.1 % when oceanic bottlenose dolphins only were present. The addition of a few pilot whales in the group increased the call rate to 50.2 % (oceanic bottlenose dolphin high ratio) before it decreased when the ratio of oceanic bottlenose dolphin to pilot whale was lower (Figure 4.4A).

In the case of mean frequency, when moving from *oceanic bottlenose dolphin only* to *oceanic bottlenose dolphin low species ratio*, the probability of being in a higher mean frequency state (states 4 and 5) increased when any pilot whales were present, while the probabilities of low frequency vocalisation (states 1, 2 and 3) occurring gradually decreased once pilot whales were present (Figure 4.4B). While the probability of being in state 1 was 57.2 % in the presence of only oceanic bottlenose dolphins (e.g., *oceanic bottlenose dolphin only*), it decreased by 98.3 % (down to approximately 1.0 %) when ≤ 33 % of the group were oceanic bottlenose dolphins.

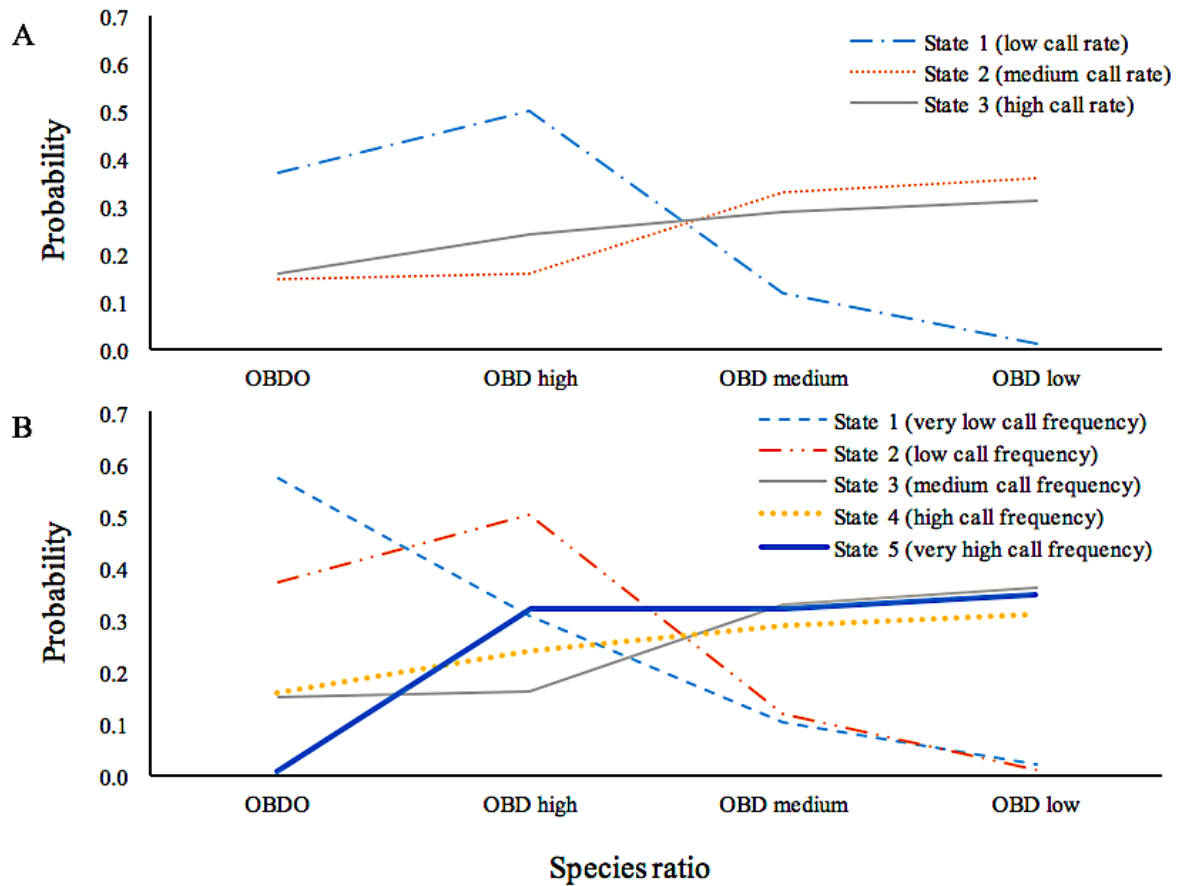


Figure 4.4: Stationary distributions for different values of species ratio TTCh and A) call rate and B) mean call frequency of oceanic common bottlenose dolphins (*T. truncatus*). Note, OBDO = groups with oceanic bottlenose dolphins only, OBD high = groups with high ratio oceanic bottlenose dolphin to pilot whale (*Globicephala* sp.) they are in association with, OBD medium = groups with medium ratio oceanic bottlenose dolphin to pilot whale they are in association with, OBD low = groups with low ratio oceanic bottlenose dolphin to pilot whale they are in association with.

The transition rates between states are shown in Figure 4.5. For call rates, when oceanic bottlenose dolphins were in the low-call rate (state 1), the between-state transition probabilities hardly changed as oceanic bottlenose dolphin ratio changed (Figure 4.5). Conversely, the probability of switching from state 2 to state 1 and 2 to 3 appeared to be heavily influenced by oceanic bottlenose dolphin ratio. In particular, when transitioning from 2-1 it steadily increased to 45.2 % as the ratio of oceanic bottlenose dolphins decreased. When transitioning from state 2 – 3, probability takes a relatively high value (22.1 %) when oceanic bottlenose dolphins were with a small number of pilot whales. Probability dramatically dropped when the dolphins were in groups with a medium (down to 6.1 %) or low ratio (down to 4.3 %) compared to pilot whales. Overall, the oceanic bottlenose dolphins were more likely to leave the low-call-rate state when they were with pilot whales and leave the high-call-rate state when they were with a proportionally larger number of pilot whales. Additionally, they were more likely to remain in this comparatively silent state when proportionally more pilot whales were present.

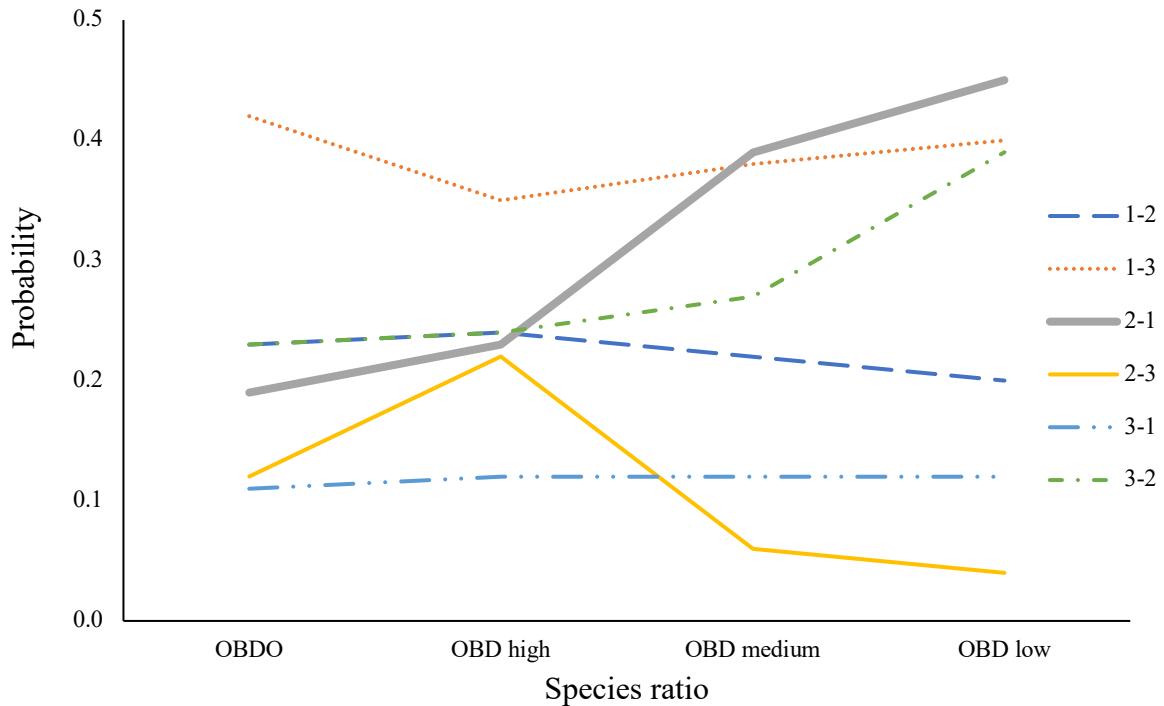


Figure 4.5: Between-state transition probabilities for different species ratio TTCh and call rate of oceanic common bottlenose dolphins (*T. truncatus*). Note, OBDO = groups with oceanic bottlenose dolphins only, OBD high = groups with high ratio oceanic bottlenose dolphin to pilot whale (*Globicephala* sp.) they are in association with, OBD medium = groups with medium ratio oceanic bottlenose dolphin to pilot whale they are in association with, OBD low = groups with low ratio oceanic bottlenose dolphin to pilot whale they are in association with.

Oceanic bottlenose dolphins were also more likely to leave the low-frequency state when they were in lower ratio to pilot whales and utilise the high and very high-frequency states when they were in low ratio. The rates of transition between states with *species ratio TTCh* as a covariate for mean frequency are given in Figure 4.6A & B. The between-state transition probabilities appeared to be heavily influenced by species ratio. In particular when transitioning from state 1, the highest value (34.0 %) was observed when the dolphins were in *oceanic bottlenose dolphin medium* groups, after steadily increasing from 22.4 % in oceanic bottlenose dolphin only groups. Overall, the dolphins were more likely to leave the low-frequency state (state 1) when they were in higher ratio to pilot whales (oceanic bottlenose dolphin only and oceanic bottlenose dolphin high) (Figure 4.6A) and used the high and very high-rate states (states 4 and 5) when they were in low ratio (oceanic bottlenose dolphin low; Figure 4.6B).

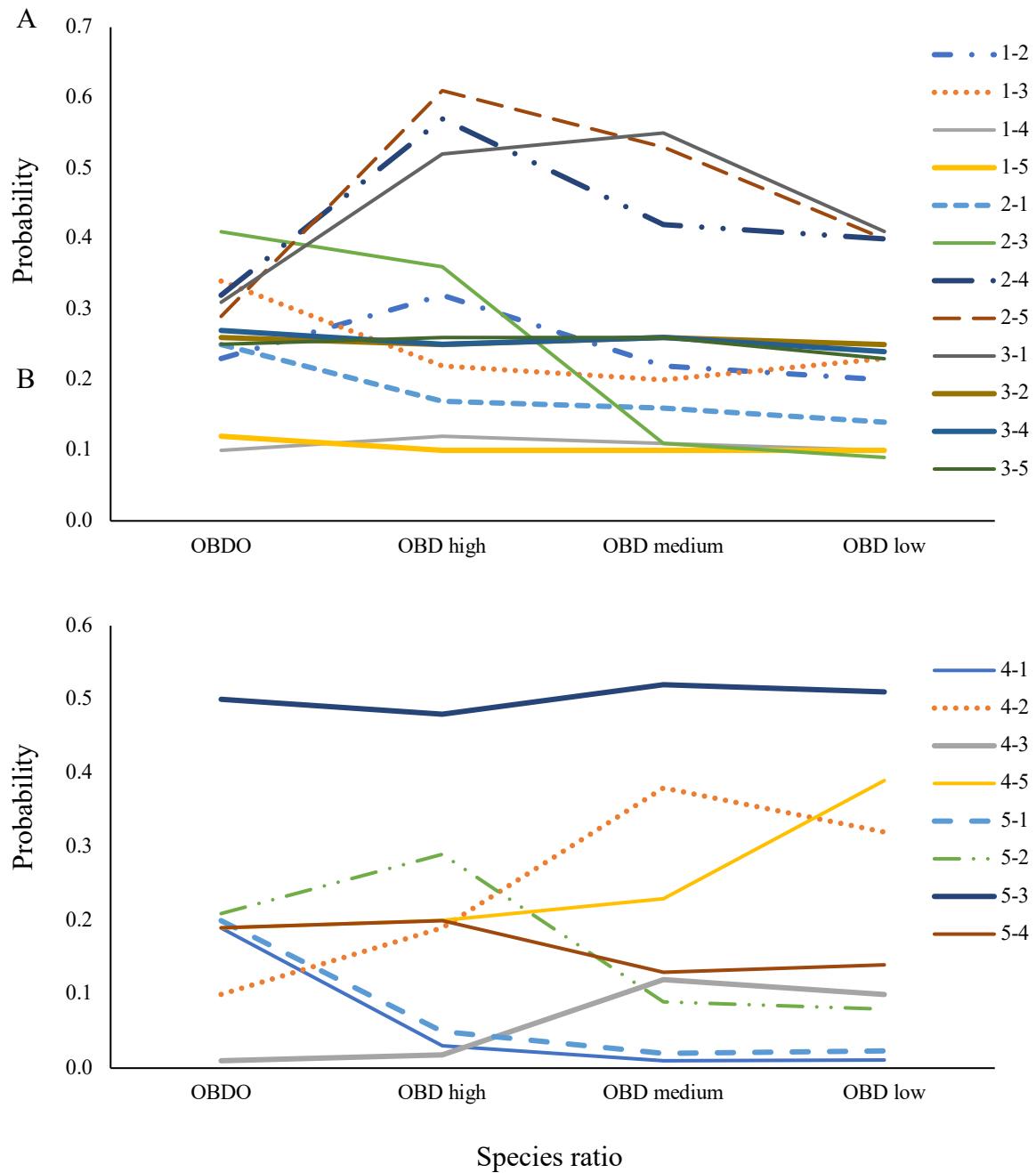


Figure 4.6: Between-state transition probabilities for different species ratio TTCh and mean call frequency of oceanic common bottlenose dolphins (*T. truncatus*) Note, OBDO = groups with oceanic bottlenose dolphins only, OBD high = groups with high ratio oceanic bottlenose dolphin to pilot whale (*Globicephala* sp.) they are in association with, OBD medium = groups with medium ratio oceanic bottlenose dolphin to pilot whale they are in association with, OBD low = groups with low ratio oceanic bottlenose dolphin to pilot whale they are in association with. A) transitions from state 1 – 3 and B) transitions from state 4 – 5

No states showed high persistence, resulting in a pattern of shorter periods of each state. Transition from a low-call-rate (state 1) to a high-call-rate (state 3) state and *vice versa* often took place abruptly, rather than gradually via the medium-state. The decoding of call rate

indicated that the dolphins persisted 11.0 %, 41.3 %, and 16.2 % of the time for states 1, 2, and 3, respectively (Figure 4.7).

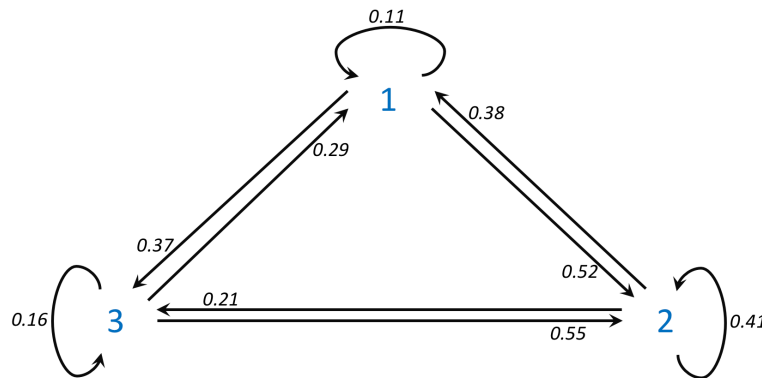


Figure 4.7: Transition matrix for three state model of call rate in the presence of varying species ratio TTCh of oceanic common bottlenose dolphins (*T. truncatus*). Note, State 1 = low call rate, State 2 = medium call rate and State 3 = high call rate. Key: Blue numbers = state, black number = transition rate, arrow direction = direction of transition between states.

The same pattern was apparent in mean frequency models (Figure 4.8), where dolphins also persisted in their mean frequency state 9.2 %, 18.2 %, 23.1 %, 23.5 %, and 12.7 % of the time in states 1, 2, 3, 4, and 5, respectively. Consequently, the dolphins appeared to stay in the state with medium vocalisation rate and frequency (states 3 and 4) compared to the states with low and high rates and frequency vocalisation (states 1, 2 and 5).

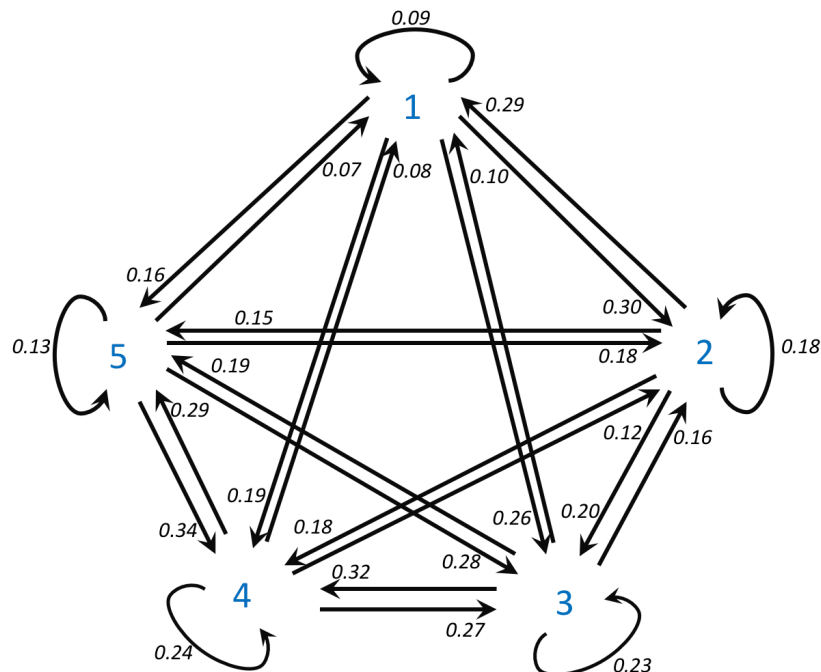


Figure 4.8: Transition matrix for five state model of mean call frequency in the presence of varying species ratio TTCh of oceanic common bottlenose dolphins (*T. truncatus*). Note, State 1 = very low, State 2 = low, State 3 = medium, State 4 = high and State 5 = very high mean call frequency. Key: Blue numbers = state, black number = transition rate, arrow direction = direction of transition between states.

4.3.5 Further investigation: covariate interaction

4.3.5.1 The effect of tactile/posture rate on call rate (multi-modal communication)

Both model selection criteria (AIC and cross-validation) indicated the negative binomial model with *tactile/posture rate TTCh* as the second best-performing one-covariate model for call rate, with minimal difference between this and the top AIC model (species ratio TTCh) (Table 4.5). It also outperforms the baseline three- and five-state model (cf. Appendix 4.19). This underlined the potential importance of *tactile/posture rate TTCh* in subsequent analysis (Table 4.5). In order to assess *tactile/posture rate TTCh* effect on call rate in different *species ratio TTCh* contexts, hidden Markov models were run on sequences of call rate for four separate scenarios - oceanic bottlenose dolphin only, oceanic bottlenose dolphin high, oceanic bottlenose dolphin medium, and oceanic bottlenose dolphin low to assess stationary distributions. The estimates of mean negative binomial distributions within each of the states of hidden Markov model, including *tactile/posture rate TTCh* are presented in Appendix 4.19.

Tactile/posture rate TTCh was categorised as low tactile/posture rate (< 2 per minute) and state 2 as high tactile/posture rate (≥ 2 per minute), based on the rate of contact observed. The stationary distribution of call rate (Figure 4.9) was then considered. Overall, when moving from *low tactile/posture rate TTCh* to *high tactile/posture rate TTCh* groupings, the probability of being in state 1 increased. The probabilities of being in moderate or high call states also decreased (Figure 4.9). The inverse relationship of call rate and *tactile/posture rate TTCh* was more pronounced as the ratio of oceanic bottlenose dolphins reduced. For oceanic bottlenose dolphin only, the probability of being in state 1 (lowest call rate) is 62.3 % when *tactile/posture rate TTCh* is high, this increased when in oceanic bottlenose dolphin low ratio sub-groups with the probability of being in state 1 is 87.9 % when *tactile/posture rate TTCh* is high (Figure 4.10).

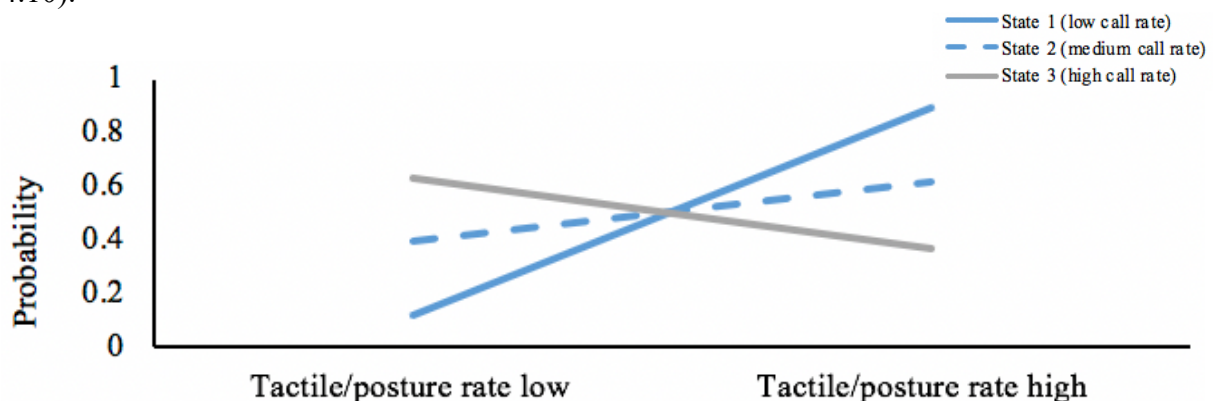


Figure 4.9: Stationary distributions for different values of tactile/posture rate TTCh and call rate of oceanic common bottlenose dolphins (*T. truncatus*).

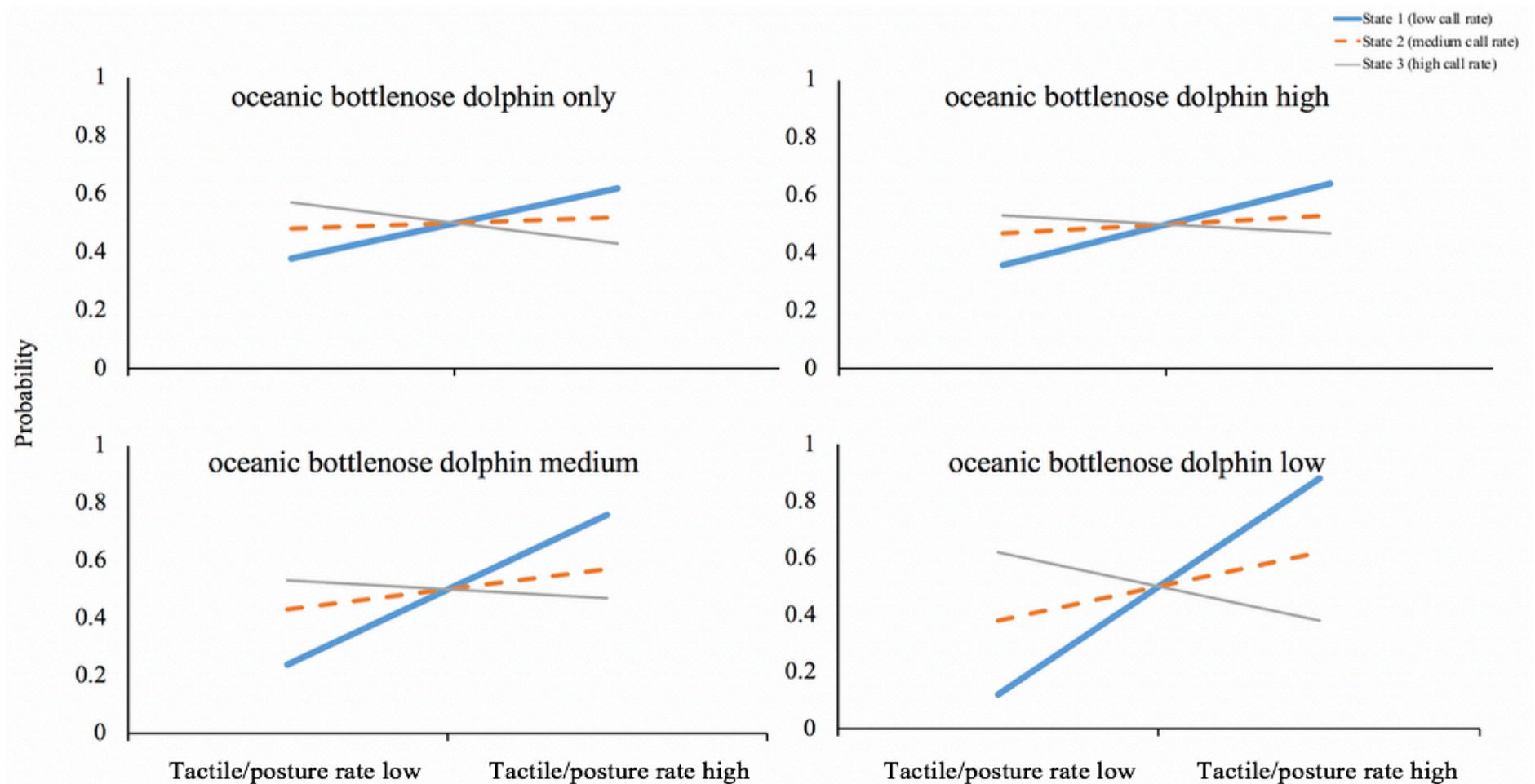


Figure 4.10: Stationary distributions for different values of tactile/posture rate TTCh and call rate of oceanic bottlenose dolphins (*T. truncatus*) in four different species ratio contexts. Note, oceanic bottlenose dolphin only = groups with oceanic bottlenose dolphin only, oceanic bottlenose dolphin high = groups with high ratio oceanic bottlenose dolphin to pilot whale (*Globicephala* sp.) they are in association with, oceanic bottlenose dolphin medium = groups with medium ratio oceanic bottlenose dolphin to pilot whale they are in association with, oceanic bottlenose dolphin low = groups with low ratio oceanic bottlenose dolphin to pilot whale they are in association with.

The rates of transition between states are given in Figure 4.11. For *tactile/posture rate TTCh*, the probability of switching from call rate state 1 and 3 appeared to be heavily influenced by *tactile/posture rate TTCh*, whereas state 2 did not appear to change. In particular, the probability of transitioning from 1-3 was higher when in a low *tactile/posture rate TTCh* (24.1% low vs 11.3% high). When transitioning from 3-1, transition probability was highest of all values (26.9 %) when oceanic bottlenose dolphins were in a high *tactile/posture rate TTCh*. Overall, oceanic bottlenose dolphins in a low-call-rate state were more likely to leave it when *tactile/posture rate TTCh* was low and leave the high-call-rate state when *tactile/posture rate TTCh* was high.

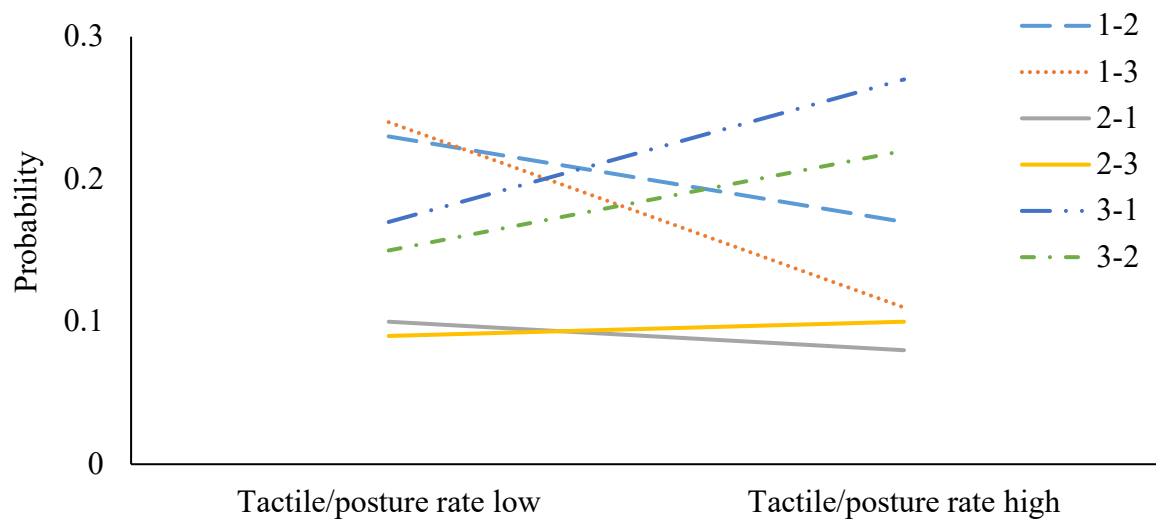


Figure 4.11: Between-state transition probabilities for different tactile/posture rate TTCh and call rate of oceanic common bottlenose dolphins (*T. truncatus*).

The rates of transition between states in different species ratios are given in Figure 4.12. For *tactile/posture rates*, the probability of switching call rate states appeared to be influenced by not only *tactile/posture rate TTCh* but also *species ratio TTCh*, especially 1 and 3. In particular, the probability of transitioning overall was higher and more varied when in low ratio. As an example, when transitioning from 3-1 in *tactile/posture rate TTCh* scenarios the probability was 20.1 % when oceanic bottlenose dolphin only and 50.4 % oceanic bottlenose dolphin low (Figure 4.12).

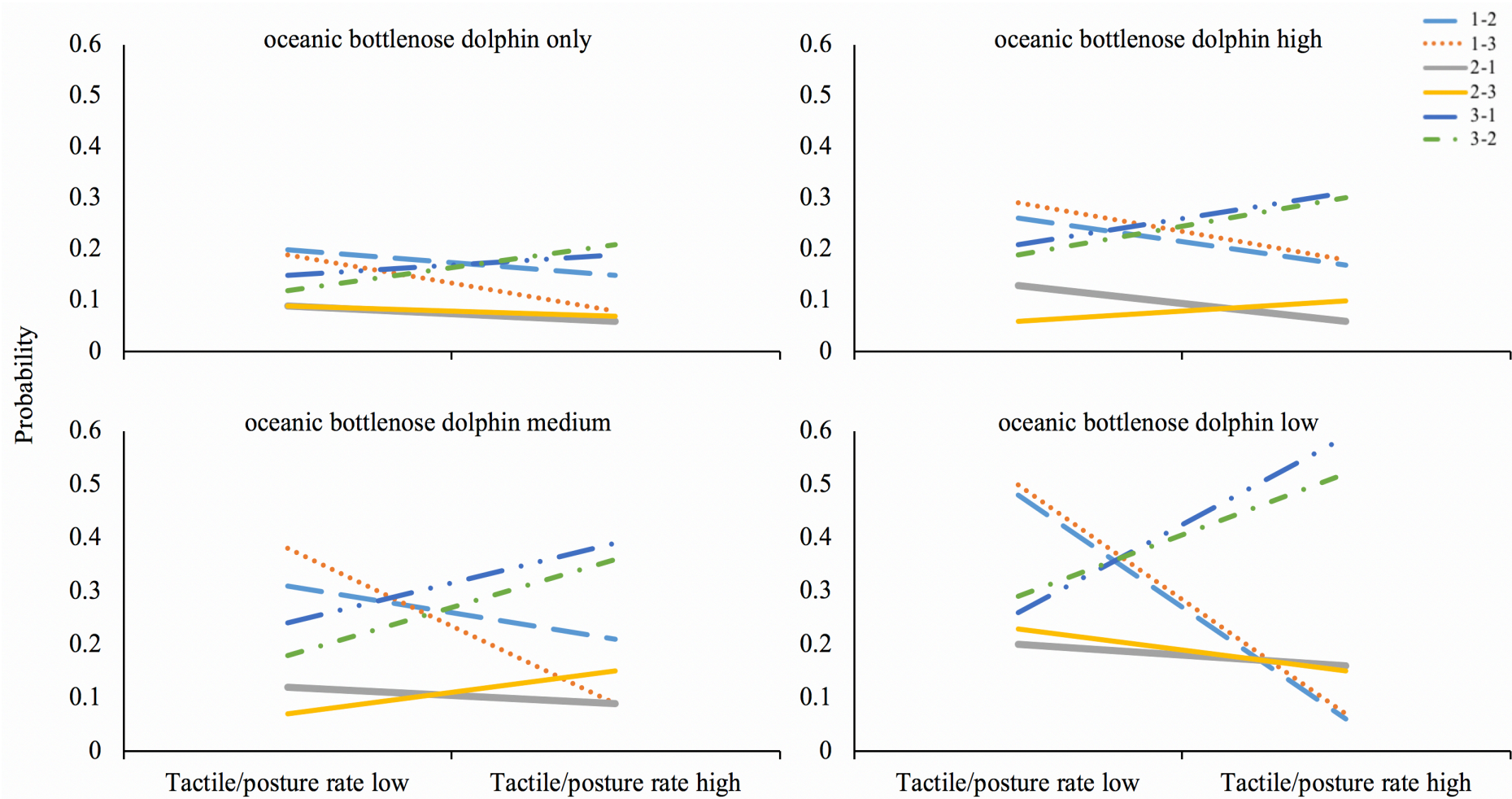


Figure 4.12: Between-state transition probabilities for different tactile/posture rate TTCh and call rate of oceanic bottlenose dolphins (*T. truncatus*) in four different species ratio contexts. Note, oceanic bottlenose dolphins only = groups with oceanic bottlenose dolphin only, oceanic bottlenose dolphin high = groups with high ratio oceanic bottlenose dolphin to pilot whale (*Globicephala* sp.) they are in association with, oceanic bottlenose dolphin medium = groups with medium ratio oceanic bottlenose dolphin to pilot whale they are in association with, oceanic bottlenose dolphin low = groups with low ratio oceanic bottlenose dolphin to pilot whale they are in association with.

