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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