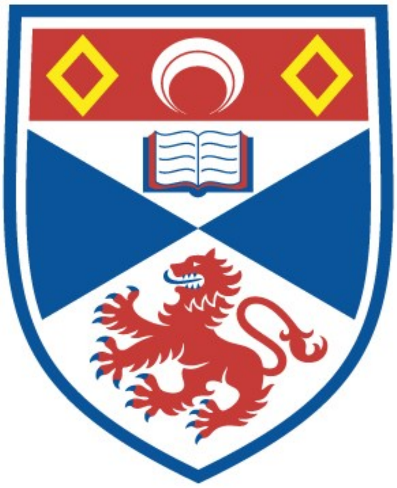

VOCAL BEHAVIOUR AND ABUNDANCE OF BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) IN ST ANDREWS BAY.

Nicola J. Quick

A thesis submitted in requirement for the degree of
Doctor of Philosophy,
School of Biology,
University of St Andrews.

July 2006

Declaration

I, Nicola Quick, hereby certify that this thesis, which is approximately 35,200 words in length, has been written by me, that it is a record of work carried out by me, and that it has not been submitted in any previous application for a higher degree.

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TABLE OF CONTENTS

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When the great innovation appears, it will almost certainly be in a muddled, incomplete, and confusing form…..for any speculation which does not at first glance look crazy, there is no hope. - *Freeman Dyson*

Bottlenose dolphin breaching in St Andrews Bay (Photo © Nicola Quick)

ABSTRACT

The aim of this thesis was twofold. Firstly I investigate the fine scale abundance of the population of wild bottlenose dolphins off north-east Scotland and secondly I provide further insights into the vocalisation capabilities of bottlenose dolphins with the use of acoustic localisation and behavioural observations.

Photo-identification undertaken during focal follows allowed sighting histories of individuals to be established. These histories were run through three abundance estimation techniques to establish the abundance of bottlenose dolphins in St Andrews bay. Results showed differences in estimation techniques, but all concluded that a large proportion of the bottlenose dolphin population found off north-east Scotland are present in the St Andrews bay area during the summer.

The development of a mobile two dimensional hydrophone array allowed accurate localisation of calls to positions around the research boat that could then be correlated with surface observations of dolphin groups. By localisation of stereotyped sequences of whistles, to identify caller position, I was able to show a context related use for these sequences as a precursor to subgroups joining. These sequences were unlikely to occur by chance and the whistles in these sequences were shown to have stereotypy matching that seen in signature whistles. Stereotypy of these whistles was further investigated through a computer based categorisation program where the percentage similarity of contours was investigated when assigning whistles to like categories. Finally, whistle rates were shown to significantly vary with activity type and increased whistle rates were observed during direction changing and socialising compared to surface travel. These increased rates suggest a communicative function related to behavioural activity, as group size was shown to not be a significant predictor of increased whistle rates.

CHAPTER ONE

GENERAL INTRODUCTION

Communication in marine mammals

Communication involves the provision of information by a sender to a receiver via some form of signal (Bradbury and Vehrencamp 1998). Sensory perception is vital in communication and terrestrial animals utilise senses of vision, hearing, touch, taste and smell in varying degrees. Humans for example rely most heavily on vision and hearing as the basis of our communicative ability is manifested through language. Alternatively, rodents (e.g. Prairie voles, Thomas and Kaczmarek 2002), insects (e.g. bumblebees, Stout and Goulson 2002) and other mammals (e.g. badgers, Hutchings *et al.* 2002) have been shown to frequently use olfactory abilities often in the form of scent-marking for a range of communicative functions. Throughout the natural world the diversity of ways in which organisms communicate is indeed varied and dependent on a spread of factors including social relationships, environmental pressures and genetics.

Observations of terrestrial animals have led to much information about life histories, population structure, associations and communicative abilities. For marine mammals, which are fully aquatic, direct field-based observations are more restricted by inaccessibility and mobility of study subjects. The study of recognisable individuals within cetacean populations has led to information regarding social affiliations, birthing intervals, and ranging patterns but many years of study are required to build up sample sizes and recognise patterns. Furthermore visual observations are limited in their power to determine which individuals within a group are involved in a behavioural or communicative event.

Fully aquatic organisms persist in a medium vastly different to terrestrial organisms. The propagation of underwater sound is approximately five times that of airborne sound (Tyack and Miller 2002), thus increasing the importance of audition compared to that of vision, which is reduced underwater. Acoustics plays an important role in communication between marine organisms in general and marine mammals specifically (Reynolds *et al.* 2000). Of the marine mammals that use acoustics for communication, odontocete cetaceans are well known. In particular the acoustic ability of the bottlenose dolphin (*Tursiops truncatus*) has provided the focus of many studies (For examples see Caldwell *et al.* 1990, Janik 1999, Reynolds *et al.* 2000).

The ability to study signal production in cetaceans has improved rapidly over the past few decades with the use of hydrophone arrays and complex recording systems. However, details on how cetaceans use acoustic signals in communicative events are still limited and more study is needed to try and understand their communication systems.

The bottlenose dolphin

Odontocete cetaceans are distributed throughout the world's oceans. The bottlenose dolphin (*Tursiops truncatus*) in particular is one of the most widespread odontocetes occurring in pelagic as well as coastal areas in both tropical and temperate waters (Leatherwood and Reeves 1983). Indeed the diversity of habitats and ranges in body size of bottlenose dolphin populations from around the world has led to suggestion that there are several species or subspecies of *Tursiops* (for review, see Hoelzel *et al.* 1998).

Studies of bottlenose dolphin populations have occurred throughout the species range; examples include The Bahamas (Parsons *et al.* 2003), South Africa (Saayman *et al.* 1973), Southern Argentina (Würsig and Würsig 1977), The Adriatic (Bearzi *et al.* 1997) and New Zealand, (Lusseau *et al.* 2003). However, three long-term studies in Sarasota, Florida (Wells 1991), Shark Bay, Western Australia (Smolker *et al.* 1992) and the Moray Firth, Scotland (Wilson 1995) yield the majority of information on this species.

Bottlenose dolphins have been shown to live in a fission-fusion grouping pattern (Wells 1991, Wells *et al.* 1980, Connor *et al.* 2000), where social groups frequently split into sub groups and then fuse again. These changes in composition vary in temporal scale and are likely to be strongly influenced by the pressures exerted by the distribution of resources and the risk of predation as has been suggested in other groups such as primates (Clutton-Brock and Harvey 1977). The variation in habitat of bottlenose dolphin populations suggests that intraspecific variation in social structure in response to these environmental pressures is likely to exist. Baird and Whitehead (2000) have shown differences in social organization of two sympatric groups of killer whales off Southern Vancouver Island and suggest this relates to differences in foraging ecology. Consequently, inferences drawn between populations of the same species that inhabit different ecological environments may be questionable. Strong male-male bonds or alliances are found in Shark Bay in Western Australia (Connor *et al.* 1992), Port Stephens in south-eastern Australia (Möller *et al.* 2001), the Bahamas (Parsons *et al.* 2003) and Sarasota (Wells 1991), but appear to be absent from the Moray Firth (Wilson 1995).