4.4 Discussion

A holistic view of sub-surface behaviour, including call vocalisations, tactile, and posture behaviour of odontocete populations, is rare. This is due to the problems associated with defining and recording the signals to be measured and how to compare them. This study demonstrates that the presence of other species affects the call, tactile, and posture behaviour of oceanic bottlenose dolphins in Far North waters, and that groups with and without pilot whales utilise the studied signal exchange parameters differently depending on behaviour. Although the full biological implications of changes in call rates and parameters remain uncertain, these changes help us understand the dynamics of inter-specific groupings and aid formulation of management recommendations by defining appropriate units of management.

4.4.1 Call behaviour in intra- and inter-specific groups

This study provided evidence for oceanic bottlenose dolphin call plasticity beyond the factors previously described in the literature for species-specific call differentiation, including variation in gross morphology, phylogeny and geographical constraints (Jefferson et al., 2008; Tezanos-Pinto, 2009; Zaeschmar et al., 2013, 2014). In inter-specific groups, behaviour state affected both oceanic bottlenose dolphin and pilot whale call plasticity with intermediate frequency and duration when travelling, and higher frequencies and duration (in the case of oceanic bottlenose dolphins) when socialising. This is compared to calls emitted in the same behavioural states in intra-specific groups. During inter-specific interactions, call similarity decreased during social states, and intra-specific group calls were discriminated from each other.

However, the call characteristics do have overlapping elements, particularly in the frequency domain. The shift of calls away from intermediate frequency and duration values may reflect a decrease in the increment in this overlap. It has previously been suggested that frequency of conspecific interactions may influence signalling utilised (Janik, 2000; Watwood et al., 2004). Infrequent associates may predominantly utilise unambiguous signalling, while frequent associates can employ subtle cueing (Dudzinski et al., 2009; Smith, 1977). The relatively high number of mixed groupings between these two species (Chapter 2, Zaeschmar et al., 2014) may be contributing to signal convergence through complex and less random interactions (Haavie et al., 2004; May-Collado, 2010; Quérrouil et al., 2008).

The body of literature pertaining to dolphin signal exchange is extensive, with examples of plasticity occurring in both the frequency and time domain of calls (May-Collado, 2010; Murayama et al., 2014). In addition, modification to cope with changes in conspecific interactions (Janik, 2000; Tyack, 1986; Watwood et al., 2004), stress response (Esch et al., 2009a), and background noise (May-Collado & Wartzok, 2008; Morisaka et al., 2005c) have been described. Inter-specific signal exchange and the role (if any) of signal matching, however, is not well studied in cetaceans, despite exploration of the effects of this behaviour in other taxa, e.g., passerine birds (Garamszegi et al., 2007; Gorissen et al., 2006).

4.4.2 Multimodal signal exchange in intra- and inter-specific groupings

This study indicates the use of vocal signals (calls) is influenced by the contact (tactile and posture) rate of individuals. The more the group engage in photic and mechanical tactile behaviour, the less the dolphins communicate through calls. As such it appears that oceanic bottlenose dolphins are using visual and tactile cues to locate each other and synchronise their behaviour, reducing their dependency on call signal exchange.

Signal exchange behaviour in oceanic bottlenose dolphin and pilot whale interactions showed a wide spread use yet subtle distinctions. This indicates the function of communication may vary as a result of group composition and behaviour. Communication behaviour serves numerous functions, e.g., during foraging events (coordinated hunting: Coscarella et al., 2015; Ridgway et al., 2015), parent-offspring interaction (synchronous swimming, surfacing, breathing: Fellner et al., 2012; Mann & Smuts, 1999), play (Bel'kovich, 1991), and mate competition (synchronous surfacing: Connor et al., 2006). In addition, the behavioural contexts associated with inter-specific interactions differ (e.g., aggressive/non-aggression, foraging/travel in any combination, Cusick, 2012), illustrating the complexity and underlying functions of signal exchange in these groupings. The current study quantifies the dynamics of signal exchange both intra- and inter-species. Results from oceanic bottlenose dolphin and pilot whale align with the current literature, especially findings that different surface behavioural states are correlated with call rate behaviour. A good example of this in the literature, is from Taruski (1979), where pilot whale mean call rate was significantly different during milling and transiting. Further to this, Taruski (1979) also linked vocal states to the level of arousal (low, moderate, and high), though this did not result in a viable explanation for call behaviour and thus system complexity was not captured by arousal alone.

4.4.3 Inter-specific interactions

Within this dataset, which was primarily recorded when socialising, interactions between oceanic bottlenose dolphins and pilot whales were antagonistic. This aligns with long-term inter-specific aggression noted in other delphinid populations (e.g., Atlantic bottlenose and spotted dolphins, Cusick & Herzing, 2014). These interactions are generally described as not including reversals of aggression, dynamic shifts, or bi-directionality (Acevedo-Gutiérrez et al., 2005; Frantzis & Herzing, 2002; May-Collado, 2010; Psarakos et al., 2003; Quérouil et al., 2008).

The ratio of pilot whale: oceanic bottlenose dolphin was key factor on the response of oceanic bottlenose dolphin vocal and tactile/postural behaviour. A higher ratio of pilot whale to oceanic bottlenose dolphin was the most important factor in call changes. The behaviour noted was similar to mobbing behaviour, observed in many species, which is defined as multiple individuals chasing after another individual (and/or species) as a cohesive unit (e.g., red-winged blackbirds (*Agelaius phoeniceus*): Consla & Mumme, 2012; Olendorf et al., 2004). In aggressive events, oceanic bottlenose dolphins, like the species targeted by mobbing behaviour (Consla & Mumme, 2012; Olendorf et al., 2004), adapted their behaviour in the presence of pilot whales. The effect of pilot whale groups on oceanic bottlenose dolphins was observed at multiple levels: call rate, call frequency, and tactile/posture rate.

Group synchrony is an example of cooperation (Drea & Carter, 2009; Noë, 2006). Cooperation during aggressive events can be especially important between unevenly sized individuals. This is particularly true for the smaller-sized cooperating individuals that can act together to counteract the inherent benefits of a larger individual (Cusick, 2012). Pilot whales, which are significantly larger than oceanic bottlenose dolphins, may use a combination of chase behaviour and physical size in order to physically dominate the oceanic bottlenose dolphins (as observed in spotted dolphins (*Stenella frontalis*) and bottlenose dolphin in the Bahamas, Cusick & Herzing, 2014). When synchronous and acting as a single unit, the likelihood of oceanic bottlenose dolphins initiating an interaction was increased when compared to individuals acting independently. Consequently, a single pilot whale would be affected by the summation of multiple individual oceanic bottlenose dolphins. This is similar to another form of mobbing reactionary behaviour which puts participants on a similar level and minimises aggression effects on each individual, ultimately maintaining overall group cohesion (Olendorf et al., 2004).

The current study additionally demonstrated that group size, ratios, and behaviour (both state and event) may change within and between encounters. This has been well-described during non-aggressive inter-specific encounters by Herzog & Johnson (1997). In Far North waters, inter-specific groups are larger on average than intra-specific groups (Chapter 1, Appendix 1.1). Furthermore, within inter-specific focal groups oceanic bottlenose dolphin individuals often outnumber pilot whales in both group size and in the number participating in interaction events (Chapter 2). Oceanic bottlenose dolphins in Far North waters live in fission - fusion societies (Tezanos-Pinto et al., 2009). This is unlike the matrilineal social structure of pilot whale noted as noted in other areas (e.g., Stephanis et al., 2008). This means there is a possibility that the full oceanic bottlenose dolphin population are not consistently together, unlike the stable social groups of pilot whales (e.g., Connor et al., 2000). Hence, frequent group size (and behaviour) changes within and between encounters are not surprising. In Far North waters, group size during inter-specific encounters altered relatively frequently. This is similar to observations in Shark Bay, Australia, where multiple group size changes can occur, especially in intra-specific aggression (mate access, Connor et al., 2011; Mann et al., 2008).

The combination of context factors during an aggressive encounter, e.g., location or time, likely affected the aggression observed. The reason for the inter-specific aggression in Far North waters between oceanic bottlenose dolphins and pilot whales may result from the need to defend against inter-specific copulation (e.g., hybrid formation: Ellis, 2010; Cusick, 2012) or male mate defence (Connor et al., 1992, 2006). Aggression unlikely resulted principally from habitat and/or food competition, since pilot whales and oceanic bottlenose dolphins have morphological differences that allow foraging on different prey species. However, aggression as a driver of habitat selection, such as niche segregation (e.g., Malinowski, 2011) cannot be ruled out. Alternatively, unlike in chimpanzees (Watts et al., 2006), territorial defence is unlikely, as in Far North waters mixed associations were not spatially correlated (Cusick, 2012). Subsequent research is required to identify the degree to which encounter context effects inter-specific aggression.

Inter-specific encounters can add stress to participating individuals. Additional mechanical signal exchange during social events was assessed in this study, adding insight to the behaviour events (tactile and posture). Calls emitted had a higher mean end frequency, suggesting an upsweep in contour (particularly in low ratio groups). Thus, inter-specific call modifications may have resulted from a skew towards the ‘minority’ oceanic bottlenose dolphins. Stress-

related signal modification has been described in cetaceans. During Guiana (*Sotalia guianensis*) and bottlenose dolphin inter-specific social-reproductive interactions (formation of hybrids), aggression was the predominant event type (Acevedo-Gutiérrez et al., 2005). When the same species were in intra-specific social states, more events were described as ‘play’ (touch, tail slap, leap, body roll, and spy hop). The utilisation of upsweep contours by oceanic bottlenose dolphins in the presence of pilot whales may occur to: 1) convey stress and/or communicate with conspecifics; and 2) emit a threat(s) “in the language” of the other species (Gorissen et al., 2006, p. 267). The need to convey context with conspecifics when isolated and/or distressed could necessitate signal modification (Watts et al., 2001). Call duration was found to be longer in this study in inter-specific than intra-specific groups. By utilising an increased call duration, oceanic bottlenose dolphins may be utilising context-specific signal exchange to convey specific stress signals to their conspecifics who may not be adjacent to the signaller. As occasions were observed when no other oceanic bottlenose dolphins remained in field of view during an aggressive pilot whale dominated event, it could be suggested that conspecifics move away from the central area of the event. Further to this, during travelling events, oceanic bottlenose dolphin only group calls and inter-specific group calls were not significantly different, indicating modification primarily occurs during other behaviours, such as socialising. This may indicate that the predominantly calling individual in aggressive (social) events was oceanic bottlenose dolphins (May-Collado, 2010).

4.4.4 Study limitations

One potential source of bias is vocal masking, resulting in an underestimation of large group call rate. Call rate and frequency were still effectively measured, throughout their range. It is therefore reasonable to suggest signal masking in the spectrograms was minimal. Other data collection considerations include limited water clarity and sea conditions for subsurface behaviour. This can limit the length of follows and the ability to extend analysis to the individual level. Additionally, the stationary research vessel effect was not assessed. Whilst efforts to minimise disturbance were made (best practice manoeuvring and a quiet four-stroke engine to reduce the impact on signal exchange), it remains unquantified.

A further potential source of bias is the limited field of view of camera equipment as a result of the angle of view. Some tactile behaviour may be missed, resulting in an underestimation of tactile and posture rate. Given that a broad range of tactile/posture contact rates and types were measured for a representative range of group sizes, this suggests that visibility and field of view

error were minimal and that this error would have underestimated the effect of inter-specific groups on the tactile behaviour. However, this source of bias is noted and could be improved in further study using animal borne systems and/or mobile camera systems (Pearson et al., 2017) able to remain close to the animals. However, these methodologies also have their own limitations that must be considered, particularly for gregarious oceanic species.

The contexts and behaviours considered in this study were not exhaustive. Throughout the literature variables not considered here are documented to affect the vocalisation of delphinids. An example of this is travelling speed, as discussed by Henderson et al. (2012). The inclusion of such variables should be considered in further research. Unfortunately, hypotheses relating to signal convergence and signal stress could not be assessed fully. Future research could include integrating data from acoustic tag and directional recording systems. This would allow individual level rather than group level assessments. Overall, larger datasets that can accommodate multiple covariates in hidden Markov models could add insights to the importance of TTCh. However, the results of this work indicate that call rates alter with subsurface context and the time of shifting of those contexts. Extending the behavioural comparison of coastal bottlenose dolphins and oceanic bottlenose dolphins beyond aggressive encounters was outside the scope of this dataset (due to non-aggressive sample size). Additionally, the degree to which inter-specific mate avoidance, food separation, etc. lead to inter-specific interactions was beyond this study's scope.

Despite the identified limitations, this study is the first to quantify the dynamic of inter- and intra-specific interactions for this population. Results establish the complexity of multi-species groupings, the need to holistically examine context, and the importance of examining how contextual factors interact and change.

Chapter 5

The effect of vessels on the signal exchange of the coastal common bottlenose dolphin (*Tursiops truncatus*) in Far North waters, New Zealand



Coastal common bottlenose dolphin (*Tursiops truncatus*) presumed adult and calf in the Bay of Islands, Far North waters, New Zealand.

5.1 Introduction

Social animals rely on group signals for varying reasons, inclusive of, but not restricted to, predator avoidance, cooperative hunting (e.g., to increase foraging success), reproduction (e.g., to increase success of finding a mate), and rearing of young (e.g., sharing effort or gaining experience) (Bertram, 1978; Suzuki, 2015). Coordinated activity necessitates contact and signal transfer through a variety of pathways (Dusenbery, 1992; Grier & Burk, 1992; Johnson et al., 2009; Supin et al., 2001). While numerous studies have explored the effects of vessels and accompanying noise on the vocal signals of cetaceans (Bejder et al., 2006; Buckstaff, 2004; Lemon et al., 2006; Lusseau, 2003, 2005; Miller et al., 2008; Nowacek et al., 2001; Stamation et al., 2010; Steckenreuter et al., 2012; Williams et al., 2002), broader signal behavioural response and its consequences remains poorly understood. Further to this, no studies to date have quantified both vocal and tactile behavioural responses in relation to vessel traffic.

Sound is the most efficient medium for long-range signal exchange in the ocean (Colosi, 2016) and vocal behaviour, particularly calls, is considered the predominant mode of signal exchange (for review see Herzing & Johnson, 2015). The term ‘calls’ refers to burst pulses and whistles, which are often analysed together when quantifying vocal social behaviour rates. This categorisation is based on evidence that they can be described on a continuous spectrum (Murray et al., 1998). Additionally, a smooth transition and concurrent utilisation of whistles and burst pulses, particularly in social events, have been observed (Sayigh et al., 2013).

Calls in dolphins have an approximate frequency range of 2 – 25 kHz and are predominantly described as social in function, e.g., used in affiliative, and agonistic/aggressive situations (Caldwell & Caldwell, 1972; Dudzinski, 1996; Herzing, 2000). Calls are utilised to aid in the maintenance of group coordination, specifically mother-calf cohesion (e.g., Janik & Slater, 1998; Sakai et al., 2006; Smolker et al., 1993). Vessel noise regularly occurs in the frequency range utilised by dolphins, potentially masking vocalisations (Jensen et al., 2009; Richardson & Malme, 1995), thus increasing the dependence on tactile and/or postural behaviour. Internationally, an increase in call rate in the presence of vessels has been noted (Buckstaff, 2004; Scarpaci et al., 2000), with the magnitude of response higher in groups with calves (Guerra et al., 2014; Van Parijs & Corkeron, 2001). Numerous studies describe adaptations to vocalisations with changing vessel sound (amplitude and frequency) in cetaceans (Lesage et al., 1999; Parks et al., 2007; Scheifele et al., 2005) and dolphins (La Manna et al., 2013). This suggests that vocalisations can be adapted to counteract (to varying levels) the masking effects

(Guerra et al., 2014). However, no research to date has assessed the possible effects of vessels on tactile behaviour, and how the use of each form of communication varies as ‘noise’ increases. In New Zealand (NZ), a correlation of the group spacing of the coastal ecotype of common bottlenose dolphin (*Tursiops truncatus*, referred to hereafter as the coastal bottlenose dolphin) with vessels was observed in Doubtful Sound. Guerra et al. (2014) noted the dispersal of groups with calves was substantially larger before, during, and after interactions with tour vessels. Given that communication utilising mechanical, photic, and some forms of acoustic signals requires the proximity of individuals, its use and effectiveness as a result of group spread changes in the presence of vessel traffic may vary.

In Far North waters, NZ vessel traffic around coastal bottlenose dolphins varies significantly. In the Bay of Islands, dolphin tourism focuses specifically on viewing and swimming with the coastal bottlenose dolphin (Constantine, 2002; Peters & Stockin, 2016). Indeed, the Bay of Islands has a comparably high level of commercial swimming-with-dolphin activities (i.e. free swimming with a snorkel and fins) targeting this species compared to other regions of Far North waters and NZ (Constantine & Baker, 1997; Constantine et al., 2001; 2002; 2004; Snell 2000; Peters & Stockin 2016). Presently, there are three operators that hold permits under the MMPR (1992) to commercially interact with marine mammals and swim with bottlenose dolphins. These operators cumulatively offer up to 10 trips per day that are permitted to view and/or swim with coastal bottlenose dolphin or common dolphins in Bay of Islands waters. In addition, a fourth operator in Tutukaka runs a dive operation and is permitted to view marine mammals that they mainly encounter en-route to the dive sites, and to swim with common dolphins or bottlenose dolphins. Collectively, these operators may exert high human disturbance levels on dolphin populations in the region, along with the recreational vessel traffic documented in the region (Constantine & Baker, 1997; Constantine et al., 2001; 2002; 2004; Snell 2000; Peters & Stockin 2016).

The primary goal of this chapter is to explore the subsurface social behaviour of coastal bottlenose dolphins in Far North waters utilising call parameters as the dependent variable. This includes the potential effect of relevant biotic/abiotic and surface/subsurface explanatory variables, including, but not limited to, tactile behaviour, calf presence and vessel traffic. The following questions were explored:

- 1) Do coastal bottlenose dolphins modify call rate, frequency and/or duration in the presence of vessels and/or with photic and mechanical behaviour changes?

If so:

- 2) How is coastal bottlenose dolphin call rate, frequency and/or duration in the presence of vessels and/or with photic and mechanical behaviour changes?
- 3) How does the use of tactile (mechanical), posture (photic), and call (mechanical) signal exchange parameters change in relation to one another in different vessel scenarios?
- 4) Does group composition (i.e., groups with and without calves) result in altered signal exchange in different vessel scenarios?

5.2 Materials and methods

5.2.1 Data collection

Data collection consisted of concurrent surface and sub-surface observations on coastal bottlenose dolphin, which was consistent with the methods used in previous chapters (refer to Chapters 2 – 4). In summary, data were collected during line transect surveys conducted year-round from March 2013 to September 2015, between sunrise and sunset (Chapter 2). Data were collected from the research vessel *Te Epiwhania*, a 5.5 m Stabicraft vessel powered by a 100 hp four-stroke engine. Data collection parameters and limitation for survey are summarised in Chapter 2, Section 2.2.

5.2.1.1 Surface observations

Surface data were recorded utilising either an HTC Touch Pro2 Windows Mobile device or Acer Iconia B1 tablet computer with associated Garmin GLO GPS device. CyberTracker (CyberTracker Conservation, Version 3.296+) software was programmed to record continuous GPS tracks (with GPS recordings every 30s and additionally with every data input) (as per Chapter 2). Surface observations were taken every minute (data collected are detailed in Chapter 4, Section 4.2.1.1.1. and 4.2.1.1.2.).

5.2.1.1.1 Group composition and size

Every minute, the group size, direction of travel, and proximity of individuals within groups were recorded. Dolphins were considered to be in groups when any number of individuals were apparently associated, with the same predominant movement direction and < 5 body length apart (e.g., Constantine et al., 2004; Dwyer, 2014; Shane, 1990a, 1990b; full definition in Chapter 2, Section 2.2.1). Additionally, the elliptical spread area was included ([group

size/spread area]*100) in the estimation of group density (number of dolphins/100 m²), and could be interpreted as group cohesion, or a measure of proximity among dolphins (as per Guerra et al., 2014). Additionally, surfacing synchrony was assessed. The instantaneous point at which any part of the individual's body breaks the water surface was termed *surfacing* (Hastie et al., 2003). *Surfacing synchrony* was quantified by recording the number of animals surfacing in sequential 3-second intervals for a 30-second period directly after each 1-minute behavioural and vessel observation. A 3-second interval was selected to minimise bias due to multiple surfacings within one interval by the same individual. The decision was made based on coastal bottlenose dolphin dive behaviour literature, which showed that the dive durations of < 3s are rare (following Hastie et al., 2003).

Group size of dolphins was logged according to three categories of individuals: the absolute *minimum* counted, the absolute *maximum* believed to be in the group, and the *best estimate* for the most likely number (Dwyer et al., 2016). For analytical purposes, group composition was logged according to the presence or absence of immature individuals (i.e., adult only, adults with juveniles, adults and/or juveniles with calf/neonate groups, as per Currey et al. 2007; Guerra et al., 2014). *Group composition* was confirmed as per Chapter 2, Appendix 2.2 and as demonstrated in Figure 5.1.



Figure 5.1: Example of a neonate coastal common bottlenose dolphin (*T. truncatus*) displaying foetal folds and flanked by presumed adult coastal bottlenose dolphin September 2013-2015, in Far North waters, New Zealand.

5.2.1.1.2 Surface behaviour

To determine the predominant *behavioural state* of a focal group, the group was scanned left-to-right to encompass all individuals (as per Dwyer, 2014). This minimised potential bias due

to conspicuous individuals or behaviours (Mann, 1999). Dolphin group behavioural state (as per Chapter 2) was recorded every minute while recording subsurface behaviour, as well as the response of the dolphins to vessels/swimmers. Responses were defined relative to the movement direction of the dolphins in relation to vessels/swimmers (Chapter 2). Behavioural events were defined as recognisable instantaneous behaviours (see Appendix 2.2 for full definitions).

5.2.1.1.3 Vessels

Every minute, the *number*, *type*, *speed* (maximum speed vessel if multiple present), and proximity of vessels within 300 m of the closest dolphin was recorded. An encounter including vessels (additional to the research vessel) was considered initiated whenever a vessel was within 300 m of a focal group (categories were research vessel only, +1, +2, +3, +4, and +5). The distance of 300 m (verified by reticular binoculars) was chosen because under the Marine Mammal Protection Regulations (referred to as MMPR hereafter, 1992), all vessels must slow to idle or no wake speed when there is an intention to view a marine mammal (Regulation 18(l)). Proximity to focal group was assessed as the minimum distance (verified with reticular binoculars) of a vessel to the research vessel (which was adjoined to the closest dolphin and utilised as a proxy for the focal group).

Vessel types were categorised into four independent groups: *permitted* (licenced swim with or view dolphin vessels), *non-permitted* (commercially operated vessels not holding a permit/licence to swim with or view dolphin), *research* (any vessel involved with research activity), and *private* (all vessels not included in the other categories, i.e., privately-owned kayaks, jet skis, yachts etc.). All categories were further assessed by *propulsion type* (e.g., inboard, outboard, jet, paddle, sail). *Vessel speed* was estimated by assessing distance (in metres) travelled in 20 seconds and categorised by seven different speeds (0 – 5, 6 – 10, 11 – 15, 16 – 20, 21 – 25, 26 – 30, 30+ knts).

Though the acoustic signature/noise of vessels can vary greatly depending on the specific propulsion method (e.g., inboard diesel, outboard, petrol, jet vs propeller), engine size (e.g., 30 hp four stroke outboard vs 350 hp turbo charged inboard), skipper, service record, hull condition, etc., these parameters are not accurately observable in the field and therefore vessel speed and number were the parameters recorded as a proxy for vessel noise. This follows

previous research and is deemed valid in this application (Arveson & Vendittis, 2000; Buckstaff, 2004; Guerra et al 2014; Jensen et al., 2009).

5.2.1.2 Subsurface mechanical (tactile and call) and photic observations

Mechanical acoustic (call) recordings were obtained with a calibrated Cetacean Research Technology Inc. C75 omnidirectional hydrophone with built-in pre-amplifier (flat frequency response of 1 Hz to 85 kHz; sensitivity -209.52 dB re 1 V/ μ Pa). The hydrophone was fitted to a Tascam DR-680 digital multitrack recorder sampling at 96 kHz, 24-bit consistent (refer to Chapter 3 for further details on methods).

Additional mechanical (tactile) and photic (posture) behavioural data collected and analysed in this chapter relate to the collection of subsurface videos of dolphin behaviour, which were recorded concurrently with surface and call data (Chapter 1 – 3). Videos were recorded opportunistically from the bow of the research vessel *Te Epiwhania* (Appendix 2.1). Prior to filming, water clarity was measured (Secchi disk, for results see Appendix 4.1) and the distance of the closest group to the vessel was recorded. A custom-built video recording rig (Appendix 4.2), with simultaneously recording Go-pro 3+ (©GoPro. Inc., 2013) video cameras in an underwater housing (1080 p, 60 fps, and 180° field of view) was utilised to record tactile and posture behaviours (Appendix 4.2, as per Chapter 4). All recordings from the forward-facing GoPro were monitored via a live feed on-board the vessel using a Wi-Fi extension cable (©CamDo solutions Inc, 2013) attached to a Samsung SM-T110 tablet computer running GoPro Studio software (©GoPro. Inc., 2013, Appendix 4.2). All recordings were calibrated with a shallow water filter during filming (BackScatter Inc., 2013, Appendix 4.2). Subsurface behavioural data were recorded utilising focal sub-group and all-occurrence sampling (Altmann, 1974; Dudzinski et al., 2009, as per Chapter 4). Recording and follows ceased when no individuals were in the frame in excess of three minutes.

5.2.2 Mechanical (tactile) and photic data processing, definition and ethogram

The software Final Cut Pro 10.1 (© Apple Inc, 2016) was used to analyse frame-by-frame videos, as per Chapter 4, using a population-specific ethogram to document subsurface *tactile contact rate, type, and posture* (full catalogue Appendix 4.3 – 4.6, and examples in Appendix 5.1). Subsurface behaviour is complex, multifaceted, contextual, and difficult to observe and measure, however tactile and postural behaviour can and have been defined and interpreted

accurately, so only this subset was selected (Following Dudzinski et al., 2012, 2010; Frohoff, 1994; Östman, 1994). In summary, dolphin posture throughout tactile contact events was categorised as follows: *horizontal*, *side-down left* and *right*, *upside down*, *head down* and *head up*; and contact types as: *rub*, *pet*, *melon to genital*, *circle chase/dive*, and *touch* (in line with Dudzinski et al., 2009). Key terms and summaries are provided in Chapter 4 for posture and tactile contact behaviour (Table 4.1) and all terms in Appendix 4.4, with definitions based on Dudzinski (1996), Dudzinski et al. (2009, 2010, 2012), Frohoff (1994), and Östman (1994). Predominant position and mean contact rate were calculated every minute for the recording duration.

5.2.3 Data Analysis

All statistical analyses were conducted using free statistical software R (R Core Development Team, 2014, RStudio for Mac version 1.0.136) with the significance threshold set at 0.05, unless otherwise stated. Data were initially tested for normality and heterogeneity. All data were also tested for significant variation on a seasonal, annual, and group (composition and size) level. If significant variation was not detected, data were combined for subsequent analyses. All methods follow those detailed in Chapter 4, unless otherwise specified.

5.2.3.1 Multivariate mixed hidden Markov models of subsurface responses

All methods of hidden Markov model were comparable with Chapter 4, Popov et al. (2017) and Quick et al. (2017). In this study the observable time series are a count of call rate (calls/minute/dolphin) or mean frequency (mean frequency/minute/dolphin). A realisation of one of the N distributions is assumed for each observation. The N state-dependent distributions are assumed to be negative binomial distributions, which can handle over-dispersion in the state-dependent distribution (Popov et al., 2017). N was chosen following AIC assessment (see section 4.2.3.2.4 for AIC details), careful consideration of the dataset considerations, or a combination thereof (Popov et al., 2017).

Subsurface and surface influences on call behaviour were considered by including these variables as ‘hidden’ states (covariates) on the probability of transitions between states of call behaviour (Table 5.1). The assumption was made that the covariates provided explanatory information about coastal bottlenose dolphins and their likelihood of transitioning between call states (see Chapter 4, Section 4.2.3.2.3.1. for details). All the covariates considered in this analysis originated from instantaneous focal follow data. Since call rate was calculated based

on the number of individuals, *group size* was not included in the base comparison. Model formulation included only a single covariate at any time to avoid numerical instability for the hidden Markov model analysis performed. Additional covariates were considered separately in subsequent analyses, if required, to maintain numerical stability.

Table 5.1: Potential covariates for hidden Markov models from the original dataset of coastal common bottlenose dolphins (*T. truncatus*). * only included in mean frequency models, ** variable combined with only top models.

Covariate	Variable definition
Year	1 st September 2013 – 31 st August 2014 and 1 st September 2014 – 31 st August 2015
Month	Defined as lunar month
Water depth	Water depth at time of recording (m)
Substrate	Predominant substrate type - rocky, sandy, vegetation
BSS	1, 2, 3, or 4
Wind speed	0 – 5, 6 – 10, 11 – 15, 16 – 20 (knts)
Surface behaviour	Travelling, milling, resting, foraging, socialising, and diving (Appendix 2.2)
Calf presence (y/n)	A calf observed in the group. Refer to Chapter 2, Section 2.2.1 and Appendix 2.2, for calf definition
Vessels (number)	Number of vessels present and interacting categories were RV only, +1, +2, +3, +4, +5.
Vessel (y/n)	Vessel/vessels within 300 m yes -1- or no -0-
Speed of travel	Speed of vessel movement (m)
Vessels (approach)	Minimum distance from dolphins in 0 – 20, 21 – 40, 41 – 60, 61 – 80, 81 – 100, 101 – 120, 121 – 140, 141 – 160, 161 – 180, 181 – 200, 201 – 220, 221 – 240, 241 – 260, 261 – 280, 281 – 300, > 300.
Tactile type	Predominant tactile per minute - (Section 5.2.2 for full definition).
Posture type	Predominant posture per minute - (Section 5.2.2 for full definition).
Tactile/posture rate	Mean number of tactile/posture per minute
Detection range	Secchi disk measurements of visibility (m)
Surface cohesion	The elliptical spread area was included ($[\text{group size}/\text{spread area}] * 100$) in the estimation of group density (number of dolphins per 100 m ² , Guerra et al., 2014).
Synchrony	The number of animals surfacing in sequential 3-second intervals for a 30-second period
Group size*	Collective group size was logged according to three categories; the absolute minimum, the absolute maximum, and the best estimate (as per Section 5.2.1.1.1.; Dwyer et al., 2016; Peters & Stockin, 2016). Best estimate was modelled.
Time to change (TTCh)**	Additionally, time to change (TTCh) was included in analysis for the top covariates indicated (as per Popov et al., 2017). The time (minutes) to the nearest (before or after the current time bin) change in group call behaviour is measured. This was included as coastal bottlenose dolphin coordinate their behaviour (with calls) before, during, and after a change in context.

5.3 Results

5.3.1 Mechanical and photic effort

Call data and corresponding subsurface videos were collected from coastal bottlenose dolphins in Far North waters between September 2013 and September 2015. In Far North waters, a total of 31 encounters resulted in 827 acoustic recordings, yielding a total sample of 12,661 calls (Appendix 1.1). Simultaneously, 57 subsurface videos were recorded, totalling 7,722 seconds and 491 behavioural events. Video effort was equal across all seasons, but clarity in videos was significantly greater in autumn (mean = 3.37 m, SD = 0.61, n = 9) and winter (mean = 2.76 m, SD = 0.41, n = 8) than in spring (mean = 1.91m, SD = 0.20, n = 7) or summer (mean = 1.86 m, SD = 0.25, n = 7) ($X^2 = 8.93$; df = 3; $P = 0.002$, Appendix 4.1). The total video length did not significantly differ among various age-classes ($X^2 = 7.29$; df = 2; $P = 0.599$, n = 57 videos; Appendix 5.2, Table 5.2; Table 5.2). Recordings were also taken when coastal bottlenose dolphins were engaged in all six behavioural states and no significant difference was detected in the video length ($X^2 = 12.04$; df = 5; $P = 0.308$, n = 57; Appendix 5.2; Table 5.2). Data collection occurred with RV only and additional vessels present (1-5, Table 5.2). Vessel frequency characteristics are summarised as ranging from 10 Hz – 24 kHz, with peak frequency between 80 – 430 Hz across all areas of Far North waters.

5.3.2 Multivariate mixed hidden Markov models of subsurface responses

5.3.2.1 Covariates in hidden Markov model

Call rate and mean frequency were utilised as good proxies for call changes. First, negative binomial hidden Markov models were fitted with up to five states. This was a preliminary step to estimate the number of states that best represented the models before considering covariates. Table 5.3 summarises the model selection criteria. Comparatively small AIC values and large cross-validated (log) likelihood values indicated a better fit, respectively. The three-state model for call rate and four-state model for mean call frequency exhibited the lowest AIC and the highest mean cross-validated likelihood (Table 5.3), thus they were selected.

Table 5.2: Number subsurface samples for key variables of coastal common bottlenose dolphins (*T. truncatus*). Note, A = Adults, J = Juveniles, C = Calves, N = Neonates and CV = coefficient of variation of mean.

Variable	Variable level	Number of videos	Number of acoustic recordings	Number of 1-minute video samples
Group composition	A-J-C-N	21	301	301
	A	19	267	267
	A-J	17	259	259
Surface behaviour	Socialising	13	195	195
	Travelling	12	138	138
	Diving	11	125	125
	Milling	8	95	95
	Foraging	9	184	184
	Resting	4	90	90
Vessel (Y/N)	Y	46	672	672
	N	11	155	155
Vessels (number)	RV only	11	155	155
	1	9	140	140
	2	8	142	142
	3	12	97	97
	4	10	137	137
	5	7	156	156
Vessels (approach)	0 – 20	5	73	73
	21 – 40	3	44	44
	41 – 60	4	56	56
	61 – 80	3	53	53
	81 – 100	3	32	32
	101 – 120	2	38	38
	121 – 140	4	55	55
	141 – 160	3	62	62
	161 – 180	6	65	65
	181 – 200	3	51	51
	201 – 220	2	29	29
	221 – 240	3	37	37
	241 – 260	2	61	61
	261 – 280	4	58	58
	281 – 300	2	38	38
	> 300	8	75	75
	Total	57	827	827

Table 5.3: Model selection criteria for benchmark models for call rate and mean frequency with no covariates of coastal common bottlenose dolphins, (*T. truncatus*). AIC = Akaike’s Information Criterion, llk = maximum log likelihood, CV = mean cross-validated (log) likelihood. Blue highlight indicated best performing negative binomial model.

	Negative binomial Model	AIC	llk	CV
Call rate	1 state	5,176.30	-6,724.921	-729.314
	2 states	3,002.41	-4,122.343	-484.920
	3 states	2,463.19	-2,832.226	-431.291
	4 states	2,467.05	-2,781.117	-438.752
	5 states	2,402.35	-2,723.780	-433.527
Mean frequency	1 state	6,032.01	-1,0597.885	-704.710
	2 states	5,978.35	-1,0597.883	-671.305
	3 states	4,011.27	-1,0042.320	-662.843
	4 states	3,025.19	-9,331.026	-527.008
	5 states	4,026.96	-9,280.194	-595.046

5.3.2.1.1 Model covariates

Six negative binomial models were fitted with three- and four-states for call rate and mean call frequency, respectively (Table 5.4). Both model selection criteria (AIC and cross-validation) selected the negative binomial model with *vessels (number) TTCh* as the best-performing one-covariate model for both call rate and mean frequency. It also outperformed the baseline three- and four-state models (cf. Table 5.3). These results indicate that *vessels (y/n and number)* influenced the probabilities of transitioning from one vocal state (rate and frequency) to another.

When comparing *vessels (number) TTCh* with just *vessels (number)*, *vessels (approach)*, *speed of travel* and *vessels (y/n)*, model outcome indicated that additional information in terms of number of vessels and time to change improved the fit, as opposed to considering the vessel parameters. Further, according to both model selection criteria, *tactile/posture rate TTCh* and *calf presence (y/n)* also resulted in a considerable improvement in the fit compared to other variables and the baseline model. The *calf presence (y/n) TTCh* and *vessels (approach)* variables also considerably improved the fit for mean frequency when compared to other variables and the baseline model. The inclusion of time to change improved the fit of all top performing models, apart from *calf presence (y/n)* for mean frequency. This underlined the potential importance of the above additional variables in subsequent analysis (Table 5.4). The fit of data was assessed using pseudo-residuals (Appendix 5.3). There were very few outliers (0.7 %, n = 5, Appendix 5.3) as well as no clear pattern over time and, thus no evidence of any notable lack of fit for either dataset.

Table 5.4: Model selection criteria of negative binomial hidden Markov model models for call rate and mean frequency with 1 covariate of coastal common bottlenose dolphins (*T. truncatus*). Note: AICc = Akaike’s Information Criterion for small sample size, llk = maximum log likelihood, CV = mean cross-validated (log) likelihood. Key: pale grey highlight = top 5 negative binomial models, blue highlight = best performing negative binomial model.

	Model	AICc	llk	CV
Call rate (3-state)	detection range	2,581.03	-2,834.196	-671.010
	year	2,581.12	-2,834.202	-671.034
	wind speed	2,576.91	-2,797.705	-671.000
	BSS	2,574.07	-2,812.478	-670.127
	water depth	2,522.56	-2,804.563	-666.548
	month	2,501.09	-2,789.324	-649.115
	synchrony	2,498.15	-2,789.221	-640.329
	substrate	2,493.46	-2,789.002	-635.762
	surface cohesion	2,493.46	-2,817.381	-630.691
	posture type	2,493.01	-2,814.129	-584.192
	surface behaviour	2,491.74	-2,820.644	-530.405
	tactile type	2,401.62	-2,741.335	-506.921
	vessels (y/n)	2,348.23	-2,819.941	-411.958
	vessels (approach)	2,339.02	-2,812.275	-413.946
	speed of travel	2,338.37	-2,811.824	-412.461
	calf presence (y/n) TTCh	2,338.01	-2,811.572	-412.399
	calf presence (y/n)	2,337.34	-2,811.223	-412.217
	tactile/posture rate	2,320.94	-2,810.031	-411.257
	vessels (number)	2,320.72	-2,810.002	-411.206
	tactile/posture rate TTCh	2,320.36	-2,809.795	-410.914
	vessels (number) TTCh	2,320.07	-2,809.540	-410.342
Mean frequency (4-state)	detection range	3,391.24	-9,371.134	-532.152
	year	3,391.05	-9,371.042	-532.105
	BSS	3,387.12	-9,370.981	-531.771
	water depth	3,386.34	-9,368.173	-530.526
	wind speed	3,384.11	-9,361.249	-528.401
	posture type	3,381.04	-9,352.033	-528.357
	month	3,381.04	-9,304.761	-521.199
	tactile type	3,025.10	-9,291.334	-527.008
	tactile/posture rate	3,025.02	-9,284.377	-527.005
	group size	3,024.63	-9,074.572	-527.001
	synchrony	3,019.47	-9,072.901	-525.283
	substrate	3,015.29	-9,072.011	-523.612
	surface cohesion	3,012.27	-9,069.395	-520.920
	surface behaviour	3,003.42	-9,061.581	-518.358
	vessels (y/n)	2,974.02	-9,058.357	-517.039
	speed of travel	2,922.01	-9,056.254	-514.630
	calf presence (y/n) TTCh	2,851.33	-9,043.178	-508.552
	vessels (approach)	2,789.05	-9,031.225	-500.374
	vessels (approach)	2,778.81	-9,041.779	-472.304
	calf presence (y/n) TTCh	2,771.04	-9,040.306	-471.892
	vessels (number)	2,765.22	-9,039.540	-471.105
	vessels (number) TTCh	2,740.26	-9,038.121	-470.157

5.3.2.2 The effect of number of vessels on call parameters

Mean estimates and development of states used with hidden Markov model are all detailed in Appendix 5.4. The stationary distribution of call rate (Figure 5.2) and mean frequency (Figure 5.3) was then considered. For call rate, when moving from *1 additional* to *5+ additional* vessels, the probability of being in the state associated with fewest calls (state 1) decreased initially until more than three vessels were present, leading to an increase in call rates (Figure 5.2). Indeed, the probability of being in state 1 was approximately 60.0 % in the presence of fewer vessels (e.g., *RV only* or *RV + 1 additional* vessel), but decreased by 66.7 % (down to approximately 20.0 %) when two or three additional vessels were in the vicinity. The addition of more vessels (> 3) increased the probability of being in state 1 to a level comparable to the presence of the RV vessel only (approximately, 65.0 %, Figure 5.2). In contrast, states with moderate or high numbers of calls steadily increased in likelihood and then decreased when three or more vessels were in the vicinity.

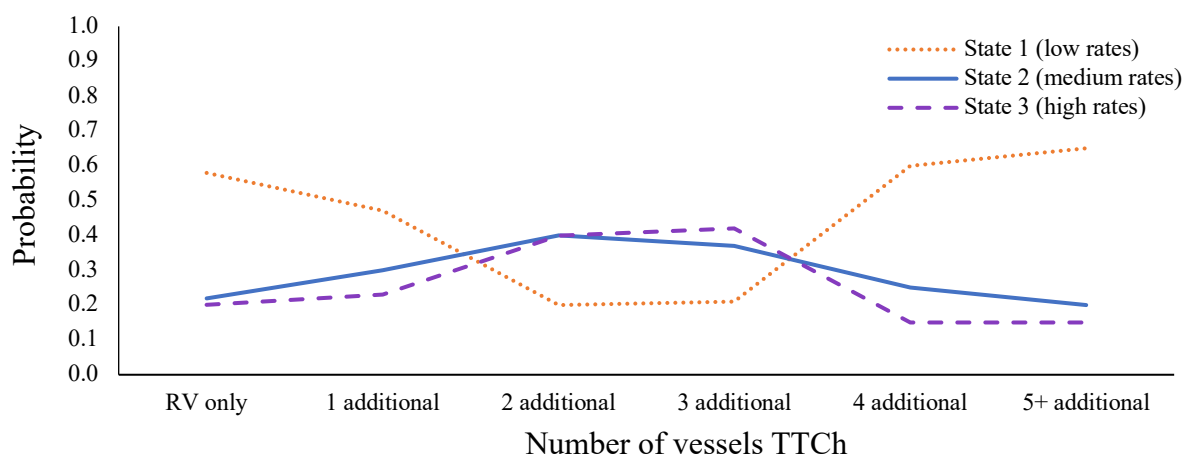


Figure 5.2: Stationary distributions for different values of vessel number (with time to change) and call rate of coastal common bottlenose dolphins (*T. truncatus*). Note: RV = research vessel.

In the case of mean frequency, when moving from *1 additional* to *5+ additional* vessels, the probability of being in the state associated with a higher mean frequency (states 3 and 4) increased in the presence of *2 additional* vessels or more, whereas the probabilities of low frequency vocalisation (states 1 and 2) occurring gradually decreased once more than one additional vessel was in the vicinity (Figure 5.3). The probability of state 1 was approximately 30.0 % in the presence of fewer vessels (e.g., *RV only* or *RV + 1 additional* vessel), decreasing by 93.3 % (down to approximately 2.0 %) when three or more vessels were present.

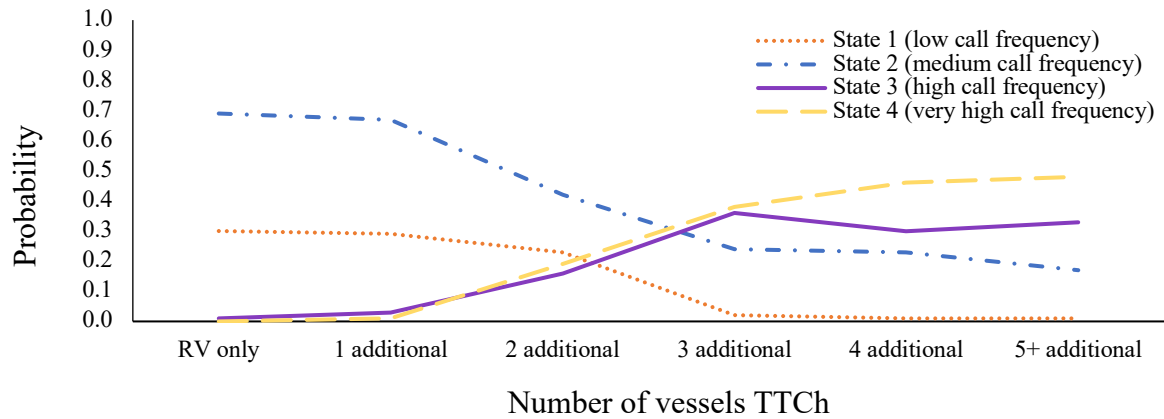


Figure 5.3: Stationary distributions for different values of vessel number (with time to change) and call frequency of coastal common bottlenose dolphins (*T. truncatus*). Note: RV = research vessel.

For comparison, in groups with calves when moving from *1 additional* to *5+ additional* vessels, the probability of being in the state associated with higher mean frequency (states 3 and 4) increased in the presence of one additional vessel or more, while the probabilities of low frequency vocalisation (states 1 and 2) occurring gradually decreased (Figure 5.4A). The converse was documented in groups with no calves where the probability of being in the state associated with higher mean frequency (states 3 and 4) decreased in the presence of three additional vessels or more, while the probabilities of high frequency vocalisation (states 1 and 2) occurring increased (Figure 5.4B).

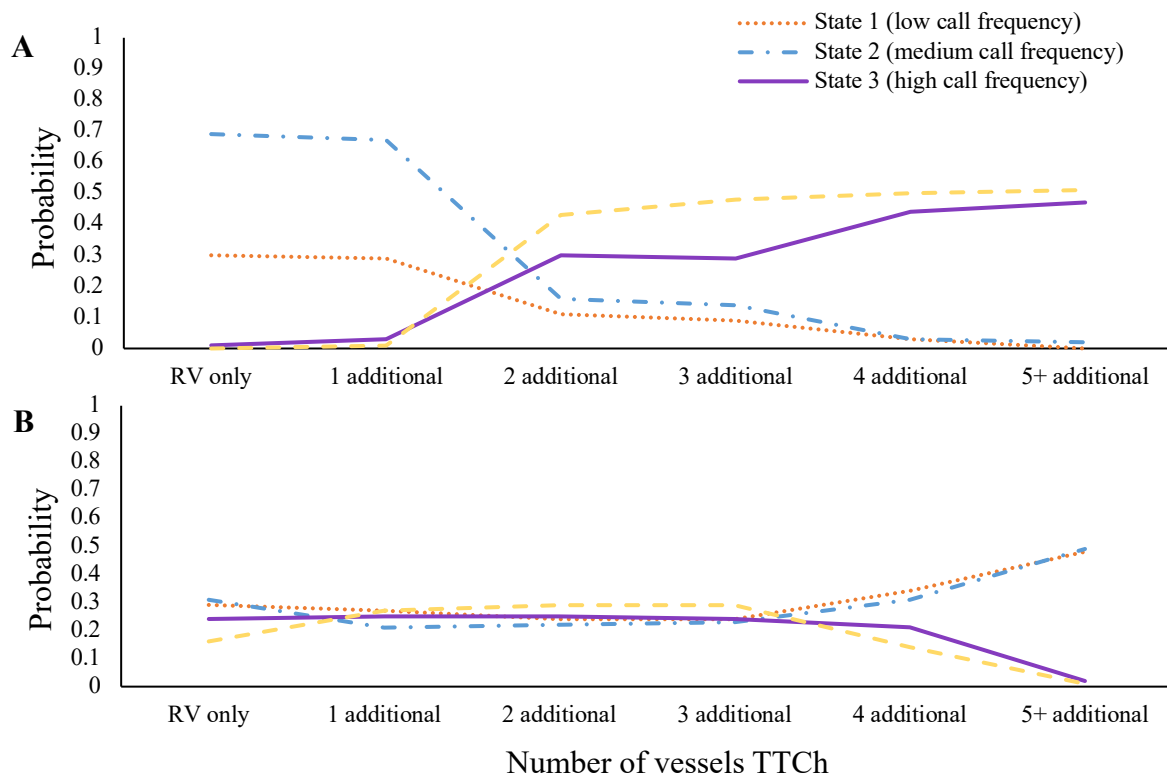


Figure 5.4: Stationary distributions for different values of vessel number (with time to change) and call frequency of coastal common bottlenose dolphins (*T. truncatus*) in groups with A) no calves and B) calves. Note: RV = research vessel.

The rates of transition between states are illustrated in Figures 5.5 and 5.6. For call rates, when coastal bottlenose dolphins are in the medium- (state 2) or high- (state 3) call-rate states, the between-state transition probabilities hardly changed when the *number of vessels TTCh* increased (Figure 5.5). Conversely, the probability of switching state 1 to 3, and state 3 to 1, appeared to correlate with the *number of vessels TTCh*. When transitioning from states 3 to 1, it was particularly high (45.1 % and 48.0 %) when the dolphins were in the presence of 3 *additional* or 4 *additional* vessels, respectively. That probability then dropped dramatically by 90.7 % and 91.3 % (down to 4.2 %), respectively, when more than four vessels were within 300 m of the dolphins. Overall, dolphins were more likely to depart from the low-call-rate state (or state 1) and the high-call state (state 3) when one to two vessels or three or more vessels were present, respectively. Dolphins were also much more likely to stay relatively silent (probability of less than 3.0 %), when they were in the presence of more than three vessels (Figure 5.5).

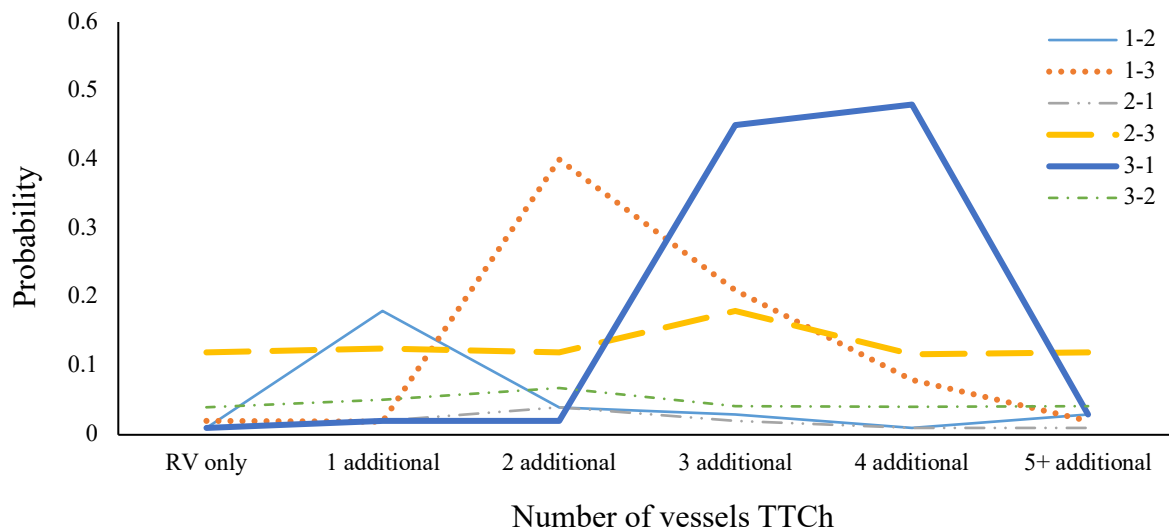


Figure 5.5: Between-state transition probabilities for different vessel number (with time to change) and call rate of coastal common bottlenose dolphins (*T. truncatus*). Note: RV = research vessel.

The rates of transition between states with *number of vessels TTCh* as a covariate for mean frequency are given in Figure 5.6. The between-state transition probabilities appeared to be heavily influenced by the *number of vessels TTCh*. In particular, when transitioning from state 1, the highest value (38.0 %) was observed when the dolphins were in the presence of three or four vessels, after steadily increasing from 10.2 % when only the RV vessel was in the vicinity. Overall, the dolphins were more likely to leave the low-frequency state (state 1) when one to two additional vessels were in the area and used the high and very high-rate states (states 3 and 4) in the presence of three or more vessels.

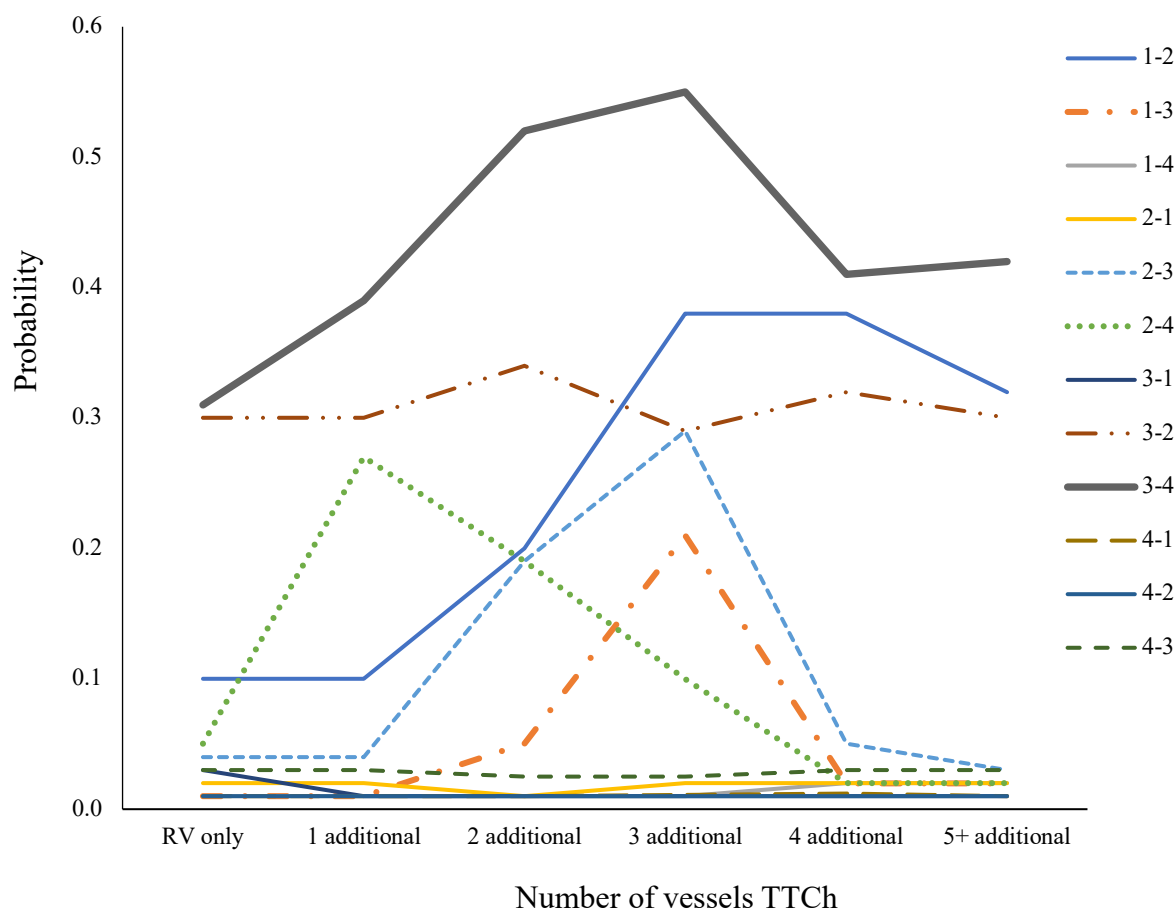


Figure 5.6: Between-state transition probabilities for different vessel number (with time to change) and mean frequency of coastal common bottlenose dolphins (*T. truncatus*). Note: RV = research vessel.

All states showed high persistence, resulting in a pattern of longer periods of each state. However, transition rates were high enough to result in comparatively frequent state changes (Figure 5.7). Transition from a low-call-rate (state 1) to a high-call-rate state (state 3) and *vice versa* often took place gradually, via the medium-call-rate state (state 2), rather than abruptly. The decoding of call rate indicated that the dolphins remained in their call-rate state 69.1 %, 62.4 %, and 86.3 % of the time for states 1, 2, and 3, respectively (Figure 5.7).

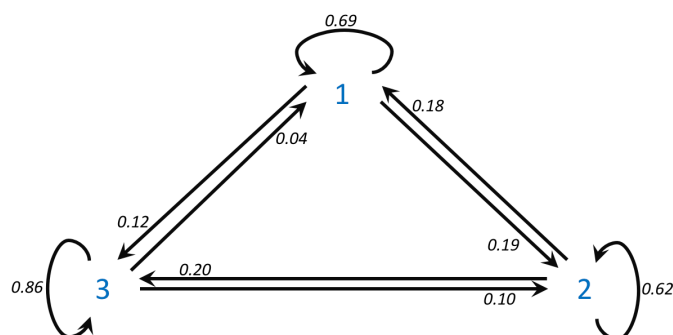


Figure 5.7: Transition matrix for three state model of call rate in the presence of different vessel numbers (with time to change) of coastal common bottlenose dolphins (*T. truncatus*). Key: Blue numbers = state, black number = transition rate, arrow direction = direction of transition between states.

Similarly, in mean frequency models (Figure 5.8) dolphins also persisted in their mean frequency state 39.2 %, 37.1 %, 48.4 %, and 41.9 % of the time when in states 1, 2, 3, and 4, respectively. The same trend was seen regardless of group composition (Figure 5.9), however groups with calves showed higher persistence in all states than in groups without calves, 43.1 vs 34.0 % (state 1), 47.3 vs 35.8 % (state 2), 56.2 vs 39.9 % (state 3), and 58.7 vs 41.4 % (state 4) of the time in groups with calves and without calves, respectively. Consequently, the dolphins appeared to stay in the state with high vocalisation rate and frequency (states 3 and 4) compared to the states with low and medium rates and frequency vocalisation (states 1 and 2).

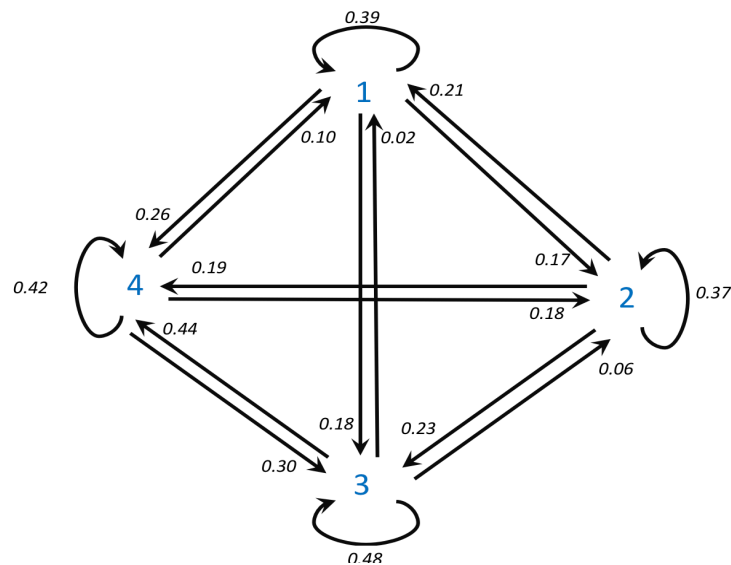


Figure 5.8: Transition matrix for four state model of mean frequency in the presence of different vessel numbers (with time to change) of coastal common bottlenose dolphins (*T. truncatus*). Key: Blue numbers = state, black number = transition rate, arrow direction = direction of transition between states.

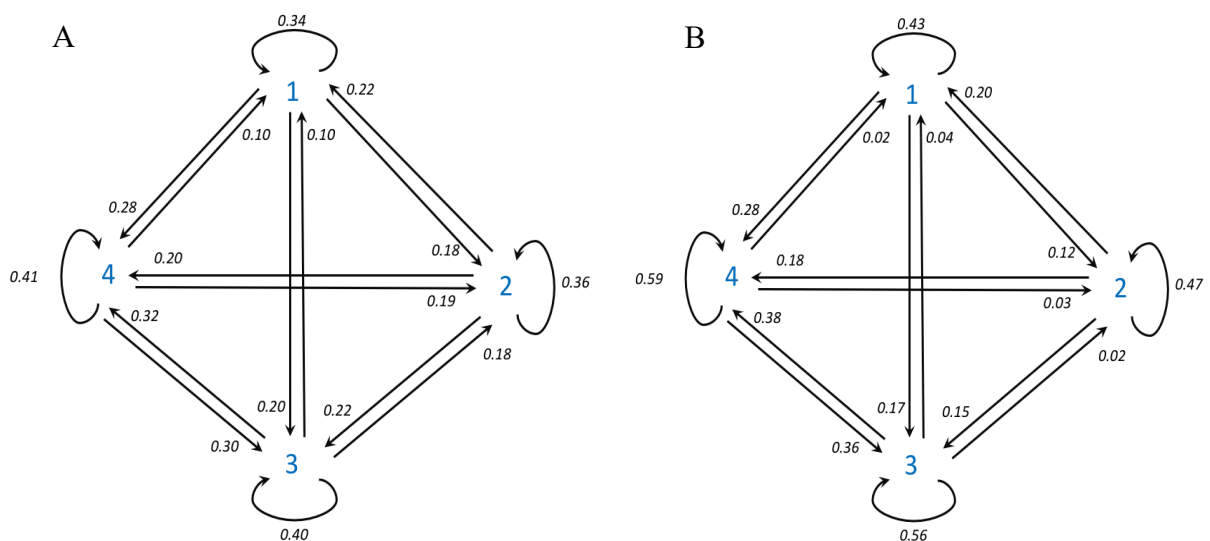


Figure 5.9: Transition matrix for four state model of mean frequency in the presence of different vessel numbers (with time to change) of coastal common bottlenose dolphins (*T. truncatus*) in groups with A) no calves and B) calves. Key: Blue numbers = state, black number = transition rate, arrow direction = direction of transition between states.

5.3.2.3 Call and tactile/posture rate in varied vessel and group composition scenarios

Model selection criteria (AIC and cross-validation) selected the negative binomial model with *tactile/posture rate TTCh* for call rate as the second best-performing one-covariate model. Given that the difference between the second and the top performing model was negligible, it is also considered for analysis. However, AIC results did not validate conducting similar analysis for mean frequency with *tactile/posture rate* (or *tactile/posture rate TTCh*) as a covariate.

In the stationary distribution of call rate, moving from low to high *tactile/posture rate* (Figure 5.10), the probability of low call rate (state 1) was highest when high *tactile/posture rate* was observed. In contrast, the probability of being in moderate (state 2) or high call rate (state 3), gradually decreased between low and high *tactile/posture rate*, respectively. While the probability of remaining in state 1 (lowest call rate) was 25.2 % when *tactile/posture rate* was low, it increased to 69.1 % with high *tactile/posture rate* (Figure 5.10).

Number of vessels had the same effect on call rate stationary distribution irrespective of the presence or absence of calves (calves presence). As vessel number increased the probability of high call rate with increasing numbers of vessels, however the probability of being in a low call rate state increased in the presence of 5+ vessels. The probability of being in the low call rate (state 1) and high *tactile/posture rate* was higher and occurred with fewer vessels within 300 m of groups with calves (+2 vessels vs +4 vessels in the absence of calves, Figure 5.11).