The aforementioned long term studies of bottlenose dolphins present three populations inhabiting very different environments and generalizations of bottlenose dolphin social structure and behaviour drawn from one study may not be applicable to the other two. Similarly the extrapolation of these studies to poorer studied populations may be misleading. Significant differences in vocal production rates between dolphins in three areas of North Carolina and the population in Sarasota (Jones and Sayigh 2002) as well as three groups along the Texas coast of the Gulf of Mexico (Ding *et al.* 1995) suggest that geographic location should not be overlooked as a source of variation within bottlenose dolphin vocal repertoires. A number of studies have focused on whistle production in the Sarasota bottlenose dolphin population (Cook *et al.* 2004, Sayigh *et al.* 1990, 1995, 1998, Watwood *et al.* 2005), due primarily to an extensive signature whistle catalogue obtained during temporary captures. In the Moray Firth a catalogue of this type does not exist and studies on the vocal repertoires of the population are limited to the work by Janik (2000a, b, c), leaving a good opportunity to build on previous studies and compare their vocal abilities with work on other *Tursiops* populations.

The population of bottlenose dolphins off north-east Scotland present an interesting population on a number of levels. They are the most northerly population of bottlenose dolphins in the world and as such experience different environmental pressures to bottlenose dolphin populations in lower latitudes. Genetic work suggests the population is genetically isolated (Parsons *et al.* 2002) and analysis of rates of discovery for adults and sub-adults do not suggest a pool of mobile individuals that move outside of the population (Wilson *et al.* 1999). These findings all point to the population being geographically isolated and definable. Previous studies have estimated abundance for this population, both for marked individuals (Durban *et al.* 2005) and also for the total population size, estimated at approximately 130 individuals (Wilson *et al.* 1999). Early studies suggested the population is resident in the Moray Firth, but a recent study shows a range expansion in the population, demonstrating that individuals range large distances around the coast (Wilson *et al.* 2004). Within the population, studies on the distribution of individuals and the social structure point to the potential existence of different social units that display differences in spatial distribution and ranging patterns (Lusseau *et al.* 2006, Wilson *et al.* 1997). The social structure of a group of dolphins will affect the communication between individuals and examining the nature of vocalisations both between individuals and within a population will aid in characterising the social structure and behaviour of that population.

Vocalisation capabilities of bottlenose dolphins

Bottlenose dolphins are able to produce a variety of different vocal signals that can be classified into three main types. The first are pulsed, broad-band sounds of short duration used in echolocation, (see Au 1993 for review) the second are less distinct pulsed sounds such as cries, grunts, brays and barks (see: Connor and Smolker 1996, Janik 2000a, Overstrom 1983 for examples) and the third are the tonal whistles which are frequency modulated narrow-band sounds (e.g. Caldwell and Caldwell 1965, Janik and Slater 1998, Sayigh *et al.* 1990, 1995).Whistles, especially signature whistles, have been the focus of many studies of dolphin sounds (Caldwell *et al.* 1990, Cook *et al.* 2004, Sayigh *et al.* 1990, 1995, 1998, Watwood *et al.* 2005), but studies of other vocalisation types have also presented interesting results.

Non whistle vocalisations

A number of studies have looked at non whistle vocalisations in bottlenose dolphins both in captivity (Overstrom 1983, Xitco and Roitblat 1996) and in the wild (Connor and Smolker 1996, Janik 2000a, Schultz *et al.* 1995). These studies have demonstrated the use of these non-whistle vocalisations in association with aggressive behaviour (Connor and Smolker 1996, Overstrom 1983), feeding events (Janik 2000a), social interactions (Schultz *et al.* 1995) and for deriving characteristics of objects (Xitco and Roitblat 1996). However, non-whistle vocalisations remain a large area for future study, with much still to be learnt about context specific use of this group of vocalisations. This thesis focuses on whistle vocalisations because of their use in communication.

Whistle vocalisations

The hypothesis that bottlenose dolphins have distinctive individualized signature whistles was first described by Caldwell and Caldwell in 1965. Their observations of a captive group of five animals led them to suggest that each dolphin tended to produce whistles which were individually distinctive and stereotyped in certain acoustic features. In fact this distinctive whistle occupied much more than 90% of the total whistle vocabulary of any one animal during the three weeks following capture (Caldwell and Caldwell 1965). The tendency of each animal to emit the same basic whistle contour in a variety of circumstances, led to a hypothesis that the individually distinctive attributes of signature whistles function to broadcast the identity of the whistler (Caldwell and Caldwell 1965). However, it is also possible that the more variable acoustic features of the same whistles may communicate other information such as motivational state and serve other functions (Caldwell *et al.* 1990). Caldwell and Caldwell (1965) state that many of their study *Tursiops* never changed their basic whistle contour in any major way other than by repetition of the same whistle, termed loops, without a pause in time. They believed that the study of cetacean communication that deals with the transfer of information via a whistle must be concentrated primarily on the individualised signature whistle and its minor variants. Their 1968 paper looks at the existence of signature whistles in the common dolphin (*Delphinus delphis bairdi*). Recordings and observations were taken of four common dolphins, one male and three females, for the period from 2 days after capture to 34 days after capture. Five major types of whistle emissions were recorded, all stereotyped and each characteristic of the animal emitting it (Caldwell and Caldwell 1968), suggesting that this species also has a system of a primary signature whistle, characteristic of the individual.

To determine which animal is producing which whistles, isolation or novel contexts (e.g. capture) have often been used in studies of signature whistles (Caldwell and Caldwell 1965, Tyack 1986, Sayigh *et al.* 1990, Janik *et al.* 1994). In these studies a high proportion of the whistles are generally of the signature whistle type. However, Janik and Slater (1998) demonstrated that undisturbed, captive bottlenose dolphins primarily used signature whistles during voluntary separations and almost only used non-signature whistles when all in the same pool. This tendency of whistle use by the animals suggests that signature whistles may function as cohesion calls (Janik and Slater 1998) and explains the increased use of these whistles in the context of isolation where a social animal would need to convey its position to close associates.

Individual recognition in highly social animals living in a fission-fusion society will be important for the maintenance of social bonds and for cooperative behaviour. The existence of male alliances and super-alliances involving many animals exhibiting differences in alliance stability (Connor *et al.* 2001) will undoubtedly require recognition between individuals and between groups, through identification of an individual trait such as the signature whistle. Within male-male alliances, members have been shown to converge on similar whistle types as the alliance develops (Smolker and Pepper 1999, Watwood *et al.* 2004), highlighting how vocal learning shapes their repertoires.

A single captive dolphin showed the capability to recognise a frequency contour independent of the frequency band used (Ralston and Herman 1995), an ability possibly underlying the recognition of conspecifics whistles. The use of playback experiments has also shown that independent offspring respond more strongly to whistles of their own mothers (i.e. animals with which a strong social bond used to exist), than to the whistles of a familiar, similar-aged female in situations of temporary restraint (Sayigh *et al.* 1998).

Additionally, Janik *et al.* (2006) have shown bottlenose dolphins are able to extract identity information from signature whistle contours even after all voice cues have been removed. Similarly, in wild unrestrained bottlenose dolphins, individuals responded to the whistle of a conspecific by emission of the same whistle type (Janik 2000b). If certain whistles do function to broadcast the identity of the whistler as was proposed by Caldwell and Caldwell (1965), then matching whistles over long distances suggests recognition at an individual level and would suggest that animals are capable of addressing each other individually. In cetacean studies the definition of a group of animals can be very subjective and is often biased by what we as terrestrial mammals consider a close association. In the marine environment the acoustic channel provides animals with the ability to maintain contact over greater distances than would be possible on land. Dolphin whistles in certain depths and sea states have been shown to have an active space enabling contact of individuals over 20 km apart (Janik 2000c). This ability bestows a greater importance to the theory of individual recognition through signature whistles that would enable the maintenance of social bonds despite many kilometres of ocean between the two associates.

Studies of the functional significance of signature whistles by wild bottlenose dolphin infants and their mothers (Smolker *et al.* 1993) and male alliance members (Watwood *et al.* 2005) revealed increased signature whistle production during separation. Additionally, significant increases in signature whistle rates during socialising compared to travelling (Cook *et al.* 2004) suggests the need for contact calls to aid in group cohesion in times of increased activity. Infants were shown to whistle more frequently than their mothers during separations (Smolker *et al.* 1993), suggesting their whistles may convey information about identity, location and motivation to reunite. In Sarasota, calves remain closely associated with their mothers for an average of more than five years (Wells 1991), for Shark Bay the average is four years (Smolker *et al.* 1992) and for the Moray Firth (Wilson 1995) high associations have been shown up to eight years (Grellier *et al.* 2003). It appears that bottlenose dolphins do not have stereotyped signature whistles at birth, but produce them by 4-6 months of age (Caldwell and Caldwell 1990). Signature whistles have then been shown to remain stable for periods up to at least 12 years (Sayigh *et al.*

1990). This suggests the possibility of influence on the structure of the calf whistle through exposure to environmental sounds and the acoustic repertoire of other animals especially the mother. In the Sarasota population, most female calves have been shown to produce signature whistles highly distinct from their mothers, whereas male calves were more likely to produce similar whistles to their mothers (Sayigh *et al.* 1990, Sayigh *et al.* 1995). This sex-related difference in signature whistle production may be due to the social structure observed in inshore bottlenose dolphin populations. It is suggested that matrilineal related females often associate together so each female may need to enhance her individuality within the group by means of a distinctive whistle (Sayigh *et al.* 1995). A recent study also supports this sex based difference, with female calves seeming more likely to model their signature whistles on members of the community with whom they associate only rarely (Fripp *et al.* 2005). However, three of the calves in this study were of unknown gender, so further study into how the whistles of these calves develop is needed. For a species exhibiting parental care it is difficult to determine if vocal development arises from genetics or auditory experience (Tyack 1997), but in the case of bottlenose dolphin calves, whistle development certainly appears to be influenced by vocal learning.

As well as signature whistles, Caldwell *et al.* (1990) reported the existence of variant whistle types. These are non-stereotyped whistles that are not individually distinctive and a diverse array may be produced by any one dolphin (Tyack 1997). As a dolphin ages it is thought that the signature whistle remains stable, but there is an increase in the production of these highly variable or variant calls (Tyack 1997). Male dolphins are thought to produce a higher proportion of variant whistle types (Caldwell *et al.* 1990) and this has been suggested as a functional response to the broadening of their network of social relationships (Tyack 1997). This is supported by the convergence of whistle types during male-male alliances (Smolker and Pepper 1999, Watwood *et al.* 2004) where social bonds appear to shape the repertoire through vocal learning.

The presence of these variant whistle types has led a few researchers to question the signature whistle hypothesis. McCowan and Reiss (1995) studied ten captive adult dolphins, (both wild and captive born individuals), from three different social groups. They concluded that the animals not only produced many different whistle types but also shared several whistle types, including a predominant one, within and across social groups. They backed up these findings with a further study in 2001 where they claimed to have replicated the approach and methodologies of studies that had concluded the existence of signature whistles. Again they report on the use of a predominant and shared whistle type, in instances of isolation, rather than signature whistles, for 12 captive dolphins (both wild and captive born individuals), from three different captive social groups (McCowan and Reiss 2001). Their argument is that these shared whistle types contain 'signature information' i.e. subtle contour variations for each dolphin that conveys the individuality of the dolphin in a similar way to the contact calls used by other species such as monkeys. The differences in vocal learning capability between cetaceans and monkeys has been reviewed by Janik and Slater (1997) and suggests that generalizations about contact calls across taxa may be misleading, especially if these calls are influenced by vocal learning as whistles in dolphins appear to be. Additionally, McCowan and Reiss present data from only 12 animals to disprove the signature whistle hypothesis which has previously been suggested by a number of independent studies that combined number over 200 individual dolphins. Two additional problems with the methods used by McCowan and Reiss are firstly the assignment of whistles to individuals based on bubblestream production. Although they previously reported bubblestreams to be a random sample across the whistle repertoire (McCowan 1995), a recent study suggests that whistles associated with bubblestreams are not randomly associated with all whistle types (Fripp 2005), a finding which has caused some debate (McCowan 2006, Fripp 2006). Secondly, the contour extraction method used by McCowan (1995) only takes twenty points across the whistle for comparison. This method appears to discount any duration differences when comparing whistles and is likely to under represent the complexity of whistles. Additionally, the long term study in Sarasota, Florida has recordings of a large proportion of the population and data on known associations and social groups. It therefore should be evident if a whistle type was shared across these associations or social groups, which appears not to be the case, although this has not been directly looked for in these data.

Vocal learning

Contextual learning is learning that affects usage and comprehension of sounds and, in relation to vocal communication, is seen as relatively common among mammals (Janik and Slater 1997). Vocal learning, however, can be described as a rarer form of social learning in acoustic communication (Janik 1999) and refers to the instances where the vocalisations themselves are modified in form as a result of experience with those of other individuals (Janik and Slater 1997). The term culture, defined as group level information or behaviour transmitted by social learning (Rendell and Whitehead 2001), has been suggested in cetaceans but has provoked a wide debate (see open peer commentary in Rendell and Whitehead 2001). Evidence for culture in cetaceans is given through the existence of vocal clans in groups of killer whales (Yurk *et al.* 2002) and sperm whales (Rendell and Whitehead 2003), where it is suggested that distinct pods or units have unique, culturally transmitted vocal dialects. Similarly, in humpback whales cultural transmission of song has been suggested (Noad *et al.* 2000).

A review by Janik and Slater (1997) concludes that while many birds are capable of vocal learning, evidence for it in mammals is rare, with the most versatile mammalian vocal learners being cetaceans, harbour seals and humans. Hoover, a harbour seal at the New England aquarium was shown to imitate human speech, (Ralls *et al.* 1985), a process only possible through vocal learning. Similarly, the song of humpback whales off the Australian east coast was completely replaced in less then two years by the song of the Australian west coast population (Noad *et al.* 2000). This change, due to the introduction of a few foreign singers, shows a speed of replacement that implies vocal learning rather than evolution of song through genetic exchange or distributional changes. One of the first detailed studies of vocal learning in the bottlenose dolphin was shown by Richards *et al.* (1984). A single female dolphin was trained to mimic computer generated sounds that were not previously recorded in her baseline repertoire of whistles and also to give unique vocal labels to objects presented to her. A further study by Herman and Forestell (1985) showed bottlenose dolphins to be capable of referential reporting of the presence or absence of named objects and a review by Kako (1999) discusses the ability of bottlenose dolphins to understand syntax.