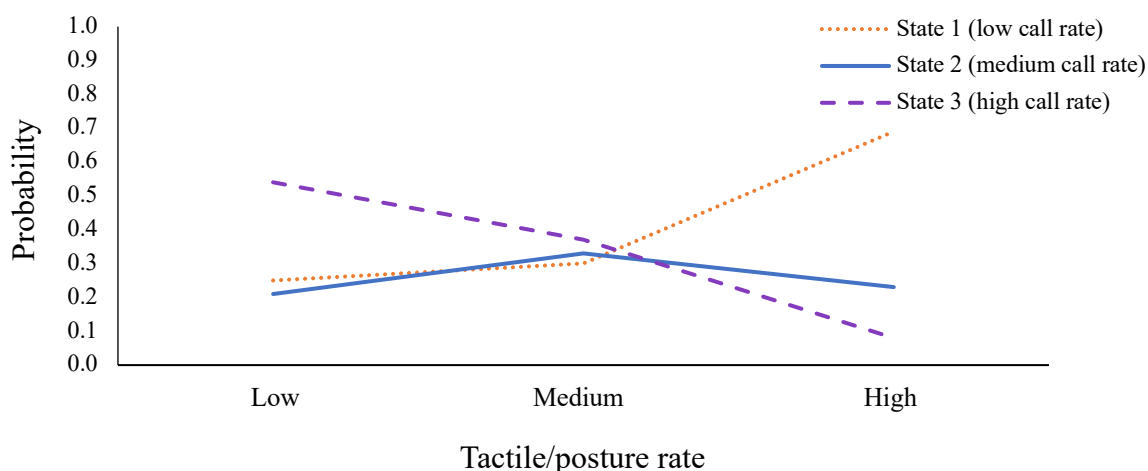


Figure 5.10: Stationary distributions for different values of tactile/posture rate and call rate of coastal common bottlenose dolphins (*T. truncatus*).

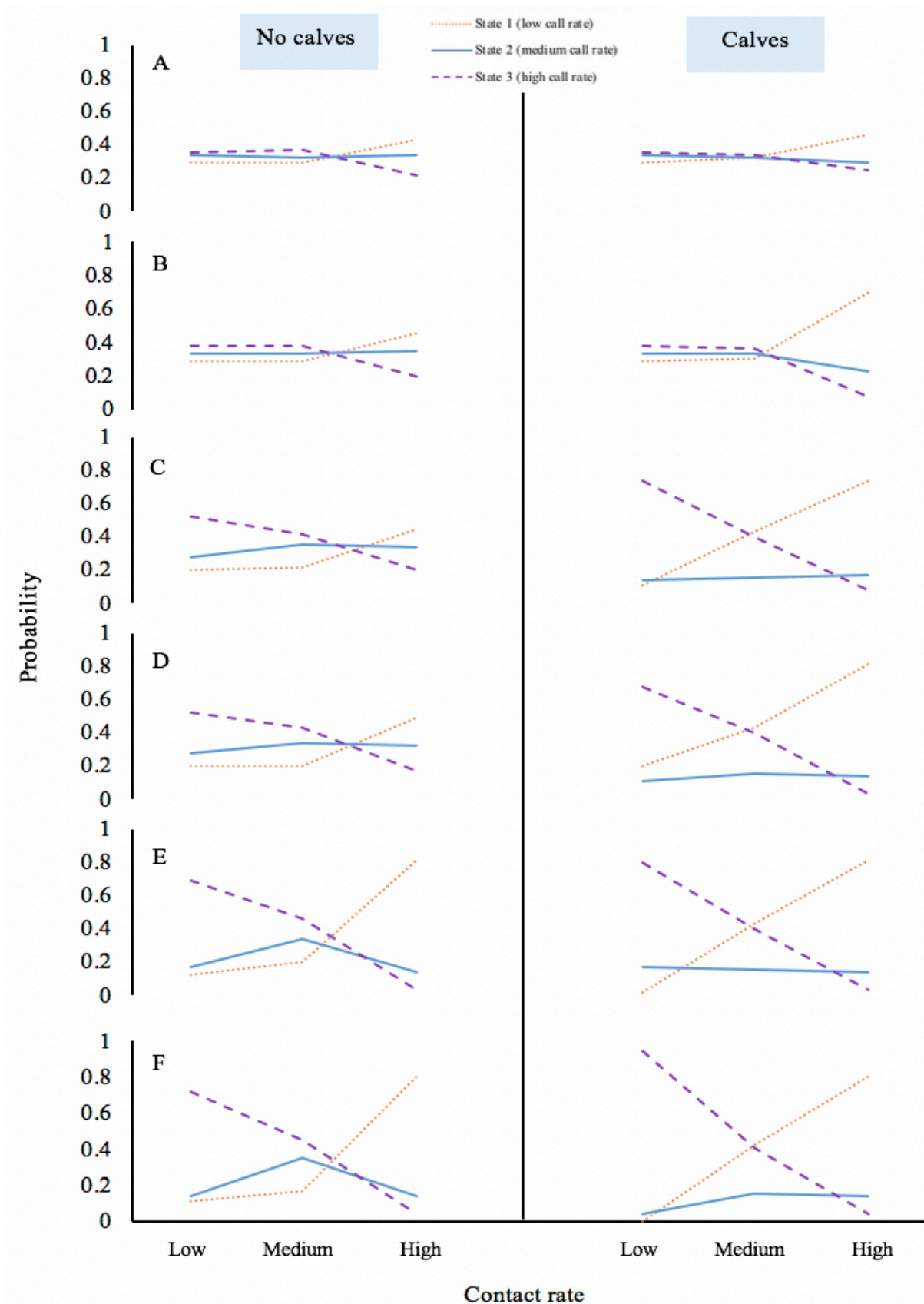


Figure 5.11: Stationary distributions for different values of tactile/posture rate and call rate of coastal common bottlenose dolphins (*T. truncatus*) in the presence of vessels with, A) research vessel only, B) 1 additional, C) 2 additional, D) 3 additional, E) 4 additional and F) 5+ additional.

The transition rates for call rate are shown in Figure 5.12. The transition of all states seemed to be influenced by *tactile/posture rate*. When transitioning from state 1 to 2 or 3, respectively, dolphins were particularly more likely to switch to these states when they had a low *tactile/posture rate* (27.0 % for 1 – 2 and 42.3 % for 1 – 3). However, that probability dramatically decreased when coastal bottlenose dolphins had a high *tactile/posture rate* (7.2 % for 1 – 2 and 3.2 % for 1 – 3 or a 73.3 % and 92.4 % decrease, respectively; Figure 5.12). The reverse was apparent when transitioning from state 3 to either state 2 or 1. The probability was particularly high when the transition was 3 – 1, with a high *tactile/posture rate* (42.4 % compared to 11.1 % with low *tactile/posture rate*, Figure 5.12). Overall, the dolphins were more likely to leave the low-call-rate state when there was low *tactile/posture rate* and leave the high-call-rate state when there was high *tactile/posture rate*.

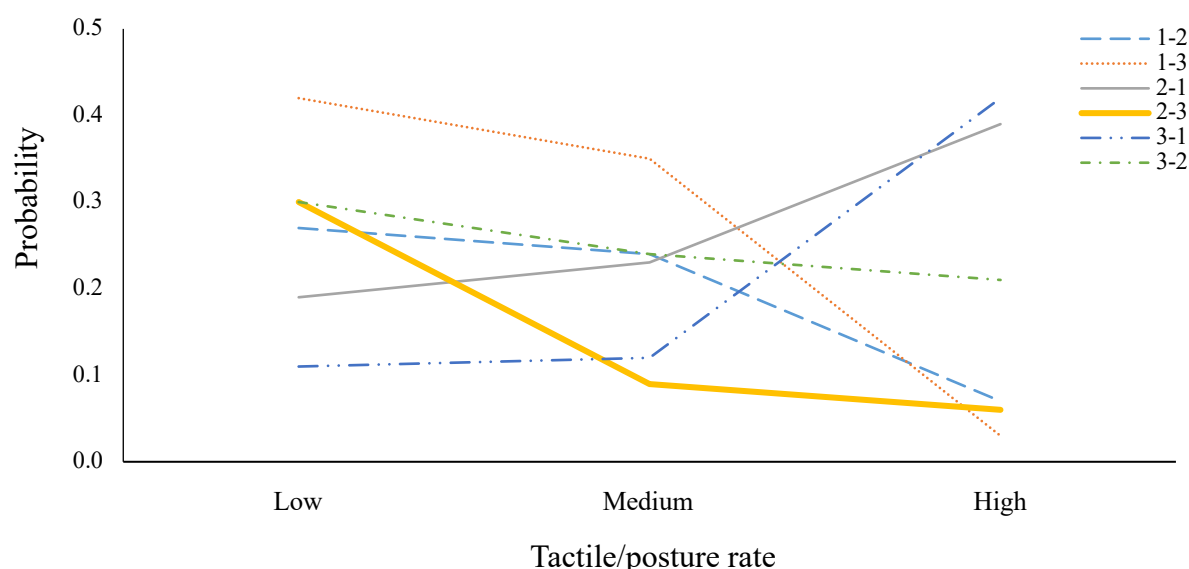


Figure 5.12: Between-state transition probabilities for different tactile/posture rates and call rates of coastal common bottlenose dolphins (*T. truncatus*).

When in the presence of vessels, a comparable trend in *tactile/posture rate* and call rate is seen as in the overall assessment. It is worth noting the probability of transition is higher overall when with calves than without calves. The between-state transition probabilities, from state 3 to lower call rates, were highest when *tactile/posture rate* was high and 2+ vessels or more were present (Figure 5.13). In addition, coastal bottlenose dolphins were also more likely to stay in this relatively silent state when *tactile/posture rate* was high. A low probability of transition to high call rate was more apparent and occurred earlier in groups with calves than groups without. Overall, the dolphins were more likely to leave the low call rate state (state 1) when *tactile/posture rate* was low and two (calves) or four (no calves) additional vessels were in the area.

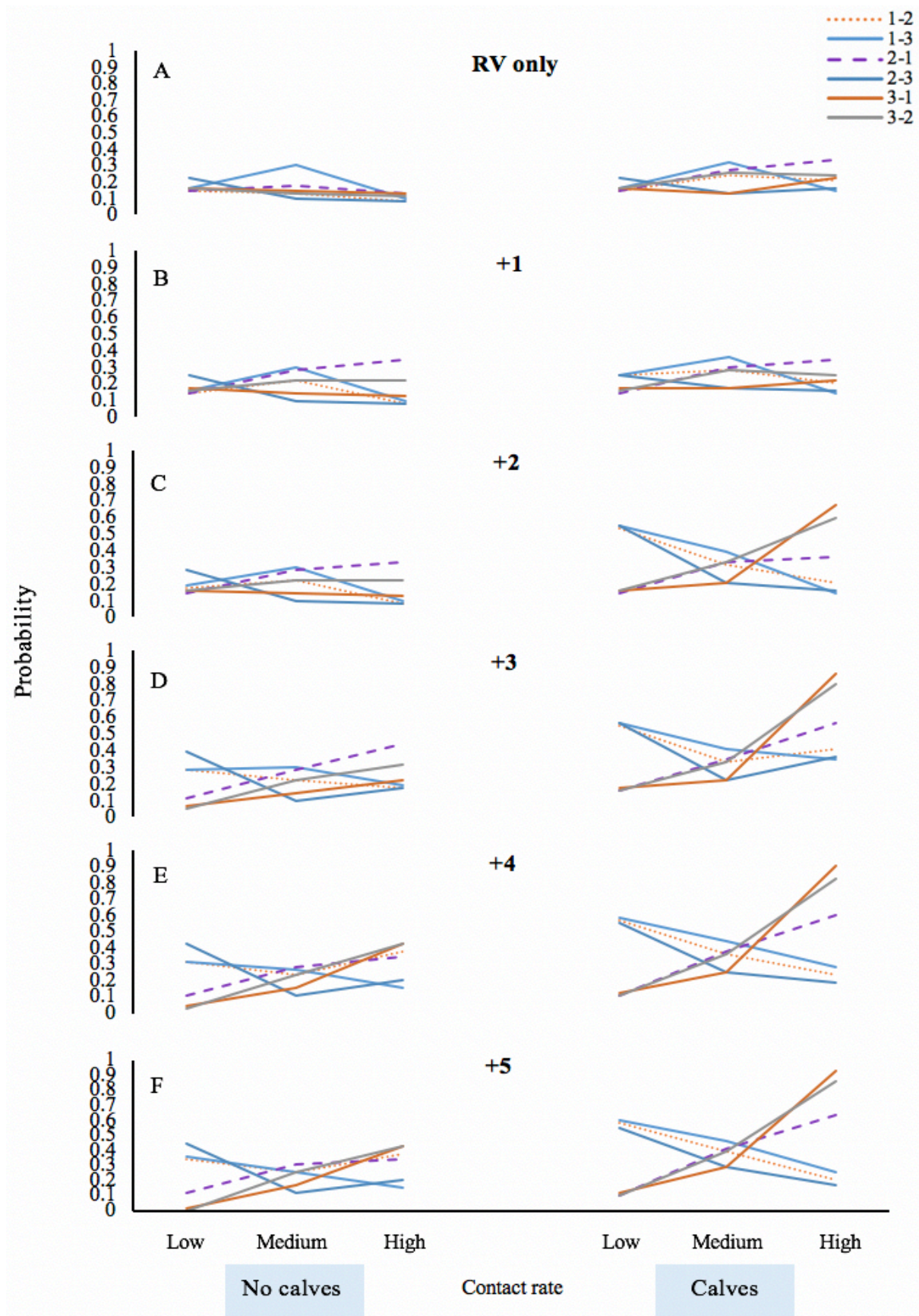


Figure 5.13: Between-state transition probabilities for different tactile/posture rates and call rates of coastal common bottlenose dolphin (*T. truncatus*) in the presence of vessels with, A) research vessel (RV) only, B) 1 additional, C) 2 additional, D) 3 additional, E) 4 additional and F) 5+ additional.

All states showed similar persistence and rates of transition between states resulting in relatively frequent changes between states (Figure 5.14). Transition from a low-call-rate (state 1) to a high-call-rate state (state 3) and *vice versa* often took place gradually, via the medium-call-rate state (state 2), rather than abruptly. The decoding of call rate indicated that coastal bottlenose dolphins persisted 29.4 %, 32.7 %, and 33.3 % of the time in state 1, 2 and 3, respectively (Figure 5.14).

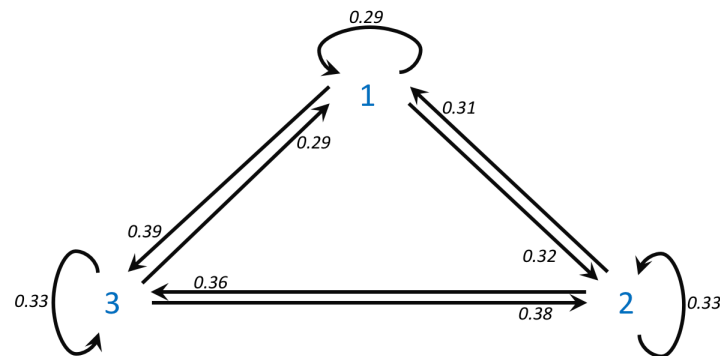


Figure 5.14: Transition matrix for three state model of call rate with varying levels of tactile rate of coastal common bottlenose dolphins (*T. truncatus*). Key: Blue numbers = state, black number = transition rate, arrow direction = direction of transition between states.

When assessing the persistence in state as a function of group type, variation between groups with and without calves was observed. In groups with calves, persistence in all states was lower than in groups with no calves (Figure 5.15). Conversely transitions between state 1 and 3 was 72.2 % (3 to 1) and 52.8 % (1 to 3) in groups with calves which was higher than in groups with no calves, 26.4 % and 30.2 % respectively (Figure 5.15). Consequently, the dolphins appeared to have a high transition rate between low and high call rate states compared to when with calves.

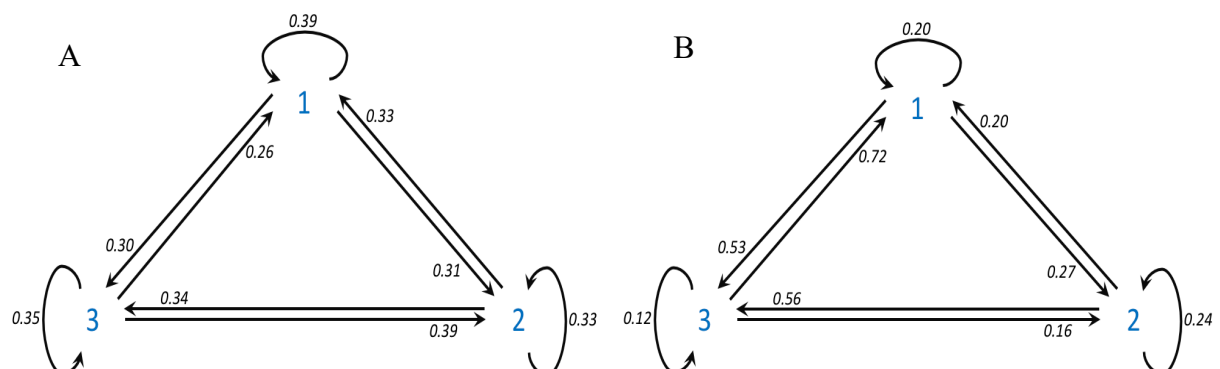


Figure 5.15: Transition matrix for three state model of call rate with varying levels of tactile rate of coastal common bottlenose dolphins (*T. truncatus*) when in groups with A) no calves and B) calves. Key: Blue numbers = state, black number = transition rate, arrow direction = direction of transition between states.

5.4 Discussion

This study demonstrates that vessels affect the call behaviour of coastal bottlenose dolphins in Far North waters, and that a correlation is observed between call and tactile/posture behaviour in the presence of vessels. Further to this, groups with or without calves respond differently to vessel presence and noise. These dolphins appear to adopt different strategies to deal with noise from vessels in close proximity. Through an understanding of communication strategies human impacts on this locally declining population (Tezanos-Pinto et al., 2013) can be better understood and managed.

5.4.1 Effects of vessels on the rate and duration of calls in coastal bottlenose dolphins

Overall, the number and speed of vessels predominantly affected rates and duration of calls. A possible interpretation of the data is that the need for vocalisation-mediated coordination increased when additional vessels were present up to a certain threshold. At this point further vocalisation-mediated coordination was no longer effective (i.e., it was masked by vessel noise) and call-rates decreased. At this same threshold, tactile/posture contact rate increased, particularly in groups with calves. Several causes have been suggested for elevated vocalisation rates in the presence of vessels (e.g., Buckstaff, 2006). This includes an altered group cohesion, an increased proximity to group members, and heightened arousal (Buckstaff, 2004; Guerra et al., 2014; Hawkins & Gartside, 2009; Scarpaci et al., 2000; Van Parijs & Corkeron, 2001). Adjusting call duration may also be a mechanism to maximise communication success.

Coastal bottlenose dolphins were more likely to: (1) leave the low-call-rate state in the presence of one to two vessels within 300m, (2) leave the high-call-rate state when three or more vessels were within 300 m, and (3) stay in a relatively silent state when more than three vessels were present within 300m. Furthermore, dolphins were more likely to: (1) leave the low-call-rate state when contact rate was low, (2) leave the high-call-rate state when contact rate was high, and (3) stay in a relatively silent state when contact rate was high. This suggests that there was an inverse relationship between call rate and tactile/posture contact rate, i.e., vocalisation-mediated coordination decreased when tactile-mediated coordination increased. This is supported by evidence from other taxa where an increase in environmental noise (overlapping with any sensory channel) has been related to adjustments in communication signal features to counteract the noise (Brumm & Slabbekoorn, 2005; Hebets & Papaj, 2005; Partan & Marler, 2005; Van der Sluijs et al., 2011). This was named “multimodal shift” by Partan et al. (2010),

P. 234 and reviewed by Partan (2013). Short-duration multimodal shifts occur in captive chimpanzees (*Pan troglodytes*) (Leavens et al., 2010), fowl (*Gallus gallus*) (Smith et al., 2011) and stickle-back fish (*Gasterosteus aculeatus*) (Heuschele et al., 2009). Field observations of multimodal shifts are rare, nevertheless it has been suggested for some taxa. For example, frogs (*Anuran* spp.) close to noisy streams utilise photic signals more than in still, and therefore quieter, areas (Hödl & Amezcuita, 2001), and jumping spiders (*Salticid* spp.) perform courting displays (photic) in open areas, while in dark nests mechanical (vibration) signals are utilised (Jackson, 1992).

In marine mammals, although some studies have found no changes in communication rates in response to vessels (Lemon et al., 2006), an increase in call rates appears to be a typical response in different populations of bottlenose dolphins. In Port Phillip Bay, Australia, bottlenose dolphin called more often around swim-with-dolphin boat operators (Scarpaci et al., 2000). In Sarasota Bay, Florida, USA, bottlenose dolphin displayed elevated call rates as a vessel started moving, and then reduced calling during and after interactions (Buckstaff, 2004). Hawkins & Gartside (2009) found that Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) had high call repetition rates during interactive behaviours with boats, such as bow and wake riding. Other cetaceans have been found to decrease their overall calling rate in response to vessel noise. For example, beluga whales (*Delphinapterus leucas*) called less often when boats approached (Lesage et al., 1999), and North Atlantic right whales (*Eubalaena glacialis*) decreased their call rate during high shipping noise (Parks et al., 2007). The effect of calf presence on the vocal reaction to vessel noise has rarely been investigated. There are two exceptions to this, Pacific humpback dolphins in Australia (*Sousa chinensis*, Van Parijs & Corkeron, 2001) and coastal bottlenose dolphins in Doubtful Sound, NZ (Guerra et al., 2014). In both studies, whistling more often occurred in the presence of vessels. This reaction was also much stronger when calves were present. The findings of the present study are consistent with those former observations in *Tursiops*. Groups with calves produced calls more often when vessels were within 300 m and with increasing vessel speeds. An increase in vocalisation rate in response to vessel noise had been previously detected in a similar study that reported call rates increased as vessels were in the presence of dolphins (200 m) and remained high even after interactions with vessels ended (Snell, 2000). The current study further established the importance of considering the presence of dependent young individuals in the analysis of reactions to vessel noise, suggesting a greater responsiveness of this demographic group in Far North waters to human effects.

The decrease in call rates and durations in groups with no calves when vessel parameters were higher (i.e., increase in speed or number) suggests that any associated elevation in vessel noise interferes with vocal signals and/or increases its cost. Groups with calves may additionally have an increased need for individuals to conserve or re-establish acoustic contact, despite the potential cost to communicate. For dolphins, vocalisations are the primary channel for communication, with contact between individuals a close second (refer to Herzing & Johnson, 2015 for review). Calls appear to be used as contact calls, with vital functions in facilitating inter-individual communication and maintaining group structure (e.g., Janik & Slater, 1998; Kondo & Watanabe, 2009). In captivity, bottlenose dolphin mothers and calves called more often when separated (McCowan & Reiss, 1995; Smolker et al., 1993). In this study, when vocals were considered in isolation, groups with calves increased vocalisations when vessels were present. Findings are thus likely to result from a need to re-establish decreased mother-calf cohesion and/or with other group members. Additionally, the fact that call rate was strongly affected by vessel speed indicates this parameter disturbs signal exchange. As a result, signal repetition might increase, partially compensating for signal masking with increased ambient source or disturbance levels. These strategies would be employed up to a threshold where energetic cost outweighs the gain in call rate, at which point a secondary communication system may be utilised. Dolphin contact behaviour may aid the formation and repair of alliances, which, as long as individuals are in close proximity (i.e., mother-calves), could facilitate group bonds in scenarios where vocal communication is no longer effective (Tamaki et al., 2006). The present study indicates that considering multiple communication channels is important in understanding vessel effects on coastal bottlenose dolphins in Far North waters, particularly in groups with calves requiring frequent contact with their mother. This is especially important in the Bay of Islands, which is a popular recreational and commercial area and has a high documented calf mortality rate (Constantine et al., 2004; Peters & Stockin, 2016; Tezanos-Pinto et al., 2015).

5.4.2 Effects of vessels on the signal use in coastal bottlenose dolphins

Call characteristics changed when vessels were present. A quantitative study of the Bay of Islands underwater environment measured the acoustic characteristics of vessels operating in that area (Snell, 2000). Tour vessels produced sound levels that were audible to coastal bottlenose dolphins over ranges of many kilometres. The four large tour vessels recorded (of which three still currently operate in the Bay of Islands) had varied broadband source levels.

Snell (2000) described little anthropogenic noise in the Bay of Islands above 20 kHz, thus the masking of echolocation clicks (which have maximum energy at 120 – 130 kHz and a range of 40-150 kHz) was improbable (Chapter 3). Calls, however, overlap with vessel noise and some masking was likely. In the present study, the fundamental frequency of calls recorded in the absence of vessel noise ranged from 0.8 to 24 kHz, with mean peak frequency at 11.18 kHz (SD = 4.17), mean minimum frequency of 6.49 kHz (SD = 3.44), and mean maximum frequency of 15.71 kHz (SD = 4.59) (Chapter 3), thus resulting in an important overlap with vessel noise.

Few studies have quantified marine mammal modifications of vocalisations as a response to vessel traffic, however it appears evident there is an effect. For example, belugas (*Delphinapterus leucas*), utilise calls of higher frequencies (Lesage et al., 1999) and sound levels (Scheifele et al., 2005) when vessel noise is higher. North Atlantic right whales increase vocalisation frequency to minimise interference with raised low-frequency vessel noise (Parks et al., 2007). A study on Indo-Pacific bottlenose dolphins (Morisaka et al., 2005c) reported dolphin calls of lower frequencies and fewer frequency modulations in habitats where vessel noise was highest. This study, however, compared calls among a population's range where dolphins are exposed to different levels of ambient noise. Thus, the observed differences in vocalisations could in some form reflect variation among areas rather than responses to a noisier acoustic environment per se (Chapter 3).

Groups with and without calves displayed opposite reactions in call adaptations to vessel noise. Overall, coastal bottlenose dolphins were more likely to withdraw from the low-frequency state when one to two vessels were present and utilise the high and very high-rate states when the numbers of vessels in their vicinity increased to three or more. An intuitive interpretation is that low frequency vocalisations were not utilised as much in the presence of vessels as they are less effective communication tools. When with vessels, groups without calves produced calls that shifted towards lower frequency bands, while groups with calves shifted towards higher frequencies. Vessel noise overlaps with dolphin vocalisations and thus could reduce the range of call propagation at a level which can be perceived by conspecifics (Jensen et al., 2009) through masking. Dolphins may, therefore, modulate their vocalisations to avoid bandwidths of loudest ambient noise or to increase communication range.

The converse reaction to vessel noise by groups with and without calves may be driven by two

factors: (1) the requirement for different forms of contact between mothers and their dependent calves, and (2) the biological limitations on hearing and sound production of calves. Low frequency sounds propagate further than higher frequency sounds (Richardson et al., 1995). Therefore, producing lower frequency calls may assist groups with no calves to reach all members of the group in a noisy environment to maintain group communication and cohesion. However, when calves were present the dolphins shifted to higher frequencies. This might be a more effective way to increase communication success over short-range distances, such as a mother and her calf or between mother-calf pairs whilst adopting alternative communication that is effective at short range (e.g., increased contact rate). In addition, calves, due to their smaller size, are likely to have better hearing at higher frequencies (e.g., Nachtigall et al., 2005). This may favour a shift up rather than down in frequency, when noise prevents communication in the usual frequency bands. In any case, even if the biological function of the observed call modifications cannot be definitively determined, it is evident that such changes illustrate a departure from optimal signal exchange conditions and may also result in some energetic cost. Whether these short-term effects result in long-term adaptations, stress, or biological consequences remains unknown to date.

5.4.3 Study limitations

In contrast to other vessels, the effect of the stationary RV was not quantified. However, a concerted effort was made to minimise disturbance and impact on the dolphins' communication through use of a quiet four-stroke engine and best practice consistent manoeuvring.

When examining vessels, a bias may occur due to vessel noise which, if loud enough, may mask calls. Additionally, masking may occur as a result of unstudied vessel variables such as the type of vessel, its propulsion type, engine revolutions, propeller type/rotation, etc. Masking would result in call rate underestimation when vessels are present. Given that call rate and frequency were still effectively measured at a range of frequencies and rates, this indicates that potential call masking in spectrograms was low. Additionally, any bias would have resulted in an underestimation of vessel effects on coastal bottlenose dolphin call behaviour.

A further conceivable bias in this type of research, is the fact that the field of view of the camera equipment is limited by water visibility and/or the angle of view. This may result in some tactile/postural behaviour being missed, leading to an underestimation of contact rate. This is additionally confounded when additional vessels are with the group. Another vessel near the

RV may block the view of the whole or part of the group for a time. Results presented here indicate a contact rate increase in scenarios with higher numbers of vessels, and no difference was observed in water visibility between areas where vessels interacted and where they did not. Given that tactile/posture contact rate and type were still effectively measured for a representative range, this suggests that visibility and field of view error were minimal and that this error would have underestimated the disturbance of vessels on the tactile behaviour of dolphins. Nevertheless, this source of bias is noted and could be improved in further studies using animal-borne systems and/or mobile camera systems in conjunction with each other to remain close to the dolphins, though these methodologies also have their own limitations to consider.

The contexts and behaviours considered in this study were not exhaustive. Throughout the literature, variables not considered here are documented to influence the vocalisation of delphinids. An example of this is travelling speed as discussed by Henderson et al. (2012). Additionally, subsurface behaviour is multi-faceted with not all modes being quantified with the utilised methodology, i.e., chemical, electromagnetic, and hydrodynamic signals. The inclusion of such variables should be considered in future research, with a focus on variables that are hard to define.

Chapter 6

General Discussion



Whangaroa harbour at dusk after a day of survey in Far North waters, New Zealand.

6.1 Overview

This thesis adds a new dimension to the study of common bottlenose dolphins (*Tursiops truncatus*, referred to hereafter as bottlenose dolphins), both within New Zealand (NZ) and internationally. It presents the first holistic assessment of two bottlenose dolphin ecotypes' behaviour in NZ. All research objectives were linked in a logical manner to the most utilised signal type, mechanical (calls), providing an extensive representation of the signal exchange behaviour of bottlenose dolphins. Chapter 2 focused particularly on gathering systematic baseline data on bottlenose dolphin density, abundance, and spatial distribution, respectively. This, in turn, allowed for the analysis of spatial and temporal overlap of ecotypes within Far North waters, i.e., assessing whether interaction is likely and whether the ecotypes are sympatrically or parapatrically distributed. Secondly, following the spatial context provided in Chapter 2, subsequent data chapters addressed the often-overlooked context of multimodal social signal use. This was done to quantify any differences between ecotypes, which may lead to the biological separation of the two. Finally, Chapters 4 and 5 further focused on determining the ecotype-specific factors acting on signal exchange that might maintain and/or effect any differences observed in Chapters 2 and the acoustic behaviour presented in Chapter 3.

This general discussion chapter synthesises the body of work within this thesis to discuss the following: a) the spatio-temporal trends of bottlenose dolphin ecotypes in Far North waters; b) the behavioural profile of bottlenose dolphins in Far North waters; c) the relationship between acoustic behaviour of bottlenose dolphins and other signal exchange forms and additional contexts (vessels, group size, and composition); d) the significance and relevance of the information, including informing the management of bottlenose dolphin in this region; and finally, e) technical recommendations and possible future research.

6.1.1 Synthesis

This thesis aimed to quantify the context-specific signal plasticity of two bottlenose dolphin ecotypes in the framework of behavioural, temporal, spatial, environmental, and group factors. Due to the utilisation of a holistic approach, the results provide important new information about multimodal behaviour in delphinids. Building from a wealth of knowledge in the Bay of Islands (e.g., Constantine et al., 2004; Hartel et al., 2014; Peters & Stockin, 2016; Tezanos-Pinto et al., 2013; 2015; Zaeschmar et al., 2014) the first quantitative information pertaining to the possibility of interaction between dolphin ecotypes in Far North waters is presented. Thus,

vital ecological knowledge is provided for informing appropriate conservation strategies. Findings can be summarised as follows:

1. Bottlenose dolphins occurred throughout most of the Far North waters surveyed, with a non-uniform distribution.
2. Ecotype was an important model factor explaining variability in spatial and temporal use of the study area. Additionally, *stratum* was a significant factor in these models (Chapter 2). Oceanic bottlenose dolphins were not detected in the Far North waters during winter and spring, whilst coastal bottlenose dolphins occurred year-round. Oceanic bottlenose dolphins and coastal bottlenose dolphins in Far North waters showed: (1) low spatial overlap; (2) no concordance in temporal space use; and (3) divergence in behavioural state (as a function of space and time).
3. Consistent differences in the social vocalisations of ecotypes demonstrated call divergence. Oceanic bottlenose dolphin vocal repertoire had higher complexity than coastal bottlenose dolphin vocal repertoire (Chapter 3).
4. Multimodal behavioural plasticity was observed in oceanic bottlenose dolphins. Call parameters of oceanic bottlenose dolphins in Far North waters varied in the presence of pilot whales (*Globicephala* sp.), and as a function of group *behavioural state*. This study provided further evidence of interspecific groups of pilot whales and oceanic bottlenose dolphins using calls with: a) intermediate duration and frequency when travelling; and b) increased duration (in the case of oceanic bottlenose dolphins) and frequencies when socialising, compared to calls produced by the same species in intraspecific groups (Chapter 4).
5. Call rates varied with mechanical (tactile) and photic (posture) context, with more frequent signal exchanges observed, not only in association with particular activities and characteristics of the social group, but also at times when those activities or characteristics were shifting. Predominant interspecific social interactions appeared aggressive. At the onset of and throughout this research, quantifying aggressive behaviour was not a central objective, but it resulted in important discussion points (Chapter 4).
6. The number of vessels predominantly affected call rates and duration in coastal bottlenose dolphins. The use of vocalisation-mediated coordination increased when additional vessels were present up to a threshold, at which point further vocalisation-mediated coordination was no longer efficient, and call-rate decreased. At this given threshold, contact rate increased, particularly in groups with calves. This suggests that a)

there was an inverse relationship between call rate and contact rate, i.e., vocalisation-mediated coordination decreased when tactile-mediated coordination increased, and b) groups with calves were more sensitive and quicker to react to vessel presence than adult only groups (Chapter 5).