The ability of dolphins to mimic man-made or computer generated sounds was further explored by Reiss and McCowan (1993) and it appears that once a dolphin learns to mimic a novel sound it is able to produce this sound without hearing the model. For wild animals this ability to mimic sounds present in their environment is particularly important in terms of response to the signature whistle of close associates. Mimicry of signature whistles was shown by two captive *Tursiops* that not only produced their own individual stereotyped whistle, but were able to mimic each others (Tyack 1986). The development of signature whistles in young captive dolphins provides some of the most convincing evidence for vocal learning in *Tursiops*. Two calves at the Miami Seaquarium developed whistles similar to the whistle used by a trainer and a third developed a whistle similar to two sub-adults who had been raised together in a pool (Tyack and Sayigh 1997). A stranded 1-2 month old calf placed into a pool with an adult female modified her signature whistle to resemble the adult female by 6-7 months of age (Tyack and Sayigh 1997), and comparison of wild and captive dolphins matched for age and sex showed the captive dolphins to have whistles that were less frequency modulated and more like the trainer's whistles (Miksis *et al.* 2002). The proven vocal repertoire and existence of vocal learning in bottlenose dolphins presents many interesting questions for future research in this species.

Objectives of this thesis

The aim of this thesis is to provide further insights into the vocalisation capabilities of bottlenose dolphins in general and the fine scale abundance of the population of wild bottlenose dolphins off north-east Scotland. Each chapter in this thesis is presented in a stand-alone format with its own abstract, introduction, discussion and references. As such each can be read in isolation, but some reference to other chapters exists and repetition between chapters occurs primarily in the methodology. In the first data based chapter (Chapter 2) I outline the localisation system used during all data collection for this thesis. Field and laboratory based trials demonstrate how the system functions and assesses the errors involved in localising dolphin whistles in the wild. In Chapter 3, I investigate the fine scale abundance of the bottlenose dolphin population off north-east Scotland, using frequentist point estimation and Bayesian models. I compare different methodologies available for abundance estimation and discuss these with reference to what is known about this population. Chapter 4 investigates the problems associated with categorising whistle contours using an automated computer program. The system uses neural networks and dynamic time warping and its categorisation abilities are discussed with reference to dolphin whistles recorded during vocal exchange events. Chapter 5 presents an analysis of the context associated with stereotyped whistle exchanges. I determine if vocal exchanges of stereotyped whistles occur more often with a given context than would be expected by chance and how the stereotypy of these whistles is comparable to signature whistles. The final data chapter (Chapter 6) explores how whistle rates are influenced by behavioural context and different group sizes in wild dolphin groups and compares this with studies on other *Tursiops* populations. Finally, chapter 7 is a general discussion outlining the main conclusions from this study and focusing on areas of future research.

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CHAPTER TWO

A MOBILE ACOUSTIC LOCALISATION SYSTEM FOR THE STUDY OF WILD BOTTLENOSE DOLPHINS

ABSTRACT

This study tested the ability of the Matlab based TOADY localisation system to assign caller position to vocalising wild bottlenose dolphins (*Tursiops truncatus*). TOADY uses the method of cross-correlation of time of arrival differences using data from a mobile 4 element distributed array positioned around a small boat. Comparisons were made between location estimates from TOADY and known playback sources of dolphin whistles during a field test. TOADY estimates of direction from the boat showed no significant difference to actual direction ($W=74.5$, $p=0.427$, $n=32$) and estimates of source depth showed variation within 1 m of the actual depths (Mean 1.65, SD ± 0.94, $n = 32$). Additionally, a lab based test, eliminating environmental effects, gave perfect localisation. TOADY is a reliable system for estimating direction and depth of a caller and has now been successfully applied to studies of wild bottlenose dolphin vocalisations.

INTRODUCTION

The study of animal vocalisations and how they relate to observed behaviour is an important area in the study of communication systems. In the aquatic environment, the problem of determining caller identification can be difficult with the observer often unable to view the animals underwater. This is further complicated in the study of cetaceans where visible signs of sound production are generally absent. Some studies of small delphinids have used the visual cue of bubblestreams or synchronised blowhole movement to assign vocalisation events, namely frequency modulated whistles, to individuals (e.g. Herzing 1996, McCowan and Reiss 1995, 2001, Miksis *et al.* 2002). However, recent evidence for bottlenose dolphins suggests bubblestreams are not representative of an animal's repertoire with only a small percentage of whistles being associated with bubblestreams and bubblestreams not being associated with all whistle types (Fripp 2005). This visual technique is further restricted to researchers studying captive animals or animals in favourable environments where water clarity allows observers to view animals through the water column. In air vocalisations have also been used to assign vocalisation events, known as pops, to individual bottlenose dolphins, but this method is restricted to one type of vocalisation, produced when animals are in shallow water (Connor and Smolker 1996).

Due to the limitations of these visual methods for assigning calls and the environmental and behavioural constraints associated with the study of vocalisation events in wild cetaceans, passive acoustic localisation is now frequently used. This method uses time of arrival differences of vocalisation events at a number of known hydrophone receivers to determine the position of the sound source. This technique has been used to study vocalisations in a number of species including spinner dolphins (Watkins and Schevill 1974), bottlenose dolphins (Janik *et al.* 2000, Sayigh *et al.* 1993) and harbour seals (Janik *et al.* 2000). This method differs from beamforming, which determines caller position by time of arrival differences of the amount of energy from a direction and frequency across a towed array and is also often used in studies of cetacean vocalisations, e.g. killer whales (Miller and Tyack 1998) and sperm whales (Teloni 2005).

In many passive acoustic localisation studies, hydrophone arrays take the form of fixed or towed arrays. Fixed arrays have been used successfully for the study of among others bottlenose dolphins (Janik *et al.* 2000), southern right whales (Clark 1980), spinner dolphins (Watkins and Schevill 1974) and harbour seals (Janik *et al.* 2000) and consist of a number of hydrophone receivers being fixed into position in the study area. However these studies rely on animals regularly frequenting the area of the array and remaining there for periods long enough to allow behavioural observations. Towed arrays can consist of a varied number of hydrophone receivers in a range of different formations. Linear towed arrays combat the problem of the array being stationed in one area and have been used in vocalisation studies of a number of species including killer whales (Miller and Tyack 1998) and spinner dolphins (Lammers and Au 2003). However, the associated left-right ambiguity inherent in the localisations from towed array data requires specific environmental conditions or behavioural traits to allow confident identification of the direction of the sound source. For example Lammers and Au (2003) were able to view their study animals through the water column and tow their array parallel to a group, something that would be difficult at a study site with poor water clarity. A similar problem exists for the mobile arrays that incorporate underwater video recordings. Dudzinski *et al.* (1995) used a swimmer operated, hand-held system of two hydrophones and a video camera to localise sounds to visual distributions of free-ranging Atlantic spotted dolphins in the Bahamas. Similarly the symmetrical star array used in a number of echolocation studies (e.g. Au and Benoit-Bird 2003, Au and Herzing 2003, Au and Würsig 2004, Rasmussen *et al.* 2004) uses images from an attached video camera to assist in assigning vocalising animals. For studies of wild, wide-ranging dolphins in temperate murky environments, the ability to observe animals through the water column is decreased, limiting the use of methodological approaches that require underwater or through water visual observations.