6.2 Ecology of ecotypes

6.2.1 Spatial/temporal variation

In Far North waters, higher frequencies and increased call complexity were recorded in locations or scenarios where ambient noise was likely to be higher; for example, in coastal areas where boat traffic was comparatively higher (the Bay of Islands and Whangaroa Harbour) in coastal bottlenose dolphins, and in ‘noisier’ larger groupings in oceanic bottlenose dolphins (Chapters 3, 4, and 5). Spatial variation in call behaviour was most apparent in coastal bottlenose dolphins, particularly in their core areas (Chapter 2) where vessel presence was also highest (Chapter 5). Duration and rate of calls in coastal bottlenose dolphins were inversely related with vessel presence. Thresholds of change were identified, and groups with calves were particularly sensitive to vessel presence and behaviour.

The different strategies adopted by groups with and without calves are likely to reflect a trade-off between an increased need for contact when calves are present and the limitations and/or costs of communicating in a noisy environment. If calves are present, the need for signal exchange is higher, as it becomes crucial to re-establish and maintain contact in mother-calf pairs or with the rest of the group. Thus, this study provides evidence that dolphins modify their vocal and tactile signals by moving away from their primary signal mode (vocal) to maximise signal exchange (visual and tactile) efficiency. Notably, this is predominantly observed in groups with vulnerable individuals that respond to changes in their environment at lower thresholds than adult only groups. The effects of vessel sound on coastal bottlenose dolphins raise concerns for four reasons. First, recreational vessel activity is not well regulated in NZ (Peters & Stockin, 2016). Second, the use of the Bay of Islands by coastal bottlenose dolphins has been reducing for an extended period of time (Peters & Stockin, 2016; Tezanos-Pinto et al., 2013). Third, as oceanic bottlenose dolphins appeared to not frequent coastal waters within the operating range of the permitted tourism industry, the oceanic bottlenose dolphin ecotype cannot be viewed as ‘rest bite individuals’ to reduce the cumulative disturbance to individual coastal bottlenose dolphins. Finally, coastal bottlenose dolphins were not restricted

in range to Bay of Islands waters only, with comparatively high-density areas in the wider Far North waters region where vessel interactions also occur. Consequently, these cumulative effects necessitate the need for further regulations regarding the coastal bottlenose dolphin. Nonetheless, protection cannot be suggested without considering the range overlap and social variations in the populations of both ecotypes and across Far North waters habitats, not just coastal bottlenose dolphin in the Bay of Islands.

6.2.2 Behavioural variation

A higher level of behavioural variation was detected in bottlenose dolphin inter- than intra-ecotype in Far North waters, particularly in call parameters. Additionally, in this study, the larger oceanic bottlenose dolphins were recorded as using significantly higher frequencies, contrary to what would be expected based on morphology alone. Other factors are, therefore, likely to affect this discrepancy (Chapters 3, 4, and 5). Social variation (e.g., isolation or affiliation) would be a more plausible explanation than morphology (May-Collado et al., 2007). Supporting this theory, shorter and higher frequency calls were common in the oceanic bottlenose dolphin ecotype (Chapter 3), with larger group sizes than the coastal bottlenose dolphin (Chapter 2). Further finer-scale social plasticity of these two parameters was also noted, beyond group size alone. The duration and frequency of calls were affected differently when oceanic bottlenose dolphins were in inter-specific rather than intra-specific groups. In larger inter-specific groups, higher frequencies and longer, rather than shorter, duration calls are produced than in intra-specific groups (Chapter 4). Understanding the dynamic associations between social structure, call rate, frequency parameters, and overall signal exchange is important to infer functionality (Chapters 4 and 5).

The use of visual, vocal, and tactile channels for signal exchange is apparent in this Far North waters bottlenose dolphin study (Chapters 3, 4 and 5). Bottlenose dolphins in Far North waters use overlapping cue types and, at times, appear to utilise more than one avenue of signal exchange, possibly to enhance the meaning intended. The inclusion of multiple signal avenues in this study illustrated the importance of holistic behavioural research. For example, surface behaviour alone was not retained in best fitting models in favour of both coastal bottlenose dolphin and oceanic bottlenose dolphin multimodal behaviour (calls, contact events, and surface behaviour state, Chapters 4 and 5). Unfortunately, a direct comparison of visual and tactile signals between ecotypes was not possible due to the parapatric nature of sightings resulting in distinctly different water visibility (1.7 – 3.4m in coastal bottlenose dolphin and

3.6 – 9m in oceanic bottlenose dolphin). Key findings supporting the plasticity of multimodal signal exchange were: a) oceanic bottlenose dolphins were more likely to use high frequency calls when in low ratio to the number of pilot whales present; b) oceanic bottlenose dolphin groups responded differently to association with pilot whales based on surface behavioural state as well as tactile and posture behavioural events (calls shorter when socialising); and c) pilot whales dominated 100 % of aggressive behavioural events recorded, suggesting oceanic bottlenose dolphins were submissive in this inter-specific interaction.

Results presented herein suggest it is not possible to infer caller motivation using frequency structure alone. Additionally, the comparatively high variation in signal (vocal and non-vocal) exchange between coastal bottlenose dolphins and oceanic bottlenose dolphins communities in Far North waters (Chapters 3, 4, and 5) may reflect the low level of interaction between these genetically indistinct populations (Tezanos-Pinto et al., 2009). There is also a limited ecotype interaction possibility during the calving season (November – March) due to oceanic bottlenose dolphin peak density in Far North waters (March – May) occurring during a different period each year (Peters & Stockin, 2016; Chapter 2). This may further increase the ecotype disparity in signal parameters over time, as the likelihood of vocal crossover during optimal calf learning is likely reduced.

6.3 Significance and contribution of research findings

Meeting the objectives of the thesis has led to a significant contribution towards a better understanding of bottlenose dolphins and their multimodal signal exchange. More specifically, ecotype-specific factors that may affect signal exchange parameters in NZ were discussed for the first time. Until now, research had primarily focused on parts of bottlenose dolphin populations subject to high tourism levels in the Bay of Islands (e.g., Constantine et al., 2004; Peters & Stockin, 2016; Tezanos-Pinto et al., 2013), Milford Sound (Lusseau et al., 2006), Fiordland (Boisseau, 2005; Currey et al., 2009; Guerra et al., 2014; Haase & Schneider, 2001) and Marlborough Sounds (Merriman et al., 2009). Consequently, there is a lack of conservation and management decisions for coastal bottlenose dolphins outside of those regions, and furthermore no management directly pertaining to oceanic bottlenose dolphins in NZ (Peters & Stockin, 2016)

In this thesis, new information about the spatial and behavioural ecology of bottlenose dolphins using Far North waters was presented. The quantification of bottlenose dolphin distributions

in previously unstudied regions of Far North waters, such as the areas north and south of the Bay of Islands and any areas frequented by oceanic bottlenose dolphins, further contributed to advancing current knowledge. Data collection was not constrained by the use of platforms of opportunity. A holistic behavioural assessment across a range of Far North waters sites was therefore conducted to produce the first assessment of spatial use of this key area by bottlenose dolphins. This provided an understanding of the likely spatial use of Far North waters by both coastal bottlenose dolphin and oceanic bottlenose dolphin ecotypes and how this spatial use varies seasonally and in response to stressors such as the presence of other species (Chapter 4) and vessel traffic (Chapter 5).

The application of multimodal behavioural analysis can sometimes be challenging, but it adds new insight into spatial use and stressors. In addition, financial constraints can also prevent researchers from using specialist equipment to document surface behavioural state in addition to mechanical (tactile) and photic (posture) behavioural event context. This study demonstrated that the use of commercially available hardware and freeware can still yield important information in the assessment of behavioural parameters (Chapters 3, 4, and 5). The application of the freeware Luscinia, for example, contributed a novel approach to the toolset of cetacean acoustics, learning from the advances in other fields of ecology, particularly ornithology. Additionally, a new method of analysing both surface behavioural state and mechanical (tactile)/photic (posture) event context for cetacean behavioural data was presented. By incorporating group composition and external factors through hidden Markov modelling, new insight was gained. While the effects of vessels were similar to those historically identified by hidden Markov modelling based on surface behavioural states, the description and modelling of multimodal behaviour (states and events) provided significantly greater insight into group behaviour than with surface behaviour alone. Further to this, more fine-scale information about bottlenose dolphin ecotypes was investigated via the comparative treatment of group behaviour. This emphasised the importance of Far North waters for bottlenose dolphins, building on historic research. Social, temporal and spatial separation between ecotypes in Far North waters and short-term responses associated with the current levels of vessel activities in the Bay of Islands have been detected and new insight added to the current knowledge of Bay of Islands coastal bottlenose dolphins. The Department of Conservation (DOC) will be able to base future management decisions on stronger scientific merit. This will aid in minimising the effects of tourism activities on localised areas of the *nationally endangered* coastal bottlenose dolphin range. Additionally, informed management can be implemented for the previously

unstudied oceanic bottlenose dolphin in Far North waters and NZ.

This study emphasises the importance of considering social, temporal, and spatial intra-species differences when managing species. Consequently, it reinforces the need to manage each local population independently. This should assist managers to develop adequate adaptive management policies for commercial dolphin-based tourism (La Manna et al., 2016). A precautionary and adaptive principle should therefore be applied: a) at locations where impact assessment is unavailable; and b) prior to the establishment of a commercial operation. For example, in the first scenario, there is now sufficient evidence to support the adaptive and inclusive management of all vessel traffic at any location in Far North waters (Peters & Stockin, 2016; Chapter 5). Such management should remain in place until it can be demonstrated that the level of tourism activities has no effect that could be considered potentially detrimental to the targeted population (Peters & Stockin, 2016).

Finally, although the Bay of Islands population of coastal bottlenose dolphins is one of the most comprehensively studied in NZ, the fine-scale distribution of these dolphins across Far North waters and their holistic behaviour, has not been systematically documented until now. Intra-species differences in behaviour between locations and ecotypes in Far North waters highlights the fact that a generalisation of the species' behaviour could be misleading. This is crucial for the management of this species because erroneous assumptions could ultimately result in inappropriate management decisions. Let us hypothetically assume, for example, that no control data could have been collected outside of the Bay of Islands and, as a result, data analyses had to be based on the behaviour of coastal bottlenose dolphins in the Bay of Islands only. The local abundance decline and behaviour changes observed historically in Bay of Islands coastal bottlenose dolphins (Constantine et al., 2004; Peters & Stockin, 2016; Tezanos-Pinto et al., 2013) may be considered to: a) reflect the global North East coast population (Chapters 2 and 5); or b) not be 'biologically significant', as the genetically non-distinct ecotypes could be recognised as one biological unit, which would result in a dramatically higher population estimate. This prospect would induce a possible change in conservation status as, in theory, additional individuals would be able to repopulate the area (Tezanos-Pinto, 2009; Chapters 2, 3 and 4). Such disparity reinforces once again the value of baseline data, the need to study each population independently at an appropriate scale, and ultimately to manage them as such.

6.4 Future work

There is rich potential for future spatial and behavioural work in Far North waters. The single spatial factor retained in the best fitting models of both ecotypes was *stratum*. The absence of background information across a large proportion of the region makes it challenging to understand any changes in spatial occurrence and behaviour across Far North waters. It would be useful to know whether oceanic bottlenose dolphins remain in the region just further from shore (e.g., in waters deeper than 200m) or whether they are part of a broader-ranging population with intermittent use of Far North waters.

To build on the study data, additional concurrent data from different (including additional previously un-surveyed) sites should be collected to provide an even pattern of temporal and spatial measurements. The use of a single dedicated RV prevented this approach in this study. To achieve this, a stationary hydrophone could be deployed in the same geographic location across different months to allow for the assessment of seasonal and monthly changes. This study also supports the need to register and include other biotic and abiotic factors when defining spatial and temporal use. One example where this could be built upon, is with the inclusion of tidal cycles. Including these data in models would further inform any temporal relationship between dolphin occurrence and distance from coastline (Harzen, 1998). Another example is the inclusion of accurate prey data. The literature on possible prey species distribution and abundance for bottlenose dolphin ecotypes and their associated species is currently lacking. In NZ, there is a paucity of information particularly on fish species such as pilchard (*Sardina pilchardus*) and anchovy (*Engraulis australis*). It is concerning that management may not have data available on the sustainability of removing these species and the impact this would have on cetaceans in Far North waters. Indeed, prey depletion effects on marine megafauna have already been recognised globally (e.g., Bearzi et al., 2008; Cury et al., 2011). Research on these fish species should not be overlooked in management priorities. An ecosystem management approach is therefore necessary. Nocturnal observations of bottlenose dolphins would be particularly useful to investigate feeding patterns. Finally, synchronised follows of groups of both ecotypes and playback experiments may result in documented avoidance behaviour and/or movements into shallower water habitats (Parra, 2006), adding insights to drivers of behaviour in Far North waters bottlenose dolphins.

Whilst coastal vessel traffic was considered, large vessel noise (i.e., shipping noise further offshore) and its effect on bottlenose dolphin behaviour could not be integrated in the analysis.

This is due to the models in Chapters 3, 4, and 5 not including data which extended to deeper waters where this type of vessel traffic occurs. Larger vessels produce lower frequency sounds, which can demonstrate a masking effect on low-frequency bands (Parks et al., 2007). This can result in displacement from areas important to larger whales for breeding and feeding, while smaller cetaceans can change locations on temporally shorter and smaller spatial scales (Weilgart, 2007). There were also other anthropogenic variables not accounted for, such as nutrient run-off from land, fish stocks, and bycatch risk. These factors might have unquantified implications for high tropic level species such as cetaceans.

The general ecosystem of Far North waters has also been the subject of comprehensive research, albeit again centred around the Bay of Islands (e.g., Bay of Islands Coastal Survey 20/20 project as summarised in Morrison et al., 2010). A spatial approach should combine what is known of the Far North waters oceanography and fish distribution with knowledge of dolphin behaviour and acoustics. As Far North waters are relatively hard to access, the areas between the limits of this study and the Hauraki Gulf (36°51'S, 174°46'E) to the South and at depths greater than 150 m remain unstudied for this species (and most other species). Stranding and opportunistic sighting data indicate Far North waters are frequented by bottlenose dolphins, if only in a transitory nature between hotspots. Preliminary findings in this study suggest great variability in spatial and behavioural use of Far North waters, which supports the need for baseline data at all locations within the range of the North East coast population. There may also be bottlenose dolphin communities that use the areas north of Doubtless Bay (34°59'S, 173°29'E), particularly around the Three Kings islands (34°09'S, 172°8'E; Anecdotal sightings, DOC, unpublished data). A population study in these areas would also be suitable as they 'bookend' the Far North waters populations.

Oceanic bottlenose dolphins behaviour in association with pilot whales was assessed in this thesis. Oceanic bottlenose dolphins have also been reported to form associations with false killer whale groups, as well as false killer whales, pilot whales and oceanic bottlenose dolphins in a three-species inter-specific association (Zaeschar et al., 2014). Unfortunately, the only encounters with false killer whales in Far North waters occurred in 2013 (unpublished data, CHP) and a comprehensive dataset was not achieved, thus no data on false killer whales were included in this thesis. Additional data collection to include all associations formed by oceanic bottlenose dolphins would therefore provide valuable insight into oceanic bottlenose dolphin behavioural plasticity. The multiple factors which may be promoting the modifications

observed (i.e., signal convergence and/or stress), including all possible social associations, should be considered. The frequency and number of recorded associations concerning false killer whales and bottlenose dolphins in Far North waters could suggest that they are an important part of each species' ecology. Future studies should therefore also expand on current methodology with the utilisation of directional passive acoustic technology provided by acoustic tags. This methodology would allow researchers to evaluate any possible factors that may promote inter-specific signal modification. Future work should assess possible influences of participants when forming inter-specific associations (e.g., Kitchen & Beehner, 2007). Individuals may have a greater chance of participating in behavioural events or display behavioural adaptations if a numerical advantage in their favour exists (e.g., Meunier et al., 2012a; Vogel et al., 2007).

Results from Chapter 3 would support the classification of ecotype from acoustic recordings. A logical next step would be the description of the full vocal repertoire of bottlenose dolphins in Far North waters. Following this, the deployment of an array of hydrophones (as mentioned above), would also allow localisation of individual calls (Quick & Janik, 2012; Schneider, 1999), the detection of ecotypes spatially and temporally, and the detection of any other vocal species in Far North waters that may be present, thus adding new insight. Knowledge of caller location may then be used to assess depth and behavioural relationships to a much greater degree. Signal behaviour (Chapter 4 and 5), and physical behaviour (Chapter 2 – 5; Peters & Stockin, 2016) have been shown to vary spatially. A comprehensive study of individual dolphin distribution and full vocalisation repertoire is feasible. This is particularly apt for hotspots within the North-East coast population, where over 20 years of collective photo-identification information exists (e.g., Berghan et al., 2008; Constantine, 2000; Constantine et al., 2004; Dwyer et al., 2014; Tezanos-Pinto et al., 2013). Additional genetic samples should also be collected from the oceanic bottlenose dolphin ecotype to add insight to the population structure, abundance, and reproductive parameters, allowing cross-ecotype comparison. However, caution should be taken in defining populations purely on genetic grounds, as it is not inclusive of ecosystem health and does not consider the effects of local extirpation and fragmentation (Taylor & Dizon, 1999).

Visual and postural signals need to be analysed further and, additionally, several larger frameworks for all species' signal exchange systems should be contemplated. Analysing discrete/graded multimodal signals, the sequence of signals and sociality combine to give

‘context’ to frameworks. This may be crucial in the interpretation of signal exchange in many species, including the bottlenose dolphin. The inclusion of multiple levels of each behaviour type in hidden Markov models will only add further insights into the complexity of bottlenose dolphin social interactions.

In conclusion, the continuation of multiple approaches to gather data on both ecotypes, including identification of threats, critical habitat, genetics, and social behaviour will reaffirm the value of these populations.

6.5 Management

Bottlenose dolphins are the most encountered cetaceans in the Far North waters. Consequently, they remain the primary target species of permitted commercial vessels in Bay of Islands. As such, bottlenose dolphins form the economic core of the marine mammal tourism industry in this region. Findings presented here indicate that management should be adaptive and broad reaching. It is recommended:

- An integrated and adaptive management plan be implemented, as per Higham et al. (2009). This management model highlights the importance of integrating multiple stakeholder perspectives in a way that is both research-informed and adaptive. Management should include the monitoring of the local population at regular intervals and across Far North waters.
- For the DOC to engage with an non-Governmental organisation or community initiative in Far North waters to provide education, on-water monitoring and hold enforcement powers.
- For the current moratorium to remain in place until at least full population analyses are completed for *Tursiops* across their broader north-east, North Island range to prevent any increases in permitted activity. This would allow site fidelity and cumulative effects to be clearly determined. Datasets with respect to Hauraki Gulf and Bay of Plenty are currently available and could be used to address this issue.
- For DOC to apply year-round management (as opposed to limiting management measures to peak periods), to encompass the seasonal distribution of both ecotypes (Chapter 2).
- For DOC to make provision for compulsory, efficient and locally relevant training for all commercial permitted operator crew annually, preferably ahead of peak season. The aim of this training is to minimise disturbance of tour boats, provide updated research information on the bottlenose population and known effects of tourism activities, as well

as to reinforce a) the importance of regulations and operator obligations under the Marine Mammal Protection Regulations (1992) and b) existing commercial permits restrictions.

- For DOC to engage in a significant public education campaign aimed at public engagement (e.g. via community initiatives) throughout Far North waters and ultimately, significant behaviour changes in private vessel owners (refer to sections 6.3 and 6.5). In light of the results presented in Chapter 5, the effects of vessel presence on communication, especially with calves, should be an included aspect.
- For DOC to mitigate the disturbance and/or potential injury to calves from vessel traffic. It is specifically recommended all racing events with high vessel speeds be excluded from Far North waters during identified peak breeding season (refer to Chapter 5).
- DOC provide compulsory area specific annual training for all un-permitted vessel skippers and crew undergoing commercial operation in Far North waters.

6.6 Concluding statement

This body of work has provided invaluable insight into bottlenose dolphin spatial and temporal use of Far North waters and the context of intra- and inter-specific behaviour. As bottlenose dolphins are a highly communicative species, they are the ideal model genus for signal exchange studies of cetaceans, with acoustic and video recordings offering a high data return per unit effort. Using a holistic approach, this study derived a wealth of information on both Far North waters ecotypes. These techniques range from the simple (calculation of vocalisation rate) to the more complex (measuring the concurrent use of mechanical and photic signals). Incorporating additional information, such as behaviour (surface and subsurface), environmental factors (biotic and abiotic), group composition, location, and species enhanced the value of the data by providing context. This is a substantial advancement on early studies, which focused largely on part of the behavioural repertoire, known population range, and only one ecotype. Subsequent studies and management bodies will be well served by a holistic appreciation of the behavioural complexities of parapatrically occurring intra- and inter-specific populations, as demonstrated by bottlenose dolphin ecotypes in Far North waters.

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Appendices



Pilot whales (*Globicephala* sp.) in Far North waters, New Zealand.

Appendix 1.1

Data summary for common bottlenose dolphins (*Tursiops truncatus*) March 2013 – September 2015, in Far North waters, New Zealand.

Key: Detections = all sightings (Chapter 2), Encounters = detections where additional behavioural data was collected (Chapter 3-5), CBD = coastal bottlenose dolphin, OBD = oceanic bottlenose dolphin

Group	Detections	Encounters	Acoustic recordings	calls	Video recordings	Video events	Group size range	Group size in frame
CBD	228	31	827	12,661	57	491	1-48	1-27
OBD (overall)	36	10	190	18,972	60	589	5-350	1-28
OBD only	15	4	86	8,031	22	139	6-70	1-26
OBD mixed	21	6	N/A	N/A	N/A	N/A	5-220	N/A
OBD mixed (sub-groups)	32	32	104	10,941	38	450	5-34	1-17
Pilot whale only	27	27	72	6,827	23	306	4-28	4-28

Appendices

Year	Month	Dedicated zones covered												CBD Sightings			OBD Sightings			CBD Sub-surface video data			OBD overall Sub-surface video data			Surface Behavioural data				
		A	B	C	D	E	F	G	H	I	J	K	L	M	On effort	Off effort	Total	On effort	Off effort	Total	Acoustic and video recording days	Visual recordings	Acoustic recordings	Acoustic and video recording days	Visual recordings	Acoustic recordings	ABSENCE data counts	ABSENCE data counts (>30min)	PRESENCE data counts	PRESENCE data counts (>30min)
spring		Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	89	513	602	0	1	1	7	10	409	0	0	0	310	130	589	440	
summer		Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	155	626	781	8	0	8	7	29	212	6	22	100	457	185	722	485	
autumn		Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	68	623	691	28	3	31	9	12	131	4	38	90	448	234	431	246	
winter		Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	24	259	283	0	0	0	8	6	75	0	0	0	359	158	1,642	1,439	
TOTAL		-	-	-	-	-	-	-	-	-	-	-	-	336	2,021	2,357	36	4	40	31	57	827	10	60	190	1,574	707	3,384	2,610	
2013	MAR	Y	Y	Y	Y					Y	Y			17	18	35	3	0	3	0	0	0	0	0	0	104	72	311	264	
	APR	Y		Y	Y	Y					Y	Y		20	73	93	5	1	6	0	0	0	0	0	0	54	0	180	138	
	MAY	Y	Y		Y		Y					Y		18	66	84	0	0	0	0	0	0	0	0	0	127	39	163	102	
	JUN											Y		17	45	62	0	0	0	0	0	0	0	0	0	42	28	41	11	
	JUL	Y			Y	Y	Y	Y		Y				29	51	80	0	0	0	0	0	0	0	0	0	88	22	179	95	
	AUG	Y	Y	Y	Y	Y		Y						23	39	62	0	0	0	0	0	0	0	0	0	35	34	8	0	
	SEP		Y	Y	Y	Y	Y	Y						31	38	69	0	0	0	1	1	48	0	0	0	43	41	22	16	
	OCT			Y					Y	Y	Y	Y		10	98	108	0	0	0	3	3	38	0	0	0	5	0	64	58	
	NOV		Y					Y				Y	Y		27	92	119	0	0	0	2	1	225	0	0	0	11	0	111	91
	DEC	Y	Y	Y	Y	Y		Y					Y		18	50	68	3	0	3	4	1	24	1	3	24	50	27	107	82
2014	JAN	Y	Y	Y	Y	Y	Y	Y	Y			Y	Y	14	85	99	0	0	0	2	4	69	0	0	0	19	0	177	131	
	FEB	Y			Y	Y	Y					Y		13	123	136	4	1	5	4	19	81	1	1	13	143	89	239	178	
	MAR				Y				Y		Y	Y	Y	9	134	143	5	0	5	0	0	0	1	12	26	62	0	113	77	
	APR			Y	Y							Y		10	136	146	8	0	8	0	0	0	3	26	64	164	75	169	57	
	MAY					Y	Y					Y		5	56	61	0	0	0	3	1	65	0	0	0	65	34	36	0	
	JUN				Y							Y		3	61	64	0	0	0	0	0	0	0	0	0	57	12	58	31	
	JUL			Y								Y		5	44	49	0	0	0	3	2	27	0	0	0	107	63	87	67	
	AUG	Y	Y			Y	Y	Y				Y		7	20	27	0	0	0	0	0	0	0	0	0	130	45	75	16	
	SEP			Y		Y	Y	Y				Y		3	42	45	0	0	0	1	2	29	0	0	0	45	29	60	52	
	OCT		Y					Y				Y		9	79	88	0	2	2	2	2	26	0	0	0	107	71	116	85	
	NOV	Y					Y					Y		2	125	127	0	0	0	0	0	0	0	0	0	85	60	700	683	
	DEC										Y	Y			6	108	114	1	0	1	0	0	0	0	0	101	0	544	440	
2015	JAN	Y				Y			Y			Y	Y	15	85	100	4	0	4	2	5	38	3	12	32	45	0	153	125	
	FEB		Y	Y			Y	Y			Y	Y		10	108	118	3	0	3	0	0	0	1	6	31	103	41	20	6	
	MAR	Y	Y				Y	Y	Y					3	95	98	0	0	0	2	11	66	0	0	0	72	38	201	83	
	APR											Y		2	85	87	0	0	0	0	0	0	0	0	0	49	35	40	32	
	MAY		Y	Y	Y						Y		Y	3	58	61	0	0	0	0	0	0	0	0	0	52	43	18	3	
	JUN		Y					Y	Y			Y		0	0	0	0	0	0	0	0	0	0	0	0	19	10	32	17	
	JUL											Y		3	3	6	0	0	0	1	4	48	0	0	0	12	0	121	89	
	AUG				Y		Y	Y		Y	Y	Y		0	0	0	0	0	0	0	0	0	0	0	0	24	9	19	7	
SEP	Y	Y	Y	Y	Y	Y	Y	Y			Y	Y	4	4	8	0	0	0	1	1	43	0	0	0	27	14	20	8		

Appendix 2.1

Research vessel *Te Epiwhania* utilised throughout this study. Owned and provided by Massey University, Coastal-Marine Research Group. Photo: B. Owen



Appendix 2.2

Common bottlenose dolphins (*Tursiops truncatus*) age and behaviour definitions following previously described categories for the North Island population (Constantine, 2002; Filby, et al., 2014; Dwyer, 2014; Tezanos-Pinto, 2009).

Age class	Definition
<i>Neonate</i>	Observable white dorso-ventral foetal folds. Often associated with uncoordinated surfacing and individuals up to 3 months old.
<i>Calf</i>	Roughly one-half or less the size of a mature adult. Often swimming in 'Infant position' with an adult.
<i>Juvenile</i>	Approximately two-thirds the size of an adult. Likely swimming with adult, but not in 'Infant position'.
<i>Adult</i>	All dolphins considered fully-grown, i.e., equal or > 3.0m in total body length.

Behavioural state	Definition
<i>Forage/feed</i>	Dolphins involved in any effort to pursue, capture and/or consume prey. Observations of fish chasing (herding), co-ordinated deep diving and no contact between individuals (as often observed when socialising), and rapid circle swimming (but not chasing another dolphin). Prey sometimes observed in the dolphin's mouth.
<i>Mill</i>	Dolphins showing frequent changes in heading. This often is described as a transition behaviour between other behavioural states.
<i>Rest</i>	Dolphins observed in a tight cluster (< 1 body length apart), engaged in slow manoeuvres with little evidence of forward propulsion. Lacking active components observed in other behavioural states.
<i>Social</i>	Dolphins observed leaping, chasing, and engaged in body contact with other dolphins involved aspects of play/copulation (including carrying seaweed).
<i>Travel</i>	Dolphins engaged in persistent, directional movement.
<i>Dive</i>	Dolphins engaged in persistent, non-directional movements; frequent periods sub-surface with short surfacings. No prey observed.

Appendix 2.3

Comparison across New Zealand, the mean best group size and range of coastal common bottlenose dolphins (*Tursiops truncatus*) are presented.

Note; SE = Standard error, S.D. = Standard deviation, Size = group size.

Location	Range	Size	SE	Reference
Bay of Islands	3–40	15.3	8.3	1996–97 (Constantine & Baker, 1997)
Bay of Islands	2–50	17.1	1.24	1999 (Constantine, 2002)
Bay of Islands	2–50	16.7	12.62	1997–99 (Tezanos-Pinto, 2009)
Bay of Islands	2–45	19.1	10.7	2003–2005 (Tezanos-Pinto, 2009)
Bay of Islands	2–50	17.9	11.72	1997–05 (Tezanos-Pinto, 2009)
Far North waters	1–48	14.4	6.2	This study coastal ecotype
Hauraki Gulf	1–82	35	23.36 S.D	Dwyer et al., 2014b
Marlborough Sounds	3–172	12	38 S.D	Merriman et al., 2009
Doubtful Sounds	1–65	17.2	N/A	Lusseau et al., 2003

Appendix 2.4

Stratum-specific estimated seasonal coastal common bottlenose dolphin (*Tursiops truncatus*) density (Density; per 1 km²) from density surface modelling analyses. Parametric bootstrapping (120 repetitions) produced standard errors (SE).

	Summer		Winter	
Stratum	Density	SE	Density	SE
Global	0.63	0.03	0.62	0.02
1	0.64	0.12	0.57	0.07
2	0.59	0.09	0.54	0.08
3	0.64	0.15	0.51	0.20
4	0.37	0.17	0.32	0.13
5	0.17	0.15	0.13	0.16
	Autumn		Spring	
Stratum	Density	SE	Density	SE
Global	0.62	0.04	0.62	0.07
1	0.61	0.10	0.62	0.03
2	0.60	0.06	0.60	0.09
3	0.61	0.07	0.58	0.17
4	0.36	0.09	0.35	0.10
5	0.15	0.12	0.15	0.18

Coastal common bottlenose dolphin group-size frequency was utilised to randomly generate group sizes in the parametric bootstrap procedure (as described in MacKenzie & Clement (2014)). Key: the number of observed groups of size s (n_s), the expected probability of detecting a group of size s within the covered area ($E(p.(s))$), and the estimated frequency of group size s (\hat{f}_s). The estimated number of groups in the covered area (\hat{N}_{gc}) was 391 in summer, 389 in autumn, 386 in spring, and 382 in winter.