Distributed arrays consist of hydrophone elements distributed in a non linear way and are often not of a form that can be towed by a small boat. However, Sayigh *et al.* (1993) report the use of a towed, linear array, deployable from a small boat for recording wild dolphins. Their system uses two hydrophones attached to small lead fishing weights and deployed through PVC pipe situated at each side of the boat. This system required the last meter of hydrophone cable to be threaded through holes drilled in the weights and enabled the cables to stream underwater at approximately 1m depth. This system enabled recordings of animals whilst underway, but is limited in design to 2 receiver elements that would make localisation, giving only 1 potential hyperbola pair, uncertain. Additionally any masking or poor recording on one hydrophone would render localisation impossible.

In this study we present a 4 element distributed array and accompanying TOADY localisation system designed to study vocal behaviour in bottlenose dolphins off the north-east coast of Scotland. The array is cost effective, portable and provides increased localisation potential due to the use of four receivers.

METHODS

The Toady localisation system

The TOADY localisation program runs in Matlab software version 6.5.1. TOADY uses the method of cross-correlation of signals from hydrophone pairs to determine the time of arrival difference between them. To determine the time delay between each hydrophone pair and calculate the cross-correlation function, waveforms of the whistles were used. Hyperbolas were calculated using rotation matrices on the equation for a hyperbola with semi-major axis *a* parallel to the *x axis* and semi-minor axis *b* parallel to the *y axis* (Equation 1), (Mathworld 2006).

$$\frac{x^2}{a^2} - \frac{y^2}{b^2} = 1 \qquad \text{(Equation 1)}$$

TOADY then references the coordinates of the array in relation to each other and the speed of sound, to produce a hyperbola for each hydrophone pair. For this trial, the speed of sound was set at 1485 m / second and the array co-ordinates were gained by measuring from a set 0, 0 point in the centre of the boat, to the hydrophone positions. A high-pass filter option is available from 0-15 kHz allowing filtering of any low frequency engine noise and event length can be set from 1000-50000 samples depending on the resolution needed. For this trial all whistle events were viewed as spectrograms within the TOADY analysis system and viewed a pair at a time with the corresponding cross-correlation function and sample lag. When all hyperbolas have been calculated and plotted, localisation accuracy can further be enhanced by scrolling for different depths set at 1m increments to bring the points of intersection closer together.

Lab based test

Prior to field trials, a lab based test of the localisation accuracy of TOADY was performed. An artificial signal was generated in Avisoft SAS Labpro with a frequency range between 4 and 9 kHz and approximately 1 second duration (Figure 1). The signal incorporated up and down sweeps in frequency and was phased in and out.

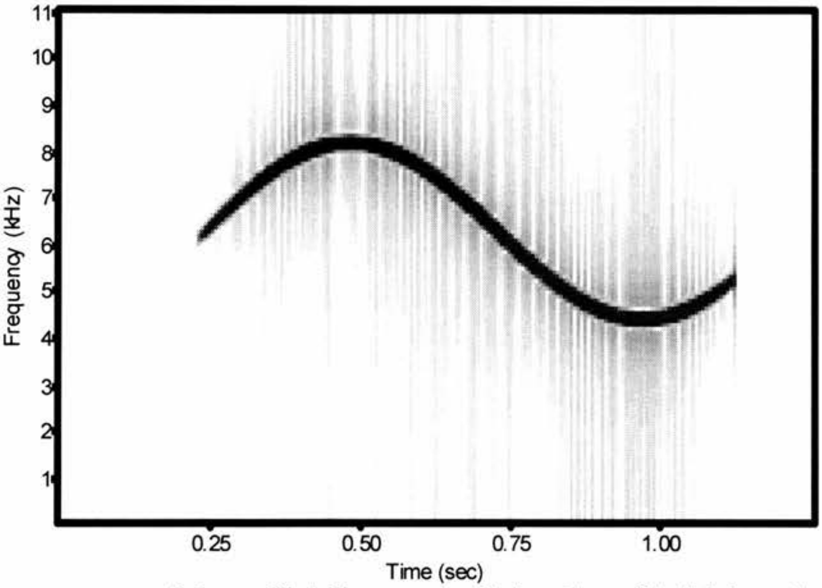

Figure 1: Spectrogram of the artificially generated signal used in lab based accuracy test

The signal was manipulated to introduce a known delay on two channels by the introduction of a period of silence whilst maintaining file duration. This mimicked the test carried out in the field by maintaining synchrony on all four hydrophone receivers. The signal was run through TOADY using the same hydrophone array coordinates to be used in the field calibration.

Hydrophone set-up

Acoustic recordings were made in the field on a 4 element distributed array consisting of three HTI-94-SSQ hydrophones and one HTI-96-MIN hydrophone, all with a frequency response of 2 Hz to 30 kHz ± 1 dB, attached to 2 meter pieces of chain using waterproof tape. The hydrophone element was attached to one end of the chain and the chain was then tensioned as the cable was attached. This tensioning meant the chain links would not rub against each other and thus create interference during recordings. The chains were secured at 4 positions from 196 cm to 208 cm apart depending on position, along the side of the boat (Figure 2). 2m chains were used to place the hydrophones at the maximum depth without risk of engine fouling.

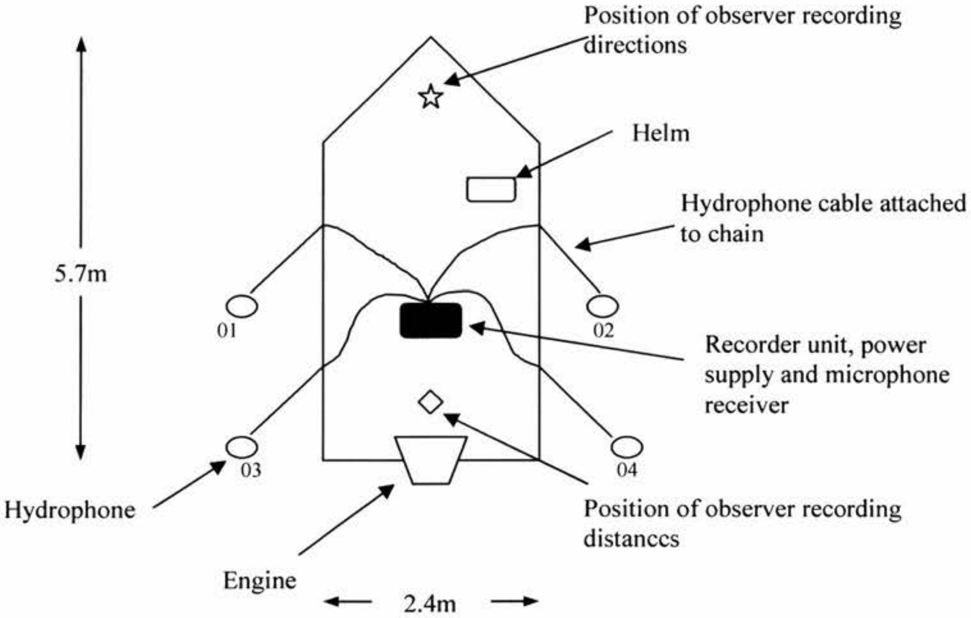

Figure 2: Diagram of the recording set-up showing hydrophone and observer positions. The values 01, 02, 03 and 04 correspond to the labels given to each hydrophone for later localisation analysis.

Calibration Trials

An artificially produced sound source, modelled on a whistle of a wild, temporarily captured bottlenose dolphin in Sarasota, Florida was used. This artificial signal was used to eliminate background noise and ensure a strong signal to noise ratio. The signal was approximately 2.9 seconds long with ascending and descending frequency loops (Figure

3). The frequency range of the signal was 6.9-17.6 kHz so within the frequency range of natural bottlenose dolphin whistles recorded for the Scottish population (see examples in Janik 2000a, b). The test signal was played through a creative nomad jukebox 3 MP3 player connected to a Magnat Classic 1000XL amplifier and transmitted through a Lubell LL-9162 scientific underwater speaker (frequency range 240 Hz to 20 kHz) The speaker was positioned off the harbour wall at Broughty Ferry Harbour, (56° 28' N, 2° 52' W), and attached to a rope of known length and positioned at 2m depth (Figure 4). The trial took place 1 hour and 20 minutes after high water (HW 4.60m, LW 1.73m on day of trial), tidal range is 5.8m (springs) to 4.0m (neaps) (Macklin *et al.* 2004).

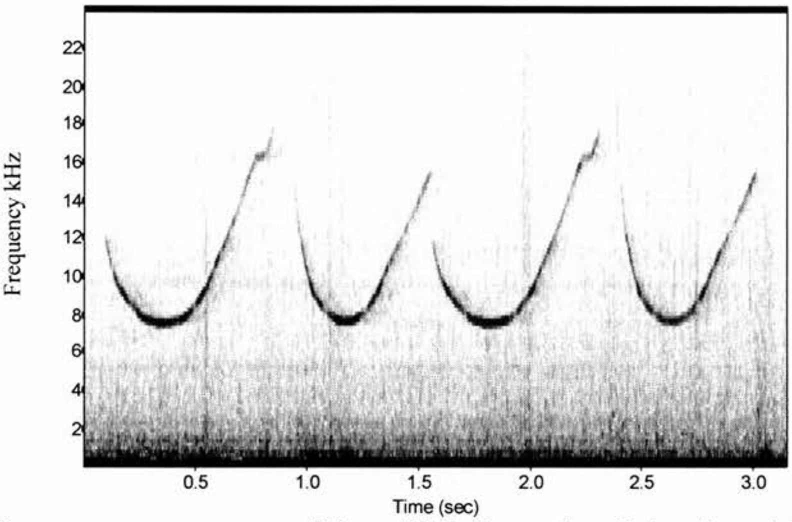

Figure 3: Frequency spectrogram of the artificially produced signal used during calibration field trials.

During the trials the boat was positioned within the main channel, at varying distances and orientations to the speaker, whilst the signal was played. Recordings were made onto an Alesis adat HD24, 24 track digital recorder (sampling frequency 48kHz, 32 bit). Spoken observations detailing the location and distance of the speaker were completed using a microphone and received on a Yaesu FRG-9600 receiver to a separate channel of the digital recorder. The recorder was powered through a 12V, 110 Ahr leisure marine battery. Distances and directions of the speaker from the boat were continually taken with a Bushnell yardage pro 1000 range finder and were spoken onto a separate track of the multi-track recorder to maintain synchrony with the underwater recordings on the array.

The trial lasted for approximately 10 minutes with the signal played on loop to ensure a number of signals were recorded from varying directions and distances.

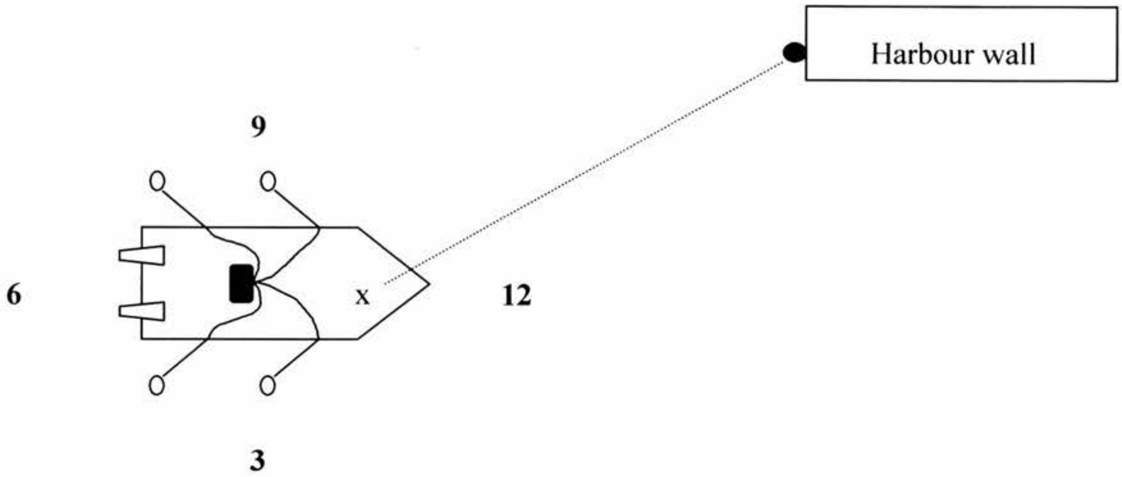

Figure 4: Diagrammatic of calibration set up. Hydrophone array is shown by open circles leading onto research boat. Location of underwater speaker is shown by closed circle at harbour wall. Numbers 3, 6, 9, 12 indicate directions from boat, based on a standard clock face that was used to assign direction to the sound source. x indicates observer position with dashed line showing an example of sound source being at approximately 11 o'clock.

The spoken recording was played back and scribed into a database and time of onset for each calibration signal was catalogued. Sections of the whistle on the first hydrophone of each pair were then manually chosen to be correlated by TOADY to the same section of the whistle on the second hydrophone of the pair. This manual manipulation allowed the sections of the whistles with the best signal to noise ratio to be used. Different sections of the whistles were chosen until the correlation function remained stable for at least 3 manipulations. If stability was not achieved after 10 attempts the whistle was deemed unsuitable for localisation. Localisation accuracy was then further enhanced by scrolling for different depths set at 1m increments to bring the points of intersection closer together.

A selection of 32 signals was chosen for localisation events (Table 1). These 32 were chosen due to their presence on all hydrophone channels, as some signals produced poor signal to noise ratio due to background noise from the engine during the trials. For each of the 32 signals, it was attempted to calculate a hyperbola for each of the hydrophone pairs. Additionally, for each event, only the hyperbola produced from hydrophone pair 1 and 2 (Figure 2) was determined in isolation, to get an idea of localisation accuracy if only 2 hydrophones were deployed.

RESULTS

Lab based test

The results of the lab based test show that when all environmental and methodological variables are removed, TOADY demonstrates a high degree of accuracy in localisation (Figure 5). Therefore any discrepancies seen in the field based calibration were due to propagation and background noise effects in a natural environment, rather than system error.

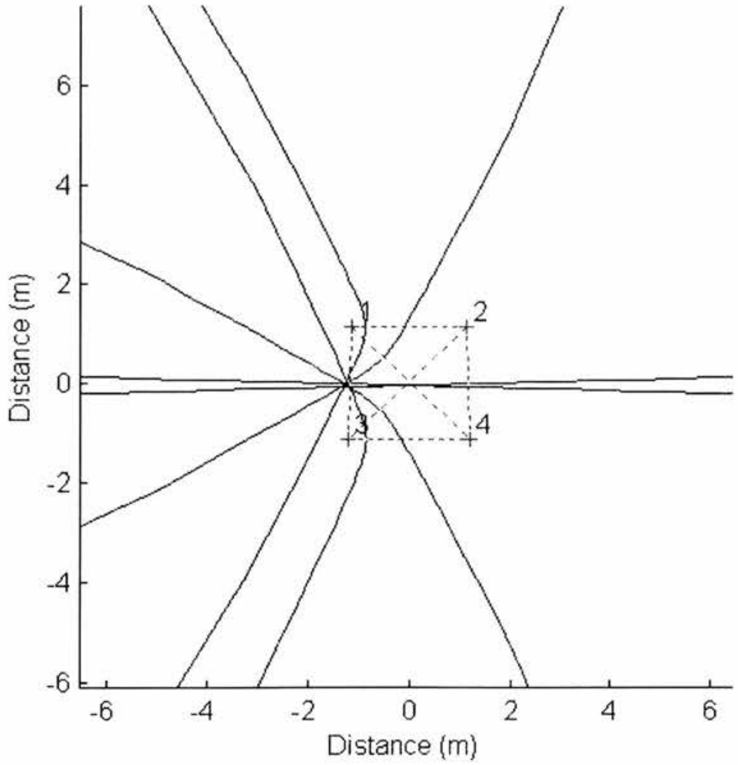

Figure 5: Plot output from TOADY showing correct localisation of the artificially produced signal. Numbers 1 to 4 refer to hydrophone positions.

Table 1: Details of each localisation event, showing actual and localised data for direction, distance and depth. For direction measurements, white boxes indicate exact matches between actual and localised directions, light grey shading indicates matches to within 1 degree of accuracy and dark grey shading represents over 1 degree of accuracy. A degree of accuracy is defined as one position around a standard clock face. End column shows direction if only one hydrophone pair is used. Two values are given for where the call could originate from. None indicates that hyperbola pair 1 and 2 produced errors so were not used in the localisation.

Event	No. of hyperbolas calculated	Actual direction (o'clock)	Localised direction (o'clock)	Actual distance (m)	Localised distance (m)	Actual depth (m)	Localised depth (m)	Direction (pair 1 and 2)
1	5	4	4	60	>10	2	1	None
2	5	4	4	>40	>10	2	2	None
3	5	1	2	83	>10	2	1	None
4	6	1	1	23	20	2	2	1 or 4
5	6	4.30	5	<20	<10	2	2	1 or 5
6	6	5	5	24	>10	2	2	1 or 5
7	6	5	5	40	>30	2	Surface	12.30 or 5
8	4	5	5	>40	>20	2	Surface	None
9	6	4	5	70	10	2	3	1 or 5
10	6	3	4	70	10	2	1	1 or 4
11	6	12	12	56	>10	2	1	12 or 6
12	5	5.30	5	25-35	20	2	2	12.30 or 5
13	6	9	8	40	>15	2	2	8 or 11
14	6	10	9	45	>15	2	Surface	8 or 11
15	4	4	4	>70	>5	2	2	None
16	5	4	3	63	>10	2	2	None
17	5	1	1	54	10	2	2	None
18	6	1	1	41	>10	2	2	1 or 4
19	6	2	1	<20	10	2	3	1 or 4
20	6	4	3.30	<20	<10	2	2	1 or 3
21	6	5	5	20	20	2	2	12.30 or 5
22	6	5	5	33	<10	2	2	1 or 5
23	6	1	1	61	>5	2	1	1 or 3
24	4	3	2	20	10	2	1	None
25	6	6	6	30-40	10	2	1	12 or 6
26	6	9	7	30-40	>15	2	4	7 or 11.30
27	6	12	12	45	10	2	Surface	12 or 6
28	6	12	12.30	<40	10	2	2	1 or 5
29	6	8	8	42	>10	2	2	8 or 11
30	6	10	10	48	>10	2	2	8 or 11
31	5	12	12.30	<40	10	2	1	12.30 or 4
32	6	12	12.30	<40	>10	2	3	12.30 or 4

Calibration Trials

Number of hyperbolas

For 69% (22 events) of all localisation events all 6 hyperbolas were plotted correctly during the localisation. Of this 69%, 95% provided accurate indications of source direction to within 1 degree of direction accuracy. Of the remaining 10 localisation events 22% (7 events) had 5 hyperbolas plotted correctly and only 9% (3 events) had 4 hyperbolas plotted correctly. No events had less than 4 hyperbolas plotted.

Direction

In total 53% of the localisation plots matched the actual directions of the sound source exactly and 97% matched to within 1 degree of accuracy. Only 1 event, 26, showed disagreement of greater than 1 degree of accuracy (Table 1). The two distributions of actual and localised direction were not significantly different from each other (Wilcoxon test for matched pairs W=74.5, p=0.427, n=32).

Distance

For arrays with short inter-hydrophone distances, error within the system will have a greater effect on localisation accuracy than it would for arrays with larger inter-hydrophone distances (Janik *et al.* 2000). For this array the maximum separation distance between hydrophones was only 2.8 meters. So to try and accurately localise whistles to distances of tens of meters will invariably produce error. The TOADY plot screen displays distances up to 1000m but for accurate viewing of the hyperbola intersect it is difficult to view plots with axes greater than 30m, so all localised distances fall within the range of 0-30m. Seven calibration events (4, 5, 6, 19, 20, 21 and 24) had source distances less than 30m away and 4 of these gave localised distance values within 10 meters of the actual distance. The other 3 gave localised distances of greater than 10 meters but always tended to the actual source (i.e. actual distance 24m localised distance >10m from the boat). For the remaining events where actual source distances was greater than 30m, TOADY could only provide estimates of distances mostly greater than 10 or 20 meters. Three events (9, 10 and 15) gave values greatly different to the actual source value and in all cases this was when the source was over 70m away. The reliability of the distance localising in TOADY is only reasonably reliable when sound sources are loud and close to the receivers.

Depth

In total 50% (16 events) of the localisation events produced the most accurate localisation when set at the actual speaker depth of 2m (Table 1). 34% (11 events) were within ±1m of the actual depth and 16% (5 events) were within ±2m. Depth accuracy was established by calculating the area of the polygon (Matlab polyarea command) in m^2 formed by the localising hyperbolas, at different depths to find the solution that minimised this area (Table 2). The mean and variation of the localised depths show good agreement with the actual depth (mean = 1.65m, SD = ± 0.94, n = 32).