	Summer			Winter			Autumn			Spring		
Size	n_s	$E(p.(s))$	\hat{f}_s	n_s	$E(p.(s))$	\hat{f}_s	n_s	$E(p.(s))$	\hat{f}_s	n_s	$E(p.(s))$	\hat{f}_s
1	0	0.68	0.30	1	0.63	0.21	1	0.63	0.20	1	0.64	0.17
2	2	0.69	0.20	4	0.65	0.40	2	0.64	0.21	1	0.65	0.19
3	1	0.71	0.17	6	0.67	0.15	4	0.67	0.31	6	0.66	0.28
4	4	0.72	0.29	8	0.68	0.08	3	0.69	0.18	5	0.72	0.23
5	1	0.77	0.09	2	0.70	0.05	1	0.72	0.09	3	0.74	0.08
6	1	0.83	0.07	1	0.73	0.03	1	0.75	0.06	2	0.77	0.04
7	2	0.85	0.05	1	0.74	0.03	1	0.80	0.06	1	0.79	0.02
8	5	0.87	0.01	2	0.77	0.03	2	0.81	0.04	2	0.80	0.01
9	2	0.89	0.01	2	0.78	0.02	2	0.84	0.03	1	0.83	0.01
10	1	0.90	0.00	2	0.79	0.00	2	0.87	0.00	1	0.86	0.00

Appendix 2.5

Estimated summer and spring oceanic common bottlenose dolphin (*Tursiops truncatus*, oceanic common bottlenose dolphin) density (Density; per 1 km²) for each *stratum* from density surface modelling analyses from March 2013 – September 2015, in Far North waters, New Zealand. Parametric bootstrapping (120 repetitions) produced standard errors (SE).

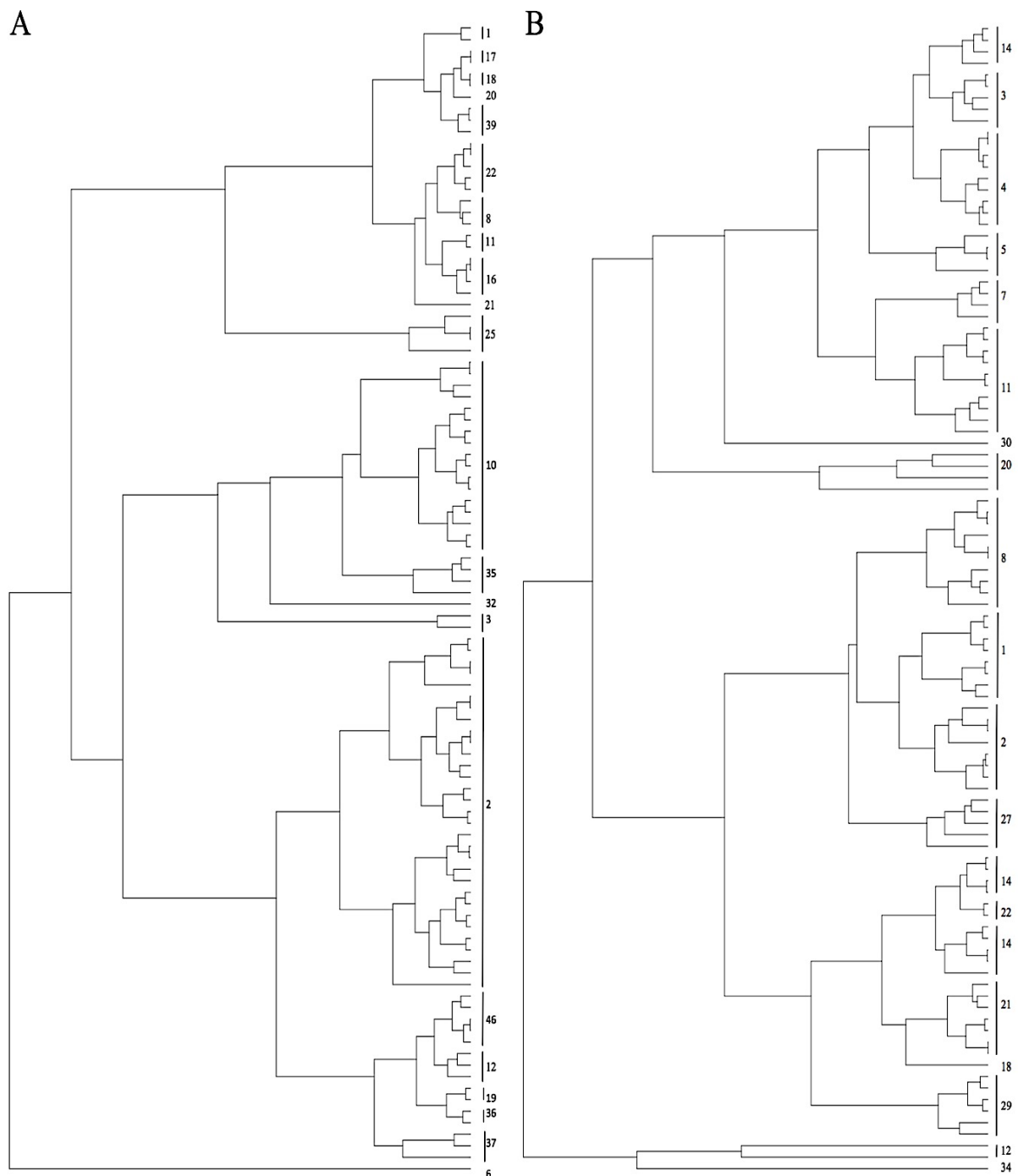
	Summer		Spring	
Stratum	Density	SE	Density	SE
Global	0.77	0.12	0.81	0.32

Oceanic common bottlenose dolphin group-size frequency was utilised to randomly generate group sizes in the parametric bootstrap procedure (as described in MacKenzie & Clement (2014)). Key: the number of observed groups of size s (n_s), the expected probability of detecting a group of size s within the covered area ($E(p \cdot (s))$), and the estimated frequency of group size s (\hat{f}_s). The estimated number of groups in the covered area (\hat{N}_{gc}) was 3914.

	Summer			Spring		
Size	n_s	$(E(p \cdot (s)))$	\hat{f}_s	n_s	$(E(p \cdot (s)))$	\hat{f}_s
10	0	0.18	0.00	0	0.10	0.00
20	1	0.23	0.01	0	0.16	0.00
30	1	0.25	0.04	1	0.18	0.01
40	1	0.25	0.04	1	0.21	0.02
50	4	0.34	0.12	2	0.31	0.11
60	4	0.49	0.13	3	0.37	0.18
70	1	0.50	0.04	2	0.58	0.23
80	2	0.72	0.23	0	0.62	0.12
90	3	0.86	0.10	1	0.64	0.15
100	4	0.89	0.28	1	0.71	0.18

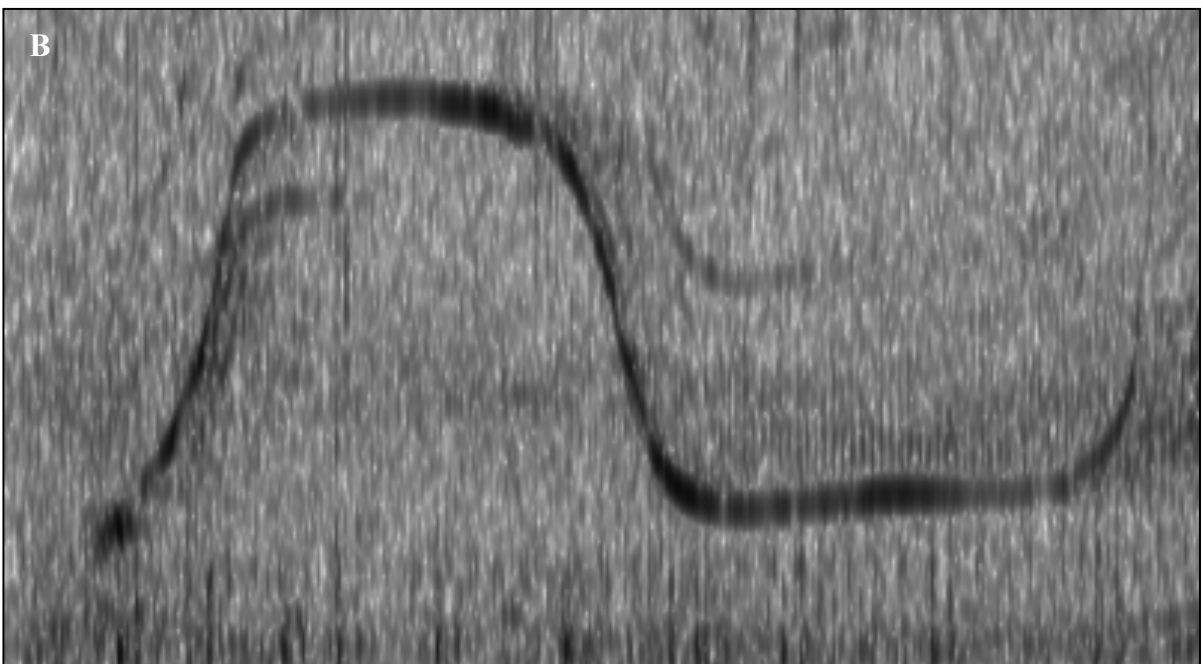
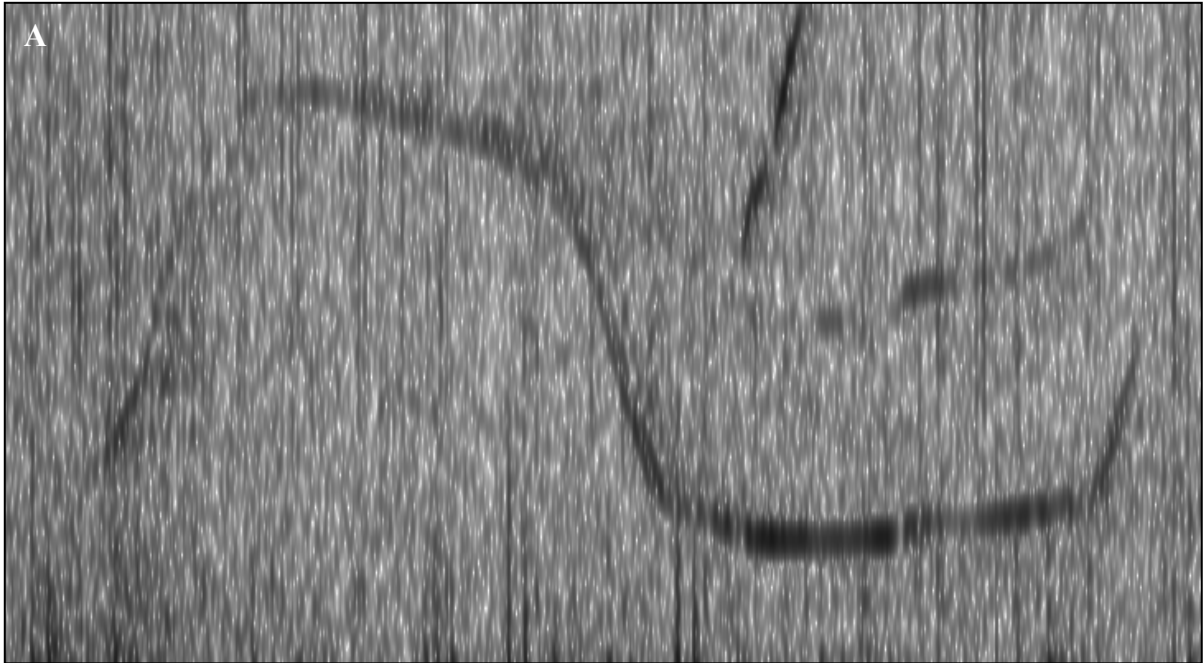
Appendix 3.1

Unweighted Pair Group Method with Arithmetic Mean dendrogram of whistle-types from A) coastal common bottlenose dolphin and B) oceanic common bottlenose dolphin (*Tursiops truncatus*) resulting from a computational comparison of a sub-set of whistle-types. Whistles are labelled by the type assigned to them by visual classification of whistle-types. The dendrogram shows a close correspondence between computational and human judgment of whistle-types.



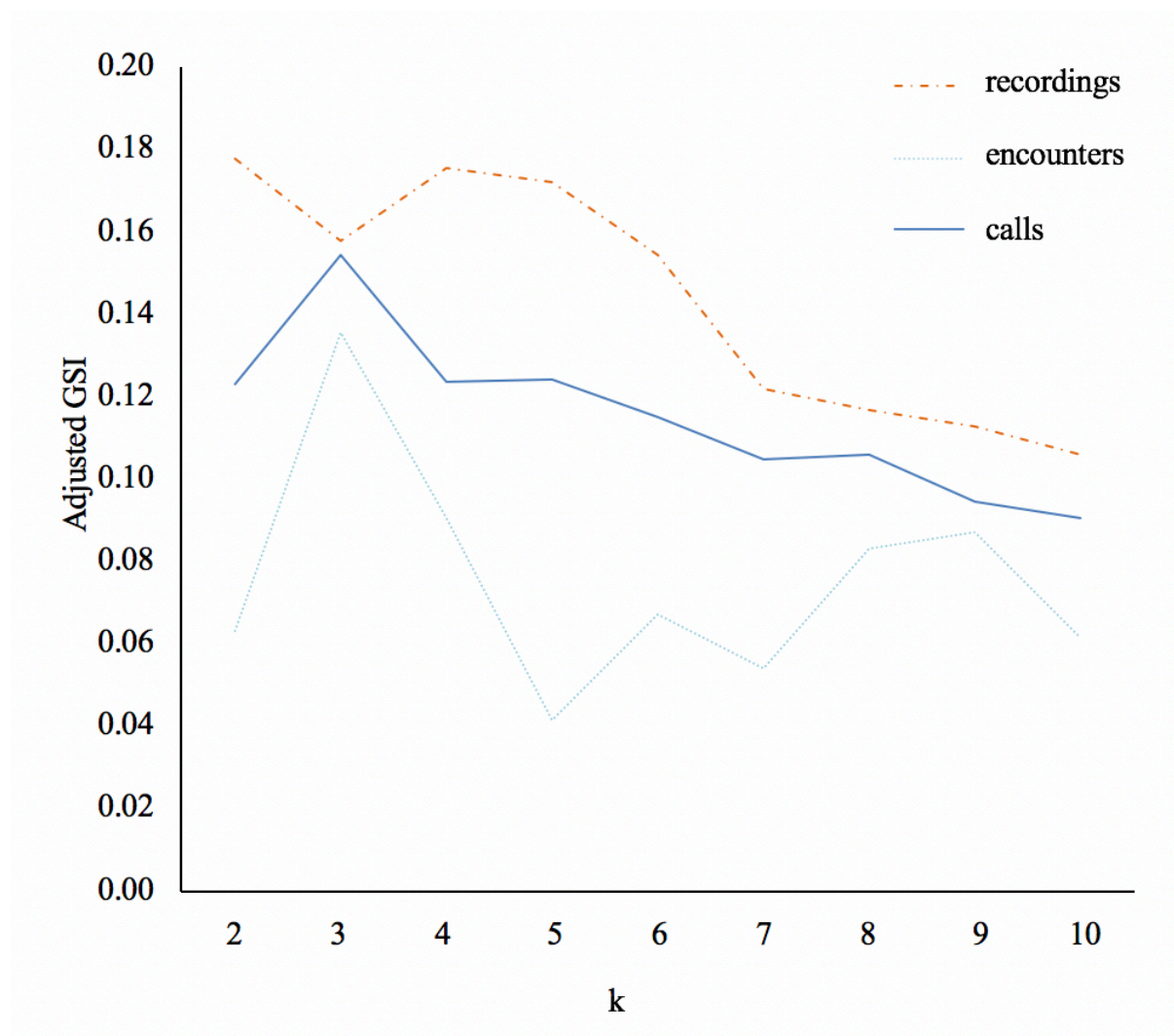
Appendix 3.2

An idiosyncratic call contour for coastal common bottlenose dolphin (*Tursiops truncatus*) recorded on two separate occasions: A) on 04/02/14, and B) on 24/07/15.



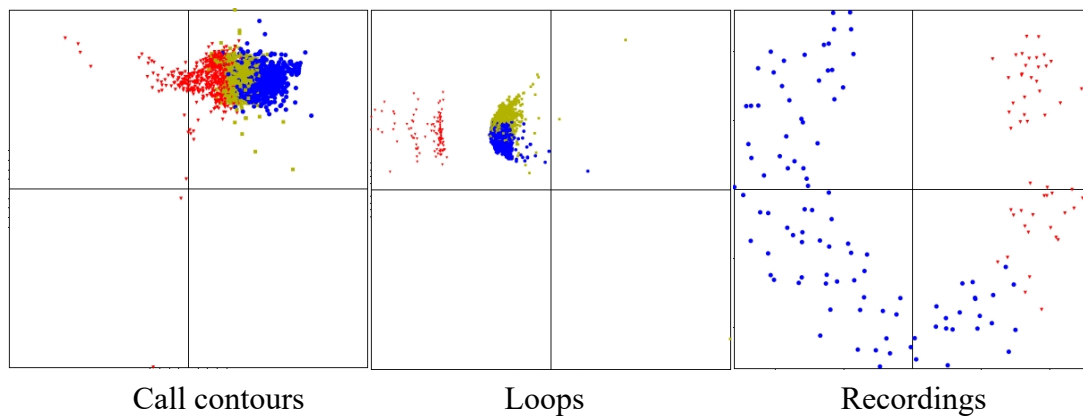
Appendix 3.3

Global Silhouette Index values of clustering options constructed through a k-medoids clustering algorithm applied to repertoires of coastal and oceanic common bottlenose dolphins (*Tursiops truncatus*) observed from September 2013 – September 2015, in Far North waters, New Zealand. A Global Silhouette Index value > 0 indicated data were clustered more than expected by chance, the higher the value the greater the clustering tendency. Higher Global Silhouette Index values tend to be produced with smaller values of k , therefore the Global Silhouette Index was corrected by comparing its output with simulated datasets (Lifjeld et al., 2016). The peak with k corresponds to the natural division of recordings.

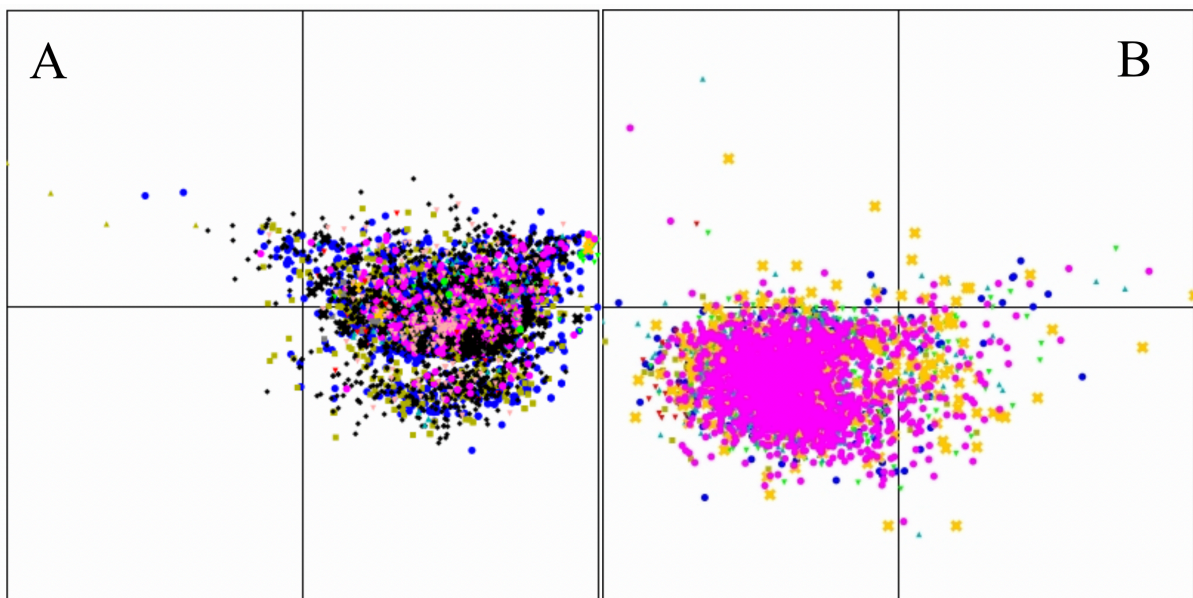


Appendix 3.4

Nonmetric multidimensional scaling clustering comparisons for coastal and oceanic common bottlenose dolphins (*Tursiops truncatus*) from September 2013 – September 2015, in Far North waters, New Zealand. Each point represents a whistle. Points that are close to one another in their graph have similar acoustic structures according to the dynamic time warping comparison. The stress of these Nonmetric multidimensional scaling ordinations ranged from 0.04 to 0.09. Scales were not meaningful for Nonmetric multidimensional scaling ordinations and were omitted. Spectrogram frequency units are 1 kHz; time units are 0.1 s.

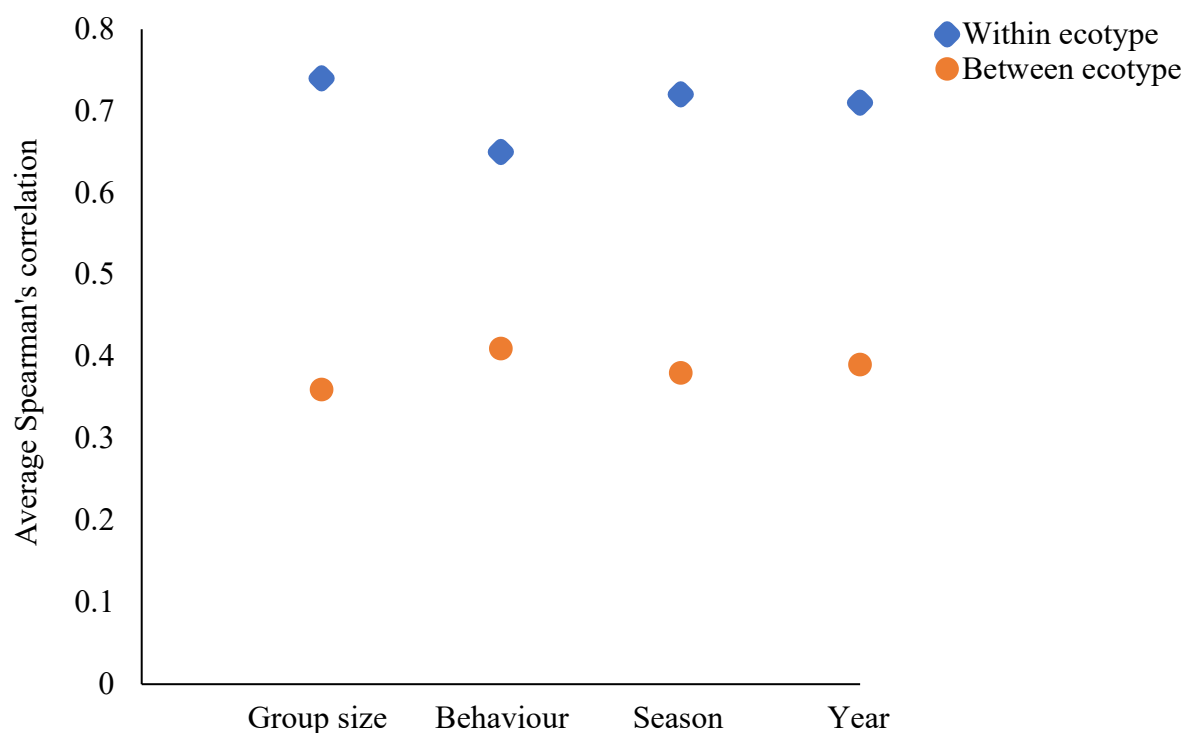


Syllable comparisons utilising nonmetric multidimensional scaling of call comparisons: (A) coastal common bottlenose dolphin and (B) oceanic common bottlenose dolphin.



Appendix 3.5

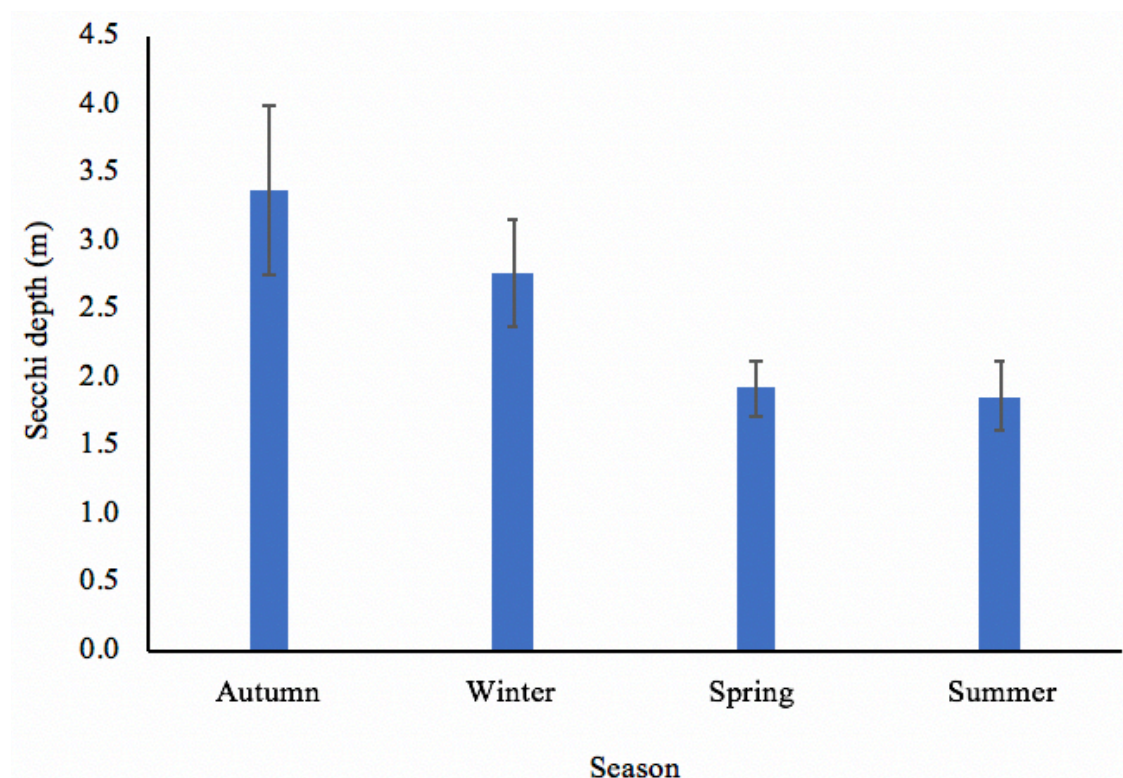
Average Spearman's correlations of call repertoire of common bottlenose dolphins (*Tursiops truncatus*) within the subclasses of each independent variable (group size, behaviour state, year, and season) from September 2013 – September 2015, in Far North waters, New Zealand.



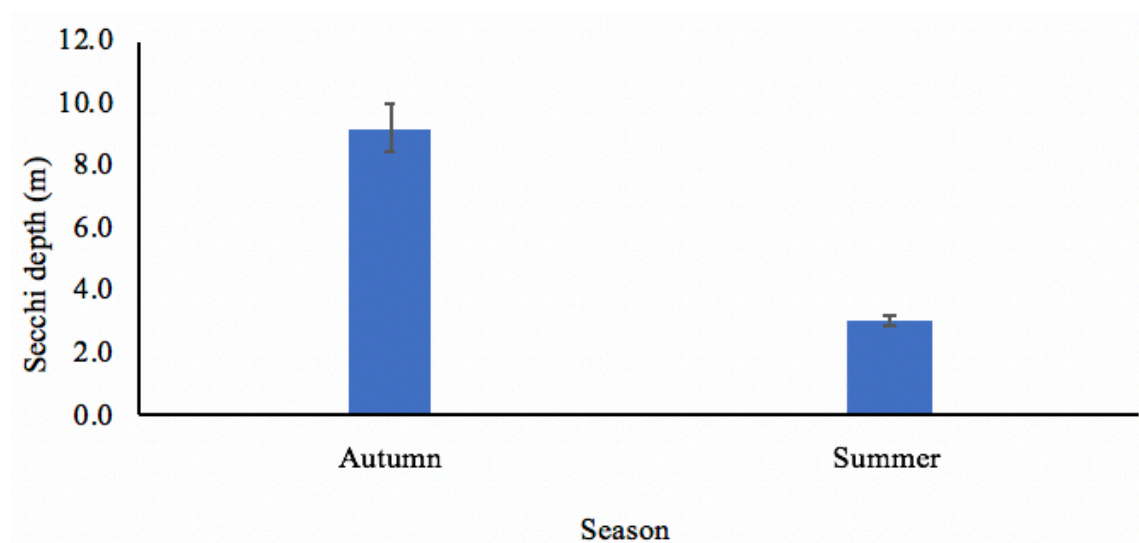
Appendix 4.1

Water visibility (measured in m using a Secchi disk) against season from September 2013 – September 2015, in Far North waters, New Zealand. SD = standard deviation around the mean.

In coastal common bottlenose dolphin (*Tursiops truncatus*)

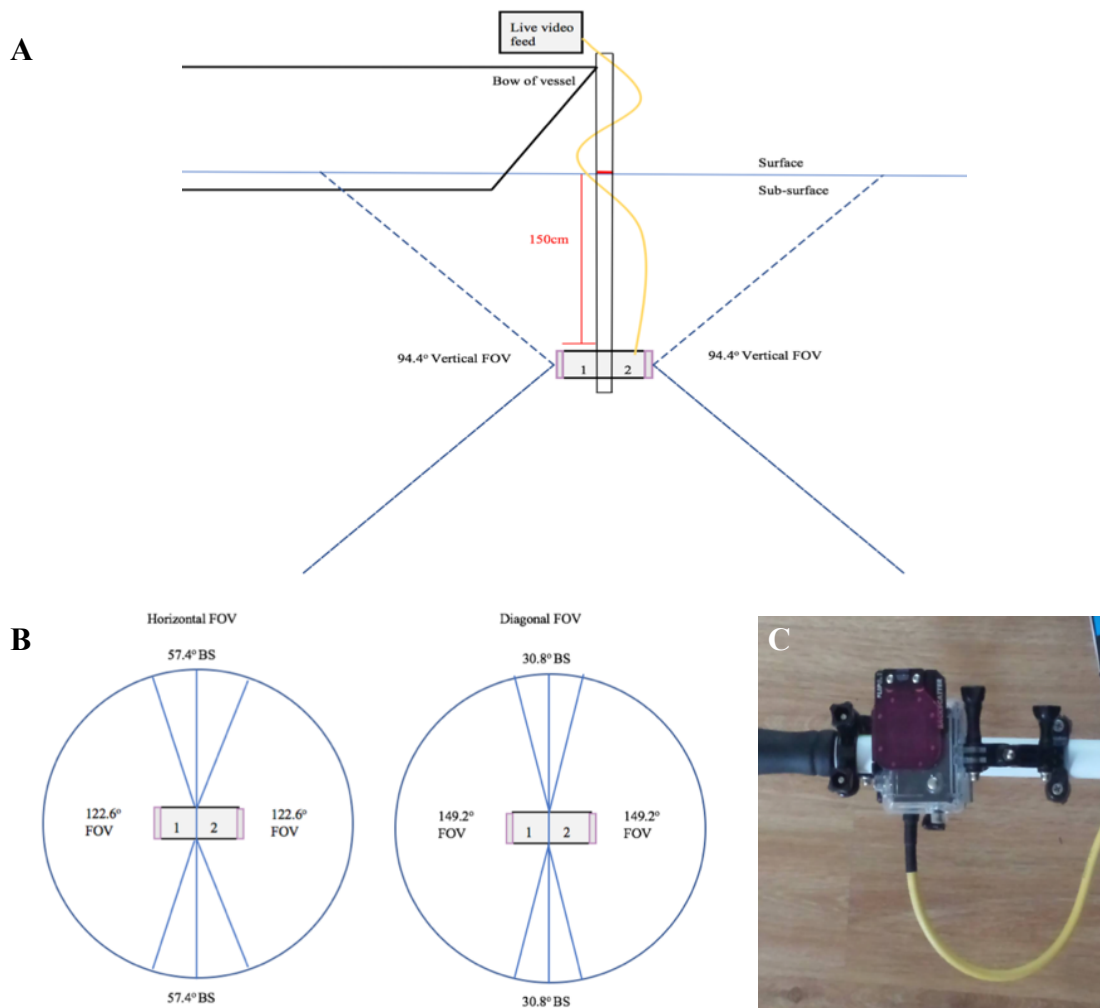


In oceanic common bottlenose dolphin (*Tursiops truncatus*)



Appendix 4.2

Custom-built video recording rig utilised to record the tactile behaviour of common bottlenose dolphins (*Tursiops truncatus*) from September 2013 – September 2015, in Far North waters, New Zealand. A) diagram of rig placement and set-up when recording, B) diagram of horizontal and lateral field of view of cameras, and C) photo of one of the cameras used. Note: BS – blind spot.

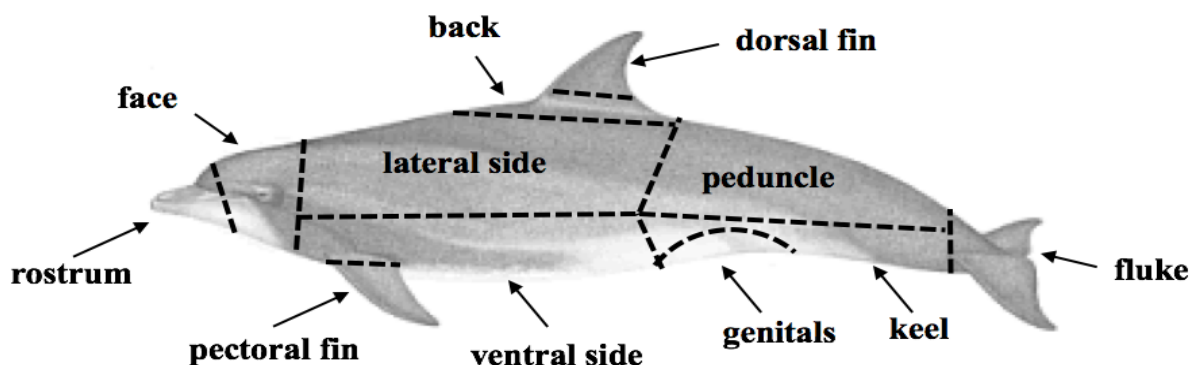


Appendix 4.3

Most common posture/contact behaviours during socialising, foraging, and mother-calf events of mixed species groupings of oceanic common bottlenose dolphins (*Tursiops truncatus*) and pilot whales (*Globicephala* sp.) recorded from September 2013 – September 2015, in Far North waters, New Zealand. A) *follow*, B) *chase*, C) *object play* (seaweed), D) *play/spy hop*, E) *contact*, F) *petting/rubbing position* (pec to lateral side), G) *petting position* (fluke to back), H) *foraging*, and I) *Echelon position* and *Infant position*. Pictures extracted from subsurface videos. Photo credit: C. Peters, T. Guerin, A. Hugill.



Eleven body part categories were used to quantify potential contact of oceanic common bottlenose dolphin and pilot whale recorded from September 2013 – September 2015, in Far North waters, New Zealand (following Dudzinski et al., 2009).



Appendix 4.4

Underwater dynamic ethogram of coastal and oceanic common bottlenose dolphins (*Tursiops truncatus*) and pilot whales (*Globicephala* sp.). Ethogram is adapted from Cusick & Herzing (2014), Dudzinski et al. (2010, 2012), and Herzing (2000).

Behaviour	Behaviour event	Description
Visual	Overall	Actions that are visually displayed, no contact is made
	Open mouth	Individual opens mouth towards another individual
	Jaw snap	Individual opens and shuts jaw rapidly
	Body jerks	Individual moves head or body in erratic motion
	Postural displays	Individual arches/contorts body in the water column stationary
Posture (single dolphin)	Overall	Positioning of one dolphin that is related or used during interaction
	Horizontal	Ventral side parallel to the sea floor
	Left-down	Right pectoral fin toward water surface and left toward sea floor
	Right-down	Left pectoral fin toward water surface and right toward sea floor
	Upside down	Individual is horizontal with ventral side toward water surface and the dorsal side toward the sea floor
	Head down	Individual in a vertical position in the water column with its head toward the sea floor
	Head up	Individual in a vertical position in the water column with its head toward water surface
	Head and fluke down	Head & flukes pointing down with respect to the body
	Head and fluke up	Head & fluke pointing up with respect to the body
	Humping surface	Snagging at surface: moving dorsal area in & out of the water
	Rest	Dolphins stationary at surface in horizontal position
	Sink	Slowly moving deeper in water column, any position
	Sink down	Vertical orientation moving deeper in water column
	Somersault	Forward flip underwater
	Spy hop	Moving head up and out of water to pecs then retracing under the water
	Sub-surface hanging float	Individual in any position, but vertical, in water column
	Suspended swim	Individual underwater in vertical position; suspended
	Flexing/S-shape	Individual positioned with its torso flexed and head up
Posture (multiple dolphins)	Overall	Positioning of one or two+ individual/s that are related or used during interaction ^[1] _{SEP}
	Abreast	Individuals in same orientation & side by side (within 2 body widths)
	Ahead	Ahead of another individual, in the same plane but to the left or right of the other's rostrum ^[1] _{SEP}
	Body contact	One individual's body contacts another's body slightly

Behaviour	Behaviour event	Description
		diagonally ^{[L][SEP]}
	Behind	One individual behind another, in the same plane ^{[L][SEP]}
	Between	One individual between 2 others ^{[L][SEP]}
	Contact	Body to body contact (individual positions identified)
	Contact position	Pectoral fin of one individual placed on lateral of another
	Meandering	Individuals in oriented parallel: repeated direction change and slow movement ^{[L][SEP]}
	Milling	Individuals in a group, changing orientation with respect to others, slow movement ^{[L][SEP]}
	Next to	Individuals within 1 body length of each other - any orientation parallel or perpendicular ^{[L][SEP]}
	Parallel	Individuals next to each other with the same body orientation
	Stopped position	Not actively moving ^{[L][SEP]}
	Perpendicular	One individual's body perpendicular to another individual
	Turn towards	One individual changes direction of travel in the water column with its new direction towards another individual
	Turn away	One individual changes direction of travel in the water column with its new direction away from another individual
Group change	Change composition	Change in the age class of group members ^{[L][SEP]}
	Change size	Change in the number of individuals in the group ^{[L][SEP]}
	Change species	Change in the species of group members ^{[L][SEP]}
Dynamic shift	Overall	Species/age class that was the initial receiver becomes the initiator and the species/age class that was the initial initiator becomes the receiver ^{[L][SEP]}
	Reaction	First aggressive behaviour in a sequence of two performed by the initial receiver towards the initial initiator. A second aggressive behaviour in sequence is scored as a dynamic shift
Tactile (body area)	Overall	Actions/behaviours that result in physical contact or touching between individuals ^{[L][SEP]}
	Tail contact	Individual/s swipe or make contact with another individual/s using tail
	Body, rostrum, pec contact	Individual/s make contact with another individual/s with body, rostrum or pectoral fin
	Head to head	Individual/s take(s) head-to-head position with another individual/s
	Melon to genital	One individual positioned with rostrum near genital region (including mammary slit). Not always implying milk transfer
Tactile (type)	Bite	One individual making contact with another individual with rostrum (mouth open)
	Rub	Active movement between one individual's pectoral fin and another individual's body

Appendices

Behaviour	Behaviour event	Description
Pursuit	Pet	Pectoral fin-to-pectoral fin contact, where active movement of at least one of the pectoral fins is observed
	Touch	Physical contact between the pectoral fin of one individual and another individual's body without active movement of either
	Overall	Actions that involve individuals following or moving after other individuals ^[1] _{SEP}
	Circle chase/dive	One individual circling another individual while swimming/diving
	Charge	Individual/s charging each other in head-to-head format, sometimes making contact
Sexual	Follow	Individual/s swimming alongside or behind another individual/s
	Overall	Behaviours that are related or used during sexual interaction ^[1] _{SEP}
	Erection	Penis is visible outside genital slit. No contact with other dolphins and no other behaviours occurring
	Side mount	Individual/s side mounts or rubs genitals against another individual/s

Appendix 4.5

Criteria for including videos in the analysis followed previously described methods of Cusick & Herzing (2014). Video recordings were only included in the analysis if the encounter length was ≥ 3 minutes (similar protocol: Melillo et al., 2009; Miles & Herzing, 2003).

Each video was deemed to contain a single encounter and correlated events. Behavioural coding and scoring utilised the software program Observer XT 13.0 formatted for Windows (Observer XT © 2018 Noldus Information Technology) and the behavioural ethogram in Appendix 4.4.

Video scoring was initiated when individuals were observed in the video field of view. Scoring terminated: 1) once the event ended and no further events were initiated for the remainder of the video recording, (2) when an individual left the field of view, or 3) when a recording stopped.

An encounter initiator was determined if at the start of a video: 1) one individual was in the field of view and was joined by a second individual and no event was occurring, or 2) multiple individuals were in the field of view and no event was occurring. If events were already occurring at the start of a video or the start was not observed (e.g., poor visibility or out of field of view) the initiator was not scored.

The outcome of an encounter was scored as observable or not observable. Observable was selected if an event ended and: 1) both individuals were in the field of view, or 2) one individual left the field of view. Not observable was selected if the event continued and both individuals left the field of view or the video recording stopped. Only complete sequences were scored. If all individuals were not in the field of view for > 5 s, scoring ceased until individuals re-entered the field of view (Altmann, 1974; Dawkins, 2007; Nowacek, 2002). If necessary, videos were viewed/scored numerous times at varying play-speeds (including frame-by-frame) to increase accuracy.

Appendix 4.6

Rater reliability

All included videos were scored by the primary observer (C. Peters). Rater reliability was ensured by randomly selecting 20 % of encounters ($n = 9$, using a random number generator in Microsoft Excel) to be scored by a secondary rater, T. Guerin (following Cusick & Herzing, 2014; Martin & Bateson, 2007; Meunier et al., 2012a & b). Reliability was calculated utilising Pearson's r correlation (r) and coefficient of determination (r^2), with correlation significance set at $r > 0.81$ ($\alpha = 0.05$) and $r^2 > 0.65$ (Gravetter & Wallnau, 2016).

Raters were consistent, with highly correlated observations. Key: Context is shown in blue.

Category	Variable	n	df	r	r ²
Oceanic	Receiver (total number of events)	9	4	1**	1
bottlenose	Initiator (total number of events)	9	4	1**	1
dolphin	Receiver (total number of encounters)	9	4	0.98**	1
	Dominant (total number of encounters)	-	-	1***	1***
Pilot whale	Receiver (total number of events)	9	4	0.99**	0.98
	Initiator (total number of events)	9	4	1**	1
	Receiver (total number of encounters)	9	4	1**	1
	Dominant (total number of encounters)	9	4	0.95*	0.97
Dynamic	Number Observed	9	4	1**	1
Shifts	Number in favour of oceanic common bottlenose dolphin	-	-	1***	1***
	Number in favour of pilot whale	9	4	1**	0.99
Reactions	Number Observed	9	4	1**	1
	Number by oceanic common bottlenose dolphin	9	4	1**	1
Group Size and Synchrony	Overall	9	4	0.99**	0.98
	Dynamic Shifts	9	4	0.99**	0.92
	Reactions	9	4	0.96**	0.97
	Changes in Group Size/Synchrony	9	4	0.99**	0.98

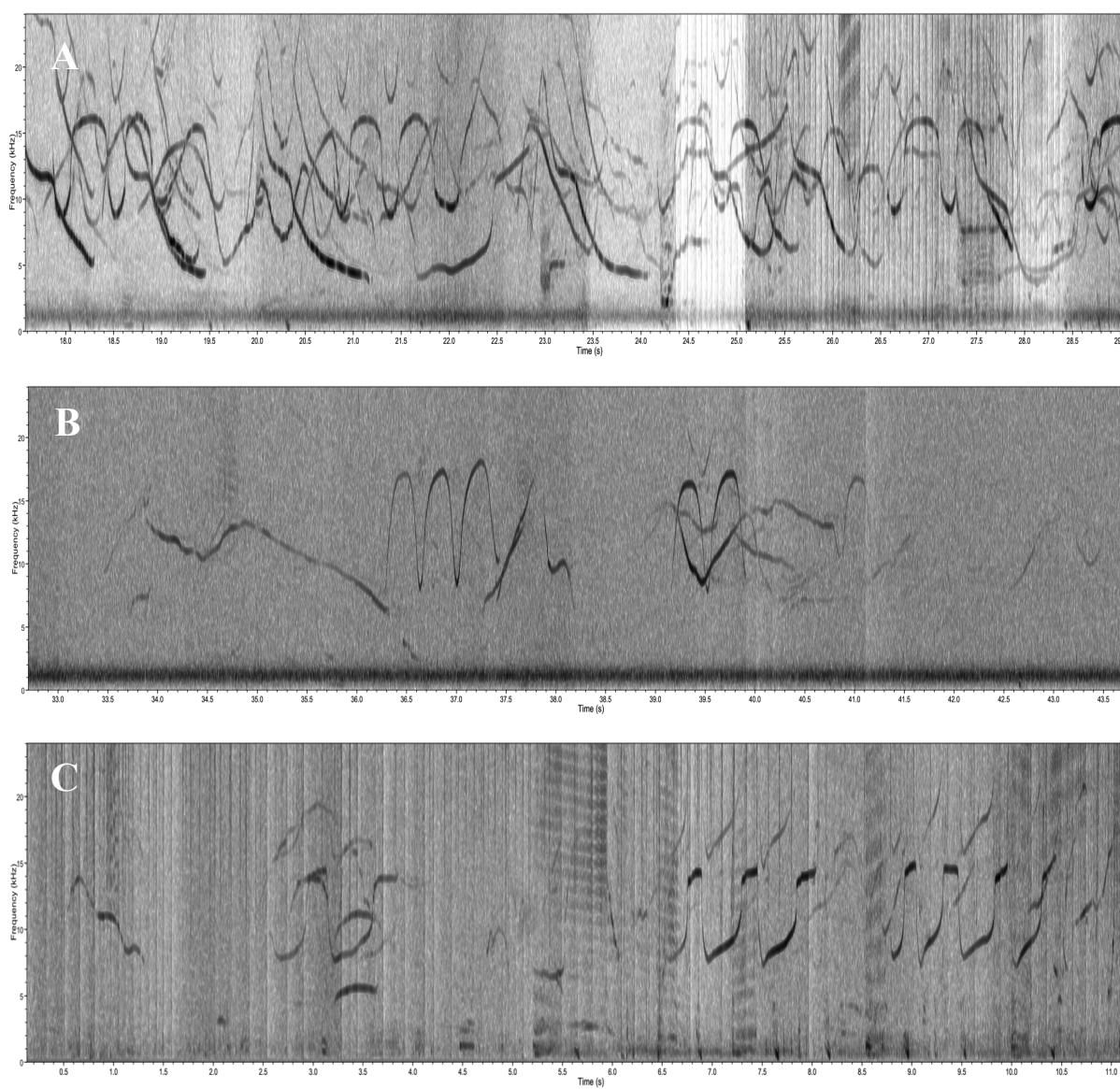
* significant at $P < 0.05$, two tails

** significant at $P < 0.01$, two tails

*** indicates correlation calculation not possible, but 100 % match

Appendix 4.7

Example spectrograms from vocalisations recorded from September 2013 – September 2015, in Far North waters, New Zealand, with A) and B) Mixed species group of oceanic common bottlenose dolphin (*Tursiops truncatus*) and pilot whales (*Globicephala* sp.), and C) oceanic common bottlenose dolphin only.



Appendix 4.8

Call parameters of oceanic common bottlenose dolphin only (*Tursiops truncatus*, oceanic common bottlenose dolphin only) and oceanic common bottlenose dolphin in mixed species groups with pilot whales, (*Globicephala* sp., oceanic common bottlenose dolphin mixed).

Call rate

As call rates (measured as number of calls per minute per dolphin) were not normally distributed, comparisons between group types were made using Kruskal–Wallis test. The rates of production of calls were compared for oceanic common bottlenose dolphin mixed subgroups and oceanic common bottlenose dolphin only to assess specific call use as a function of group type. The total rate of call production (per minute per dolphin) also varied between focal group types, being higher in oceanic common bottlenose dolphin mixed than oceanic common bottlenose dolphin only (0.31 oceanic common bottlenose dolphin mixed vs 0.52 oceanic common bottlenose dolphin only calls/minute/dolphin, $X^2 = 79.24$, $P < 0.0001$).

The total number of calls recorded

The total number of calls (measured as calls per minute), regardless of group size, was not significantly different as a result of group type (49.00 oceanic common bottlenose dolphin mixed vs 51.00 oceanic common bottlenose dolphin only calls/minute, $X^2 = 186.92$, $P = 0.081$). Within group type, the total number of calls, regardless of group size (measured as calls per minute), did not indicate a significant variation.

Further evidence of density dependence within groupings was provided by comparison of Pearson correlation coefficients. Significant positive correlations existed between group size and total call rate ($r = 0.239$, $P < 0.0001$ oceanic common bottlenose dolphin only; $r = 0.247$, $P < 0.0001$ oceanic common bottlenose dolphin mixed). Conversely, there was a significant negative correlation between group size and total call rate per dolphin for oceanic common bottlenose dolphin mixed ($r = -0.013$, $P < 0.0001$ oceanic common bottlenose dolphin). No significant correlations were found for oceanic common bottlenose dolphin only ($r = -0.005$, $P = 0.913$). Thus, it appears that as group size increased, overall vocalisation rate increased but individual dolphins tended to vocalise proportionally less for oceanic common bottlenose

dolphin mixed. Oceanic common bottlenose dolphin only group size (median = 18 individuals, range = 6 – 70, n = 86) was significantly smaller than oceanic common bottlenose dolphin mixed (median = 24 individuals range = 5 – 34, n = 104; Mann-Whitney test, $W = 392$, $P < 0.0001$). As all recordings were taken in only two areas (wider survey and Cavalli Islands) for oceanic common bottlenose dolphins, it was not possible to assess correlation between areas and call rate.

Results from cross-validated testing suggested up to 58.2 % of all calls may be assigned correctly to grouping (oceanic common bottlenose dolphin only, oceanic common bottlenose dolphin mixed), based solely on production rate during each recording. Most false classifications were the result of attributing recordings from oceanic common bottlenose dolphin only to oceanic common bottlenose dolphin mixed (46.4 %) (oceanic common bottlenose dolphin mixed to oceanic common bottlenose dolphin only (32.9 %)).

Cross-validated classification of individual oceanic common bottlenose dolphins call recordings to ecotype based solely on call rates recorded from September 2013 – September 2015, in Far North waters, New Zealand. The mean correct classification rate is 58.2 % (50.0 % expected by chance) for grouping.

Observed	Predicted	
	Oceanic common bottlenose dolphin only	Oceanic common bottlenose dolphin mixed
Oceanic common bottlenose dolphin only	53.6	46.4
Oceanic common bottlenose dolphin mixed	32.9	67.1

Appendix 4.9

Video effort

Simultaneous acoustic, surface behaviour state, and subsurface video data collection occurred. Sixty subsurface videos were recorded totalling 444.0 minutes. Video effort was not equal across all seasons, with no videos in winter or spring. Water clarity in the videos was significantly greater in autumn (mean = 9.21, standard deviation (SD) = 0.73, n = 38) than in summer (mean = 3.04, SD = 0.15, n = 22) ($X^2 = 3.71$; df = 1; $P = 0.001$, Appendix 4.1).

Two grouping types were considered: 1) oceanic common bottlenose dolphin only = oceanic common bottlenose dolphin only, (*Tursiops truncatus*), and 2) oceanic common bottlenose dolphin mixed = oceanic common bottlenose dolphin in mixed species groups with pilot whales (*Globicephala* sp.). The number of recordings made for each grouping type were found to be significantly different ($X^2 = 8.19$; df = 1; $P = 0.067$). This will be considered in all comparisons. Recordings were taken from all behavioural states.

Video recording effort of oceanic common bottlenose dolphins. Note: A = Adult, J = Juvenile, C = Calf and N = Neonate, CV = mean cross-validated (log) likelihood.

	Total videos	% of total	Total video length (s)	% of total video length	Mean length of recording	CV
A-J-C-N	20	33.3	8,921.0	33.5	382.0	0.7
A	24	40.0	9,176.2	34.5	304.1	0.8
A-J	16	26.7	8,542.8	32.1	402.7	0.9
Socialising	21	35.0	8,765.0	32.9	494.2	0.7
Travelling	18	30.0	7,229.6	27.1	495.0	0.9
Diving	6	10.0	3,851.9	14.5	237.8	0.8
Milling	6	10.0	3,437.5	12.9	493.7	1.3
Foraging	4	6.7	1,023.9	3.8	205.0	1.6
Resting	5	8.3	2,332.0	8.8	326.4	1.1
Total	60	-	26,640.0	-	304.9	-

The number of recordings made during all seven behavioural states was not equal between group types ($X^2 = 4.67$; df = 5; $P = 0.059$), though most recordings were made during socialising, travelling, and diving in all group types. Significant difference was also detected in the video length in each behavioural state ($X^2 = 60.21$; df = 5; $P = 0.923$, n = 60). However, the two most predominant behaviours (travelling and socialising) were comparable and not

significantly different ($X^2 = 34.09$; $df = 1$; $P = 0.014$, $n = 39$).

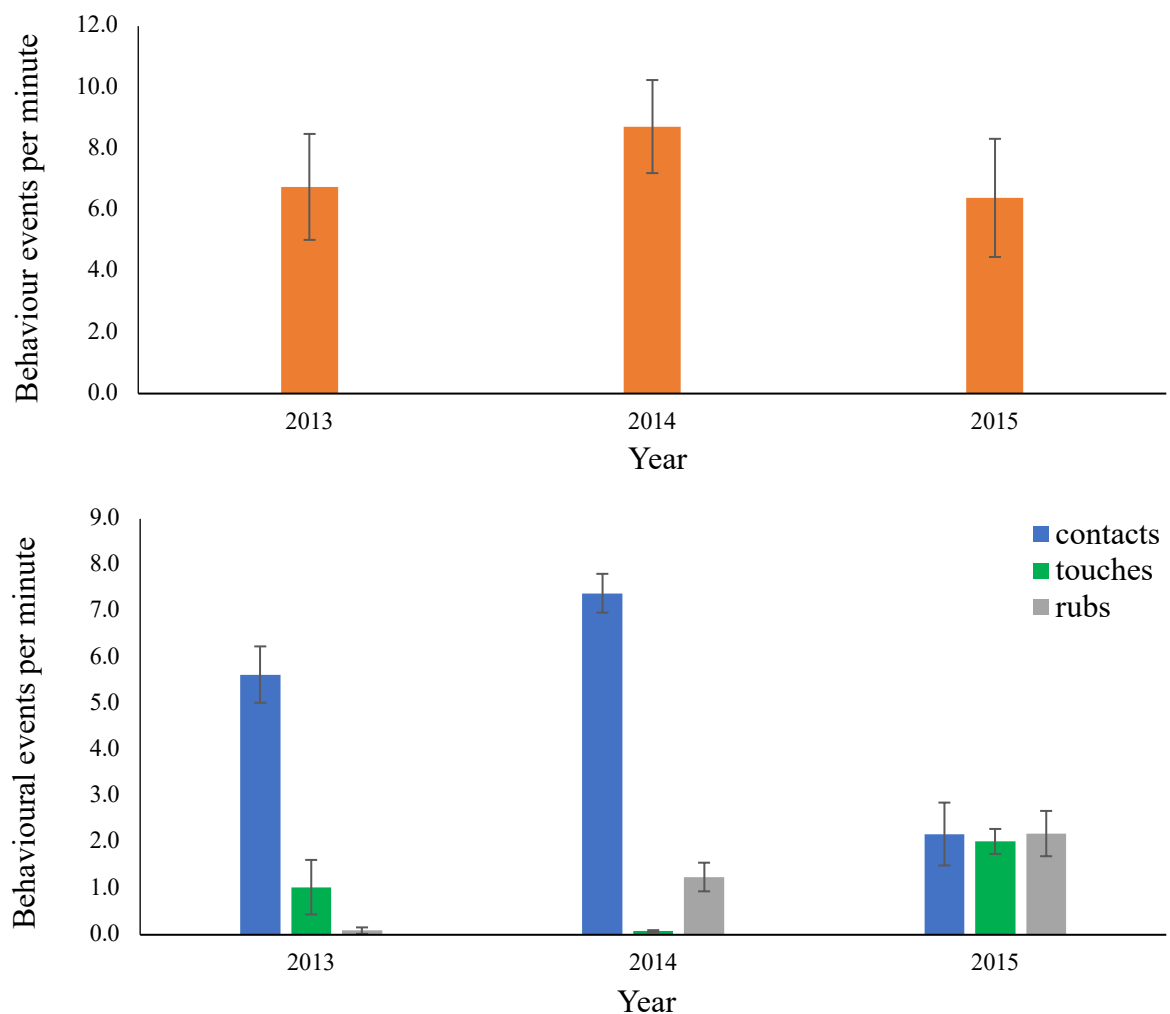
Number of recordings made in each comparison category for all behavioural states of oceanic common bottlenose dolphins (*Tursiops truncatus*) in different group scenarios.

Predominant surface behaviour	oceanic common bottlenose dolphin	%	oceanic common bottlenose dolphin only	%	oceanic common bottlenose dolphin mixed	%
Socialising	62	32.6	20	27.4	42	35.9
Travelling	40	21.1	13	17.8	27	23.1
Diving	35	18.4	19	26.0	16	13.7
Milling	19	10.0	8	11.0	11	9.4
Foraging	22	11.6	8	11.0	14	12.0
Resting	12	6.3	5	6.8	7	6.0
Total	190	-	73	-	117	-

Appendix 4.10

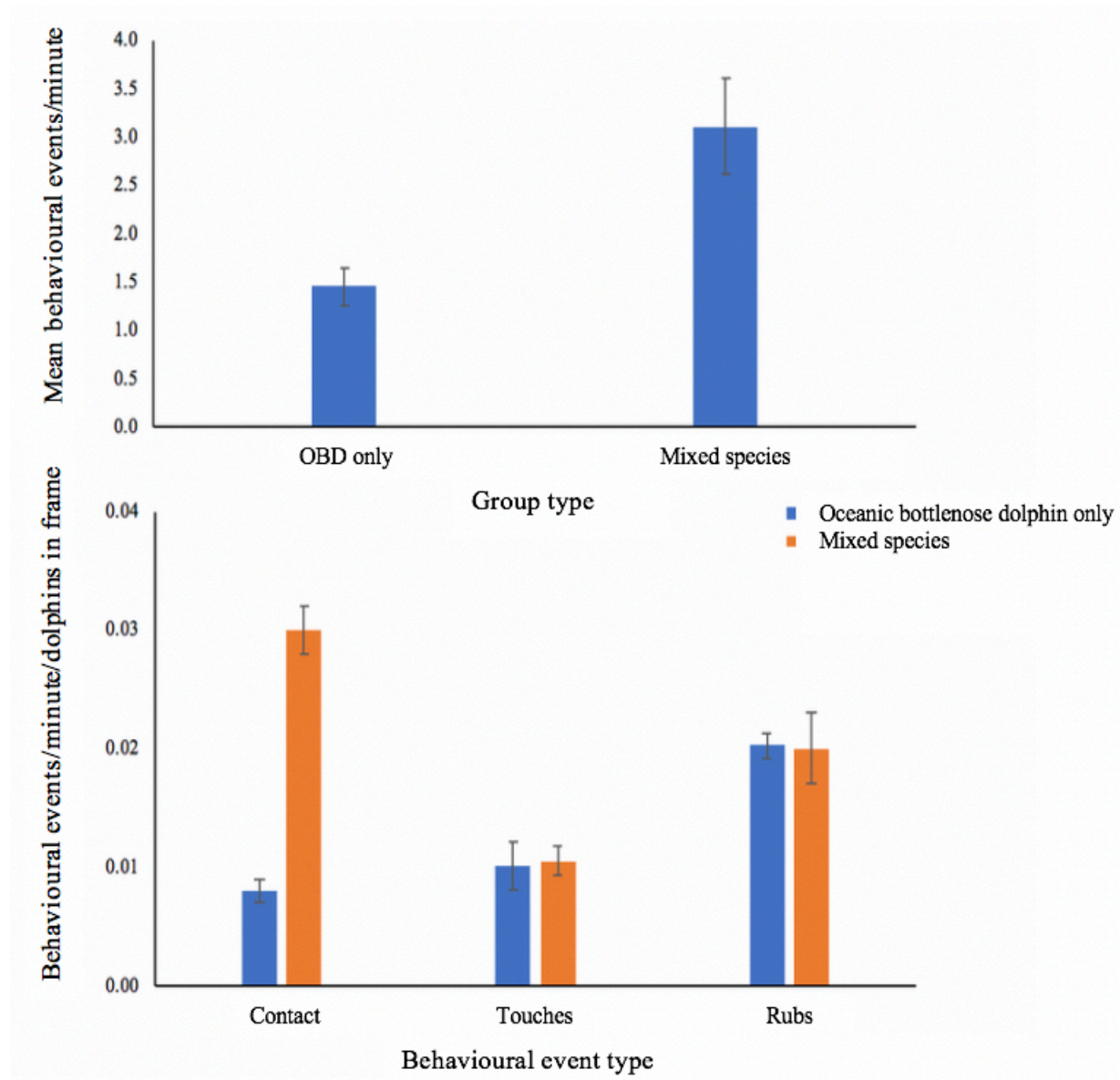
Contact frequency between single- and mixed-species groupings

Mean rates of contact types were compared for behaviour episodes for oceanic common bottlenose dolphins (in intra- and inter-specific groups) from September 2013 – September 2015, in Far North waters, New Zealand (following Dudzinski et al., 2009). The overall mean rate was 3.87 behavioural events/min, while for oceanic common bottlenose dolphin only (*Tursiops truncatus*) episodes the mean was lower, at 0.29 behavioural events/min. To establish if and how contact rate differed between oceanic common bottlenose dolphin only and oceanic common bottlenose dolphin in mixed species groups with pilot whales, (*Globicephala* sp., oceanic common bottlenose dolphin mixed), a t-test was applied to mean contact rates per minute by year/dolphin/group type. Mean contact rates/minute/year for (top) all subsurface interactions, and (bottom) contact type is presented.



Rub and touch rates did not indicate significant variation, however contacts were significantly different: contacts ($t = 0.455$, $P = 0.002$); rubs (including petting) ($t = 0.27$, $P = 0.8$); touches ($t = 1.94$, $P = 0.3$). This demonstrates that oceanic common bottlenose dolphins in intra- and inter-specific grouping used pectoral fin contact behaviour at comparable rates.

Mean interaction rates per minute per dolphins in frame across (top) group type and (bottom) group type and interaction type. All years were grouped for this assessment.



No significant differences in mean touches and rubs rate were identified between inter- and intra-specific groups. Trends were identified in contact rate. That is, oceanic common bottlenose dolphin in mixed groups (0.03 contact/min/individual) perform a higher level of touches than in oceanic common bottlenose dolphin only (0.008 contact/min/individual).

Appendix 4.11

Initiator vs receiver in oceanic common bottlenose dolphins (*Tursiops truncatus*) and pilot whales (*Globicephala* sp.) single and mixed species groups.

Methods were comparable to Dudzinski et al. (2009). For behavioural events, the individual that engaged in the event was significantly more often the initiator of the event episodes ($P < 0.001$, 76.12 % of 448 episodes). The initiator appeared to initiate contact at nearly identical rates for all groups with no significant difference identified in how often the engager was the initiator ($X_1^2 = 0.912$, $P = 0.842$). When oceanic common bottlenose dolphins initiated contact, that individual had an increased likelihood of performing contact behaviour like petting or rubbing ($X_1^2 = 3.82$, $P = 0.039$). On occasions when the initiated contact was petting or rubbing, the initiating rubber and rubbee, petting was as likely to occur as rubbing ($X_1^2 = 9.23$, $P = 0.011$). In these circumstances individuals were less likely to engage in contact behaviour ($X_1^2 = 2.57$, $P = 0.035$). Of the 589 events recorded, 392 were contact events. Two predominant contact interaction types could be ascribed the broad categorisations of mother-calf (19.13 %, $n = 75$) and aggression (59.4 %, $n = 233$).

For each group type, oceanic common bottlenose dolphin individuals were categorised into: adult, juvenile, and calf/neonate (see Appendix 2.2 for definitions; Dudzinski et al., 2009). Age categories indicated significant differences for both contactor and contactee roles when dolphins were either the initiator ($X_2^2 = 31.89$, $P < 0.0001$) or receiver ($X_2^2 = 23.71$, $P = 0.0054$). As initiator, juvenile and calf oceanic common bottlenose dolphins were the contactor more than adults, with calves as contactor more than juveniles. When interacting as receiver, juveniles assumed the role of contactor a comparable number of times to adults (50.8 % and 48.4 % respectively) and significantly more than calves (0.8 %). Juveniles, as a receiver, were contactees in instances more than double that of calves and nearly three times more than adults. All contact exchanged by oceanic common bottlenose dolphins is presented as a function of age category and role (in the initiator role as contactor or contactee and the receiver role as contactor or contactee. Key: grey background indicates significant pairings.