Localisation using only 1 hyperbola pair

For each localisation event, plots of just one hydrophone pair (1 and 2) were considered. These results (Table 1) show that for 8 events, no information was gained due to error in plotting the hyperbola. In all but 3 of the remaining events, pinpointing caller position became limited to side of vessel, rather than to the accuracy given when 6 pairs are considered. This is due to a hyperbola being a line rather than a point and it is clear that when the line is drawn the caller could be anywhere upon it, including directly under the boat, when no other information is given. These results show a clear advantage to using more than 2 hydrophones and are especially interesting due to the pair being hydrophones 1 and 2 which is the most likely formation of receivers (i.e. one each side of the boat furthest from the engine) that would be used if only two receivers were to be deployed.

Table 2: Area (m^2) enclosed by intersections for all 32 calibration events. Values were first worked out for 2m depth followed by sequential depths either side until a lowest number was established, hence some events have more areas calculated than other. Bold shows lowest area value for each event, indicating best depth estimate for sound source.

Event	0m (surface)	1m	2m	3m	4m	5m
1	4.04	**3.76**	6.22			
2		1.49	0.86	**0.49**	0.65	
3	0.77	**0.71**	1.55			
4		4.40	**3.16**	4.18		
5		1.71	**0.68**	0.77		
6		2.93	**2.28**	2.61		
7	**5.43**	8.42	12.77			
8	**7.28**	7.49	13.29			
9		2.24	1.63	**1.54**	1.61	
10	6.85	**5.92**	6.22	9.61		
11	0.64	**0.62**	1.37			
12		1.39	**0.60**	0.95		
13		5.64	**2.87**	3.76		
14	**5.31**	5.65	6.41			
15		0.96	**0.54**	1.33		
16		0.95	**0.81**	1.44		
17		3.55	**2.57**	6.50		
18		1.49	**1.37**	11.96		
19		1.50	0.45	**0.35**	0.85	
20		0.16	**0.15**	1.04		
21		10.08	**3.61**	9.37		
22		1.58	**0.63**	1.18		
23	0.42	**0.35**	3.26			
24	0.0281	**0.0279**	0.17			
25	0.194	**0.19**	0.43			
26		0.70	0.38	0.27	**0.23**	0.37
27	**0.285**	0.286	0.35			
28		2.7	**0.76**	1.64		
29		8.65	**5.83**	35.5		
30		2.35	**1.17**	1.74		
31	0.35	**0.32**	0.46			
32		1.77	0.43	**0.19**	1.90	

DISCUSSION

Calibration of a hydrophone array used in the field is vital, as local environmental conditions will change from site to site. Differences in depth and salinity have a marked effect on how sound travels through water and other topographic features such as rocks, sandbanks and currents will also affect transmission paths (see review in Spiesberger and Fristrup 1990). These differences are highlighted in this study by the discrepancies with the field based calibration and the lab based calibration. The lab based synthesised signal gave a localisation plot to the exact position of the sound, indicating that the TOADY system can accurately localise signals modelled on wild dolphin sounds. However for the field based calibration trials errors were evident. Not all localisation events in the field yielded plots with all 6 hyperbolas in place (Table 1). The reason for this instability in some pairs is unclear, but may be linked to reflections and distortions of the sound path or cross correlation on other noise sources that are not initially obvious when observing the spectrograms in TOADY. However, 70% of the calibration trials successfully plotted all hyperbolas and 100% of the trails plotted at least 4 hyperbolas, which still gives a good indication of source location, especially direction from the array. A previous study (Janik *et al.* 2000) used only 3 receivers and still received good indications of source location for this same population of dolphins localising with only 3 hyperbola pairs. 53% of localised directions of the calibration events matched precisely to the actual directions. However if 1 degree of accuracy around the actual direction is considered, then TOADY successfully localised 97% of the samples. This error is considered workable both statistically, no significant difference, Wilcoxon test for matched pairs W=74.5, p=0.427, n=32 between distributions and for field studies when considering environmental factors. The movement of the boat, effects of currents and observer influence in assigning directions make the situation in the field dynamic so changes of 1 degree of accuracy in direction would not be uncommon. Direction has been shown to be more accurate in passive acoustic localisation than distance (Watkins and Schevill 1974) and this was the case in this study, as localised distances were only weakly related to actual distances. It is known that the accuracy of acoustic localisation deteriorates quickly with distance outside the array (Watkins and Schevill 1974) and this was always going to be a concern with this array set up, because unless the dolphins are directly under the boat they will be outside the array. When animals are within 5m of the boat the localisation accuracy of distance is likely to be better but assigning certainty to localised distance measurements would be problematic and probably best avoided with this system. Cato (1998) has explored ways of estimating source distance of sounds using different numbers of hydrophones and differences in received source levels. These methods may be useful if further details on distance or source levels of sound are needed. The scanning of depths in 1m increments is used to help stabilise (bring the points of intersection for the hyperbolas closer together) the localisation procedure by placing the source at different depths, a process that is more likely to mimic the actual event. 50% of the localisation events had best localisation accuracy when set to the actual speaker depth of 2m (Tables 1 and 2) and a further 34% were within ±1m of the actual depth. The localisation plots of source depth showed variation within 1 m of the actual depths (Mean 1.65, SD ± 0.94, n = 32), indicating that the TOADY depth function gives reliable estimates of signal source depth. This gives an extra dimension to the TOADY system as error in localisation is known to increase when using a 2-dimensional array in a 3-dimensional environment (Janik *et al.* 2000) and many localisation systems assume the call is made at the water's surface. We know that wild cetaceans produce their vocalisations underwater so localising based on surface positions is incorrect. The influence of depth on localisation accuracy is a problem when using a 2-dimensional array, but this could be controlled for with the use of an extra receiver (Spiesberger 2001) or the use of a vertical array (Hastie *et al.* 2006). However, the use of four hydrophone receivers in this study enhances the accuracy of the system as a minimum of four receivers are needed when localising sounds in a 2-dimensional environment (Spiesberger 2001). The problems with using fewer receivers were highlighted by the results of the localisation using only 1 hydrophone pair. For 8 of the 32 events no information was available on caller position due to errors in the localisation. For the remaining events ambiguity in exact position arises due to the potential for the caller to be anywhere along the hyperbola. In order to confidently assign vocalisations to observations of animals in the wild, the use of more than two hydrophone receivers is a must. A further source to account for localisation error may be due to this system using receivers that although weighted by chains will experience small changes in depth with changes in boat speed and current flow. This is likely to affect the localisation process as slight changes in the receiver positions will heighten the effect of the error due to the small inter-receiver distances used in this array. However it would be extremely difficult to measure the exact changes in the receiver positions with every possible water flow rate so, for this study, receivers were assumed to move in a uniform way hence maintaining the array coordinates.

Fundamentally the TOADY system performs well, giving directions to 1 degree of accuracy 93% of the time and reliable estimates of signal source depth. The variation in localisation accuracy is known from other studies to be caused by environmental factors (Janik *et al.* 2000, Spiesberger and Fristrup 1990, Watkins and Schevill 