		Age category		
		Adult	Juvenile	Calf/Neonate
Initiator role	Contactor	27	59	63
	Contactee	31	41	2
Receiver role	Contactor	60	63	1
	Contactee	8	23	9

Appendix 4.12

Summary of means (and standard deviations, SD) for parametric parameters measured from oceanic common bottlenose dolphin (*Tursiops truncatus*) calls. Note, oceanic common bottlenose dolphin only = oceanic common bottlenose dolphin only and oceanic common bottlenose dolphin mixed = oceanic common bottlenose dolphin in mixed species groups with pilot whales (*Globicephala* sp.).

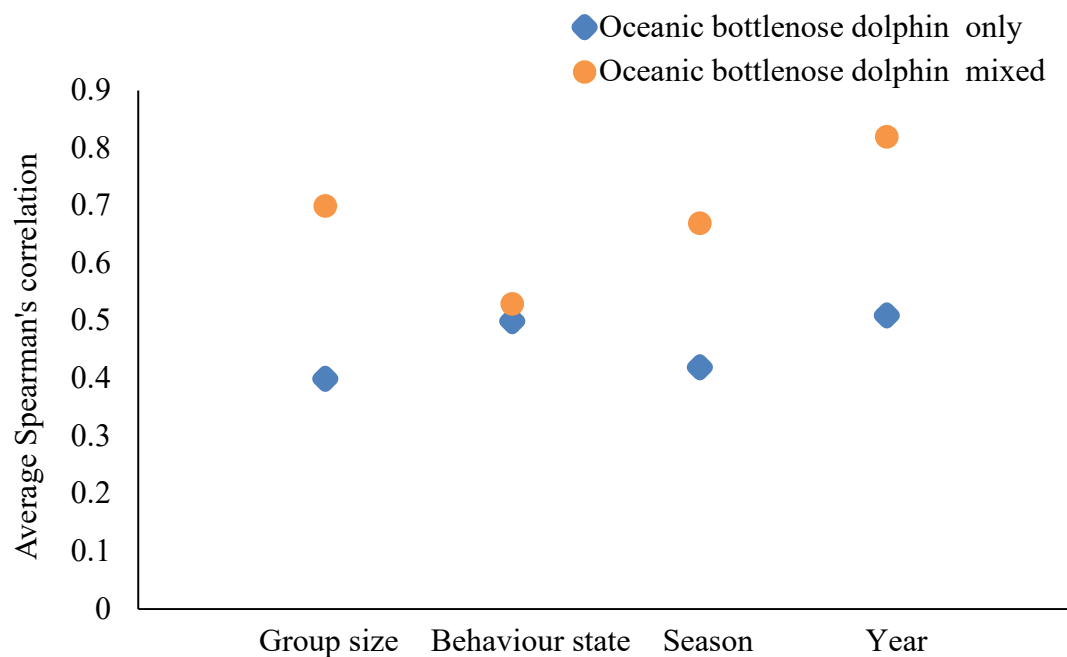
Parameter	oceanic common bottlenose dolphin only (n = 8,031)		oceanic common bottlenose dolphin mixed (n = 10,941)	
	Mean	SD	Mean	SD
Mean frequency (kHz)	11.02	2.97	11.37	3.06
Start frequency (kHz)	10.62	3.91	10.70	3.84
End frequency (kHz)	10.37	4.16	11.10	4.29
Minimum frequency (kHz)	8.08	2.79	8.48	3.00
Maximum frequency (kHz)	13.91	3.73	14.25	3.67
Frequency range (kHz)	9.02	3.02	10.57	2.84
Peak frequency (kHz)	11.02	2.97	11.37	3.06

Summary of one-way analysis of variance for frequency parameters measured from whistles recorded September 2013 – September 2015, in Far North waters, New Zealand. Group type (oceanic common bottlenose dolphin only or oceanic common bottlenose dolphin mixed) is included as a factor. Values in bold are significant at the 95 % level. * represents square root transformed data; ** represents the use of the Welch test in lieu of the *F* statistic if variances were not homogenous (i.e. for significant Levene tests).

Parameter		Levene Statistic	Levene <i>P</i>	Mean sum of squares	<i>F</i>	<i>P</i>
Mean frequency	Between Within	9.31	0.001	52.04 14.56	96.32**	< 0.0001**
Start frequency*	Between Within	2.09	0.927	0.08 0.97	10.71	0.053
End frequency*	Between Within	0.13	0.901	0.80 0.81	6.09	0.029
Minimum frequency	Between Within	4.72	0.292	0.19 3.93	57.63	0.035
Maximum frequency	Between Within	0.81	0.564	71.05 20.51	40.11	0.021
Frequency range	Between Within	0.07	0.993	109.23 16.37	38.19	0.020
Peak frequency	Between Within	12.85	0.001	58.33 11.92	67.35**	< 0.0001**

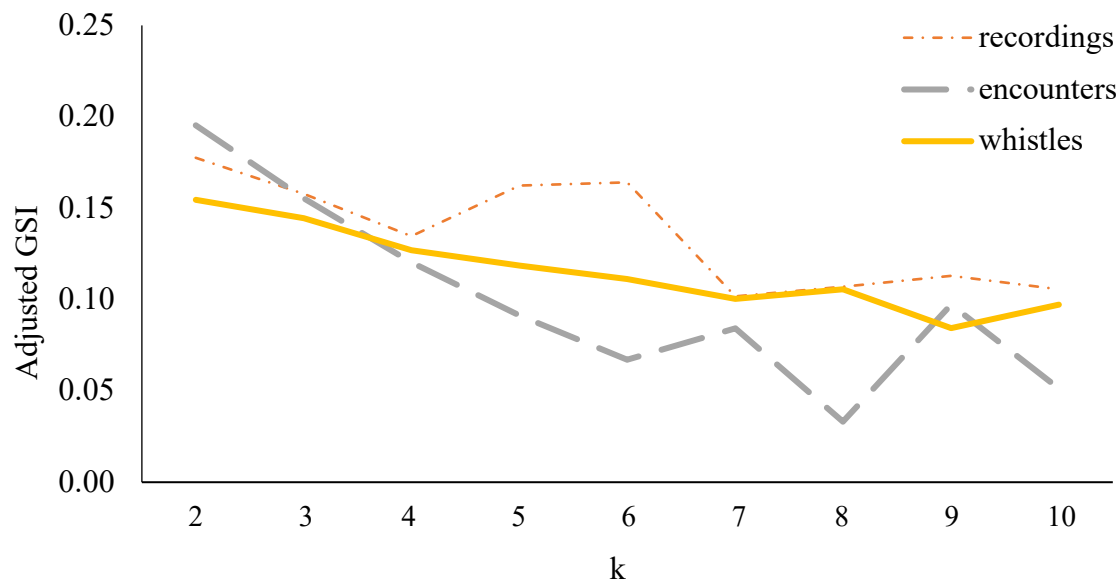
Appendix 4.13

Average Spearman's correlations of call repertoire of oceanic common bottlenose dolphin within the subclasses of each independent variable (group size, behaviour state, year, and season) observed from September 2013 – September 2015, in Far North waters, New Zealand. Note, oceanic common bottlenose dolphin only = oceanic common bottlenose dolphin only (*Tursiops truncatus*) and oceanic common bottlenose dolphin mixed = oceanic common bottlenose dolphin in mixed species groups with pilot whales (*Globicephala* sp.).



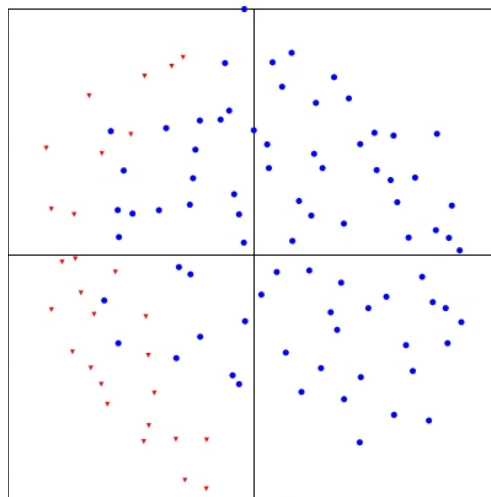
Appendix 4.14

Global Silhouette Index values for different clustering solutions produced by the k-medoid clustering algorithm applied to repertoires of coastal and oceanic common bottlenose dolphins (*Tursiops truncatus*) observed from September 2013 – September 2015, in Far North waters, New Zealand. The Global Silhouette Index has a value greater than 0 when data are clustered more than expected by chance. Higher values represent a greater clustering tendency. The Global Silhouette Index tends to produce higher values with smaller values of k, so the Global Silhouette Index was corrected by comparing its output with simulated datasets. The peak with k corresponds to the division of recordings.



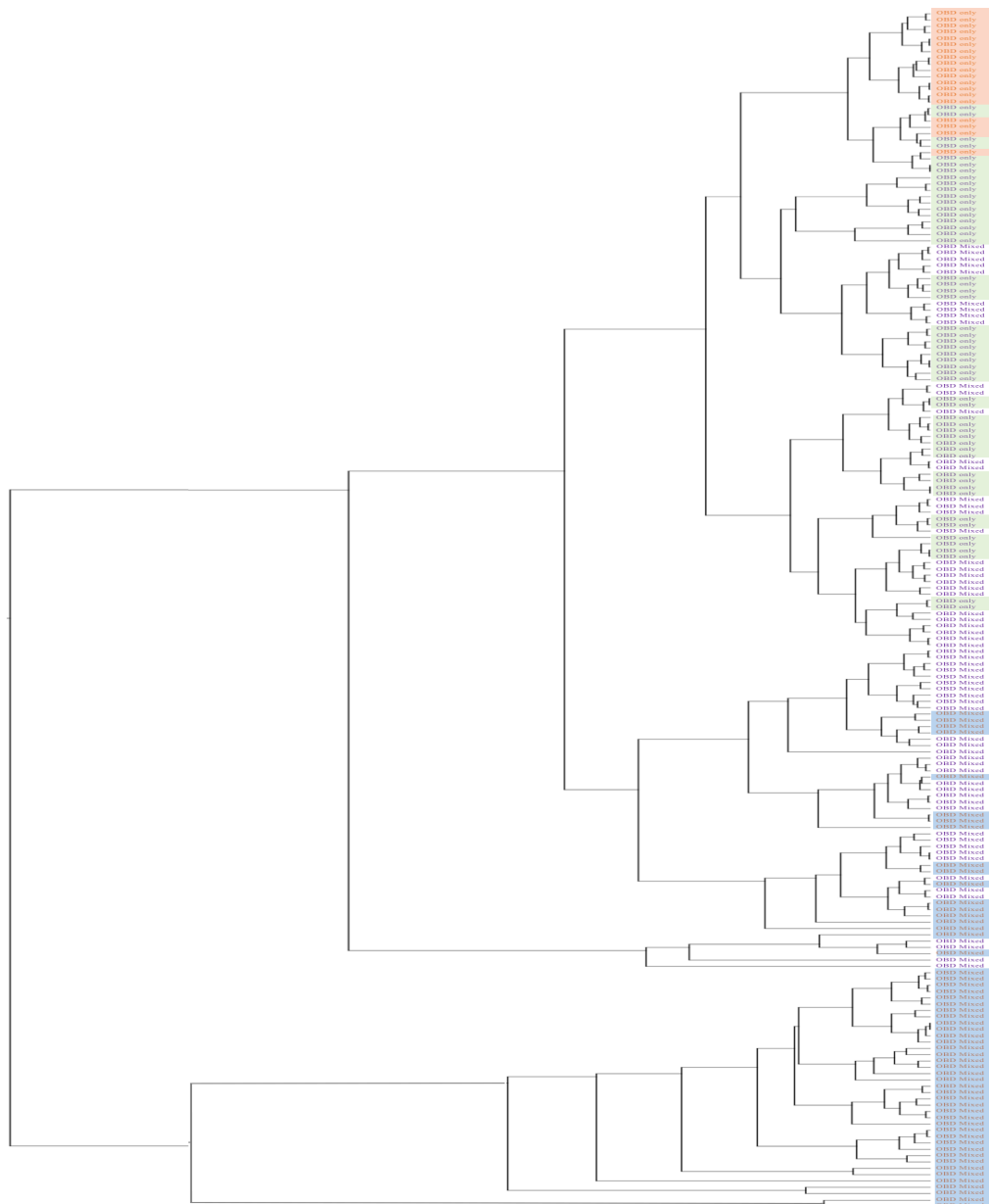
Appendix 4.15

Nonmetric multidimensional scaling of clustering comparisons for oceanic common bottlenose dolphin only (*Tursiops truncatus*) and oceanic common bottlenose dolphin in mixed species groups with pilot whales (*Globicephala* sp., oceanic common bottlenose dolphin mixed) observed from September 2013 – September 2015, in Far North waters, New Zealand. Each point represents a call. Points that are close to one another on their graph have similar acoustic structures according to the dynamic time warping comparison. The stress of these Nonmetric multidimensional scaling ordinations ranged from 0.04 to 0.09. Socialising is illustrated in blue and travelling in red. Scales were not meaningful for Nonmetric multidimensional scaling ordinations and were omitted. Spectrogram frequency units are 1 kHz; time units are 0.1 s.



Appendix 4.16

Dendrogram of encounter repertoires in different behavioural states and groupings. Recordings are from oceanic common bottlenose dolphin only (*Tursiops truncatus*) and oceanic common bottlenose dolphin in mixed species groups with pilot whales (*Globicephala* sp., oceanic common bottlenose dolphin mixed) from September 2013 – September 2015, in Far North waters, New Zealand. The dendrograms were calculated using the Unweighted Pair Group Method with Arithmetic Mean clustering algorithm from a dissimilarity matrix generated by a Dynamic Time Warp analysis. Key: orange letters/orange box = oceanic common bottlenose dolphin only socialising, orange letters/blue box = oceanic common bottlenose dolphin mixed socialising, purple letters/green box = oceanic common bottlenose dolphin only traveling, purple letters/no box = oceanic common bottlenose dolphin mixed traveling.



Appendix 4.17

Baseline models

Call rate and mean frequency were utilised as good proxies for vocal changes. First, negative binomial hidden Markov models were fitted with up to five states. This was a preliminary step to estimate the number of states that best represented the models before considering covariates. A summary of the model selection criteria for the five fits is provided below. Comparatively small values of the Akaike's Information Criterion and comparatively large values of the cross-validated (log) likelihood, respectively, indicate a better fit.

Model selection criteria for benchmark models for call rate and mean frequency (with no covariates) of oceanic common bottlenose dolphins (*Tursiops truncatus*) recorded from September 2013 – September 2015, in Far North waters, New Zealand. Note: NB = negative binomial, llk = maximum log likelihood, CV = mean cross-validated (log) likelihood. Grey highlight indicated best performing negative binomial model.

	NB Model	Akaike's Information Criterion	Likelihood	CV
Call rate	1 state	9,710.04	-4,833.782	-692.129
	2 states	7,931.27	-4,671.307	-532.017
	3 states	5,193.56	-4,328.294	-501.342
	4 states	5,005.72	-4,324.243	-500.662
	5 states	5,226.13	-4,298.331	-503.174
Mean frequency	1 state	7,831.35	-9,932.301	-892.012
	2 states	6,945.20	-9,877.472	-714.223
	3 states	6,017.42	-9,542.319	-702.192
	4 states	5,832.49	-9,583.273	-683.105
	5 states	5,280.31	-9,401.488	-669.751

The four-state model for call rate exhibited the lowest Akaike's Information Criterion and the highest mean cross-validated likelihood. Despite the model criteria pointing to the four-state model, the three-state model was selected for the following reasons. First, behavioural data model selection criteria often favour overly large numbers of states. In fact, there is a tendency in the biological literature to work with as few as two states without formal justification (Morales et al., 2004; Patterson et al., 2009; Schliehe-Diecks et al., 2012; Zucchini et al., 2008). Second, examining the Likelihood values, the greatest improvements in terms of the goodness of fit were obtained up to the three-state model. In the models with more than three states, the

likelihood further increased but at much smaller rates.

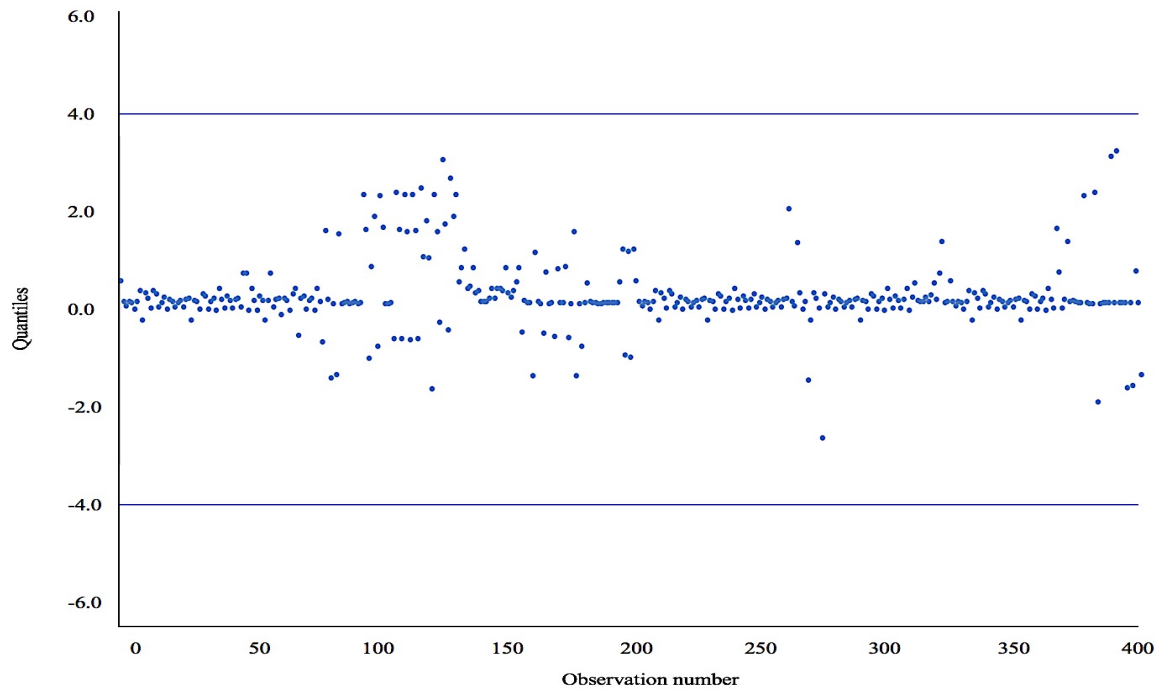
Finally, the relatively short lengths of the individual time series, including covariates in hidden Markov models with more than three states, rendered corresponding models very unstable numerically. It led to high variances in the parameter estimators due to the high complexity of the model relative to the number of observations available. While fitting a baseline model without covariates was still feasible, given the relatively small sample size, this was not the case with the more complex model formulations presented below. A three-state model therefore appeared to provide a realistic compromise between the formal assessment result of models and practicality.

The five-state model for mean call frequency had the lowest AIC and the highest mean cross-validated likelihood. As it largely outperformed all other methods, it was selected.

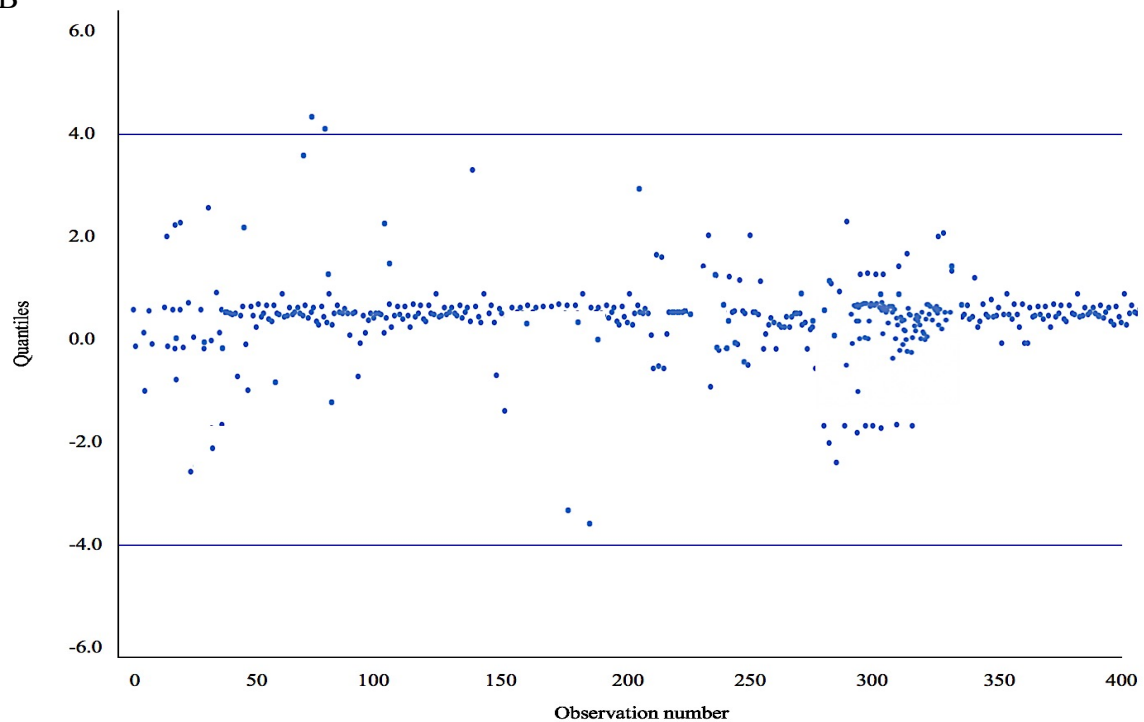
Appendix 4.18

Pseudo-residual segments in the dataset of oceanic common bottlenose dolphins (*Tursiops truncatus*) for A) call rate and B) mean frequency. The x-axis gives the observation number of the 1-min intervals. Here ∞ is set to 1 % and the solid lines give the 99.5 % and the 0.5 % quantiles of the standard normal distribution respectively. Intervals going to $-\infty$ have been truncated to 6 to facilitate plotting.

A



B



Appendix 4.19

Development of states for hidden Markov models for oceanic common bottlenose dolphins (*Tursiops truncatus*).

The mean negative binomial distributions within each hidden Markov model state for call rate and mean frequency, including *species ratio* as a covariate. Judging by the mean values, states 1 to 3 were labelled as low, medium, and high call rate, respectively. Two additional states were added for mean frequency, with states 1 to 5 labelled as very low, low, medium, high, and very high mean frequency, respectively.

		Mean
Call rate (3-state)	State 1	0.1042
	State 2	0.5201
	State 3	2.0343
Mean frequency (5-state)	State 1	08.3586
	State 2	11.0071
	State 3	12.0715
	State 4	17.1522
	State 5	21.0933

The mean negative binomial distributions within each hidden Markov model state for call rate, including *tactile/posture rate* as a covariate. Judging by the mean values, states 1 to 3 were labelled as low, medium, and high call rate, respectively.

Model	State	Mean
Call rate (3-state)	State 1	0.1013
	State 2	0.6701
	State 3	1.9992

Appendix 5.1

Examples of tactile positions of coastal common bottlenose dolphins (*Tursiops truncatus*) observed between adults (top) and adult and calf (bottom). Top left: *petting/rubbing position* (pec to lateral side), top right: *contact position* (pec to pec), bottom left: *Echelon position*, bottom right: *Infant position*. Pictures extracted from subsurface videos. Photo credit: T. Guerin (top), A. Hugill (bottom).



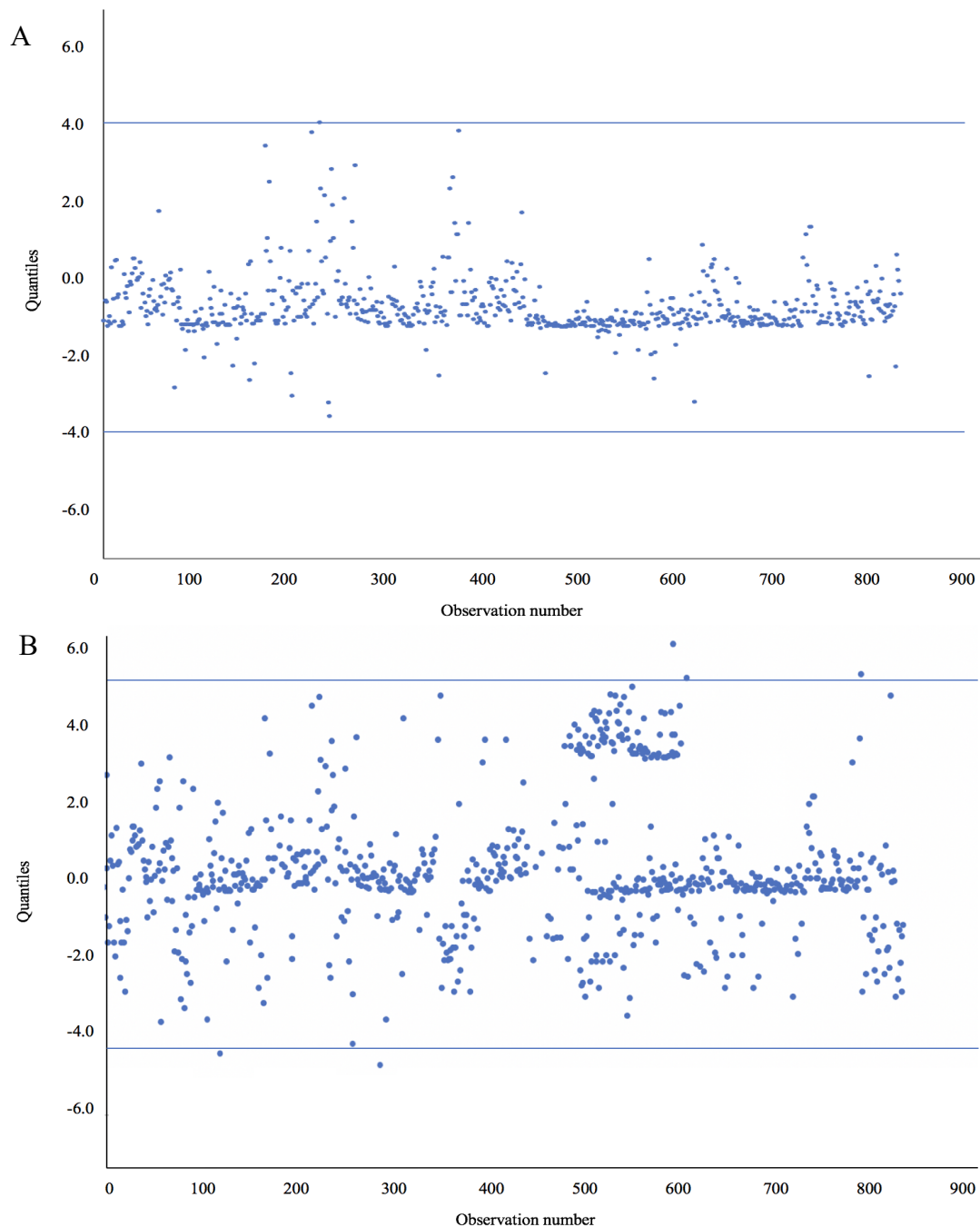
Appendix 5.2

Table 5.2: Number of video recordings made in each comparison category for surface observations of all behavioural states and age-classes of coastal common bottlenose dolphins (*T. truncatus*). Note, A = Adults, J = Juveniles, C = Calves, N = Neonates and CV = coefficient of variation of mean.

	Total videos	% of total	Total video length (s)	% of total video length	Mean length of recording	CV
A-J-C-N	21	36.8	2,728.2	35.3	152.9	0.3
A	19	33.3	2,297.4	29.8	107.9	0.8
A-J	17	29.8	2,696.0	34.9	198.6	1.0
Socialising	13	22.8	1,536.6	19.9	201.2	1.1
Travelling	12	21.1	1,390.6	18.0	195.9	0.9
Diving	11	19.3	1,105.2	14.3	123.5	0.8
Milling	08	14.0	1,427.5	18.5	201.4	1.0
Foraging	09	15.8	1,327.3	17.2	170.5	1.1
Resting	04	07.0	0,934.6	12.1	150.6	1.1
Total	57	-	7,721.7	-	167.0	-

Appendix 5.3

Pseudo-residual segments in the dataset of coastal common bottlenose dolphins (*Tursiops truncatus*) observed from September 2013 – September 2015, in Far North waters, New Zealand, for A) call rate and B) mean frequency. The x-axis gives the observation number of the 1-min intervals. Here ∞ is set to 1.0 % and the solid lines give the 99.5 %- and the 0.5 %-quantiles of the standard normal distribution. Intervals going to $-\infty$ have been truncated to 6.0 to facilitate plotting.



Appendix 5.4

Development of states for hidden Markov model for coastal common bottlenose dolphins (*Tursiops truncatus*). The mean negative binomial distributions within each hidden Markov model state for call rate and mean frequency, including *vessel number* as a covariate.

Judging by the mean values, states 1 to 3 were labelled as low, medium, and high call rate, respectively. One additional state was added for mean frequency, with states 1 to 4 labelled as low, medium, high, and very high mean frequency, respectively.

		Mean
Call rate (3-state)	State 1	0.103
	State 2	0.538
	State 3	1.845
Mean frequency (4-state)	State 1	07.445
	State 2	10.302
	State 3	12.069
	State 4	15.052

Appendix 7.1

The following publications have been produced during the PhD candidature:

- Reports

Peters, C. H. & Stockin K. A. (2016). Responses of common bottlenose dolphin (*Tursiops truncatus*) to vessel activity in Northland, New Zealand. *Final internal report to the Department of Conservation, Bay of Islands Conservancy, New Zealand*. 122pp.

Peer reviewed and freely available at:

<http://www.doc.govt.nz/Documents/conservation/marine-and-coastal/bottlenose-responses-dolphin-vessel-activity-northland.pdf>

Peters, C. H. & Stockin, K. A. (2014). Responses of common bottlenose dolphin (*Tursiops truncatus*) to vessel activity in Northland, New Zealand. *Internal progress report to the Department of Conservation, Bay of Islands Conservancy, New Zealand*. 39pp.

Peters, C. H. & Stockin, K. A. (2013). Responses of common bottlenose dolphin (*Tursiops truncatus*) to vessel activity in Northland, New Zealand. *Internal progress report to the Department of Conservation, Bay of Islands Conservancy, New Zealand*. 30pp.

- Conferences presentations and publications

Barlow, D., Hodge, K., Steel, D., Klinck, H., Baker, C. S., Chandler, T. E., Bott, N., Constantine, R., Double, M., Gill, P., Glasgow, D., Hamner, R., Lilley, C., Ogle, M., Olson, P., **Peters, C. H.**, Stockin, K. A., Torres, L. G. (2018). Documentation of a New Zealand blue whale population based on multiple lines of evidence. *Endangered Species Research*, 36: 27-40.

Dwyer, S., Stockin, K. A., Visser, I., Clement, D. & **Peters, C. H.** (2012). The importance of Great Barrier Island waters for *Nationally Endangered* New Zealand common bottlenose dolphin (*Tursiops truncatus*). Paper presented at the 4th joint AMSA-NZMSS conference, Hobart, Australia.

Peters, C. H., Guerin, T., Stockin, K.A. and Pawley, M.D.M. (2016). Density and Distribution of *nationally endangered* common bottlenose dolphin (*Tursiops truncatus*) in Far North Waters, New Zealand. Paper presented at the Institute of Natural & Mathematical Sciences Postgraduate Students Conference 2016, Albany, New Zealand.

Peters, C. H., Stockin, K.A., and Pawley, M.D.M. (2017). Acoustic divergence of common bottlenose dolphin (*Tursiops truncatus*) ecotypes in Far North waters, New Zealand. Paper presented at the Proceedings of the 22nd Biennial Conference for the Society of Marine Mammalogy 2017, Halifax, Canada.

Zaeschmar, J., Tezanos-Pinto, G., Dwyer, S.L., **Peters, C. H.**, Berghan, J., Donnelly, D., Meissner, A. M., Visser, I. N., Weir, J., Judkins, A., Brough, T., Guerra, M. and Stockin, K. A. (2017). First insights into the ecology of oceanic common bottlenose dolphin off north-eastern New Zealand. Paper presented at the Proceedings of the 22nd Biennial Conference for the Society of Marine Mammalogy 2017, Halifax, Canada.

Zaeschmar, J., Tezanos-Pinto, G., Dwyer, S. L., **Peters, C. H.**, Berghan, J., Donnelly, D., Meissner, A. M., Visser, I. N., Weir, J., Judkins, A., Brough, T., Guerra, M. and Stockin, K.A. (In Prep). First insights into the ecology of oceanic common bottlenose dolphin off north-eastern New Zealand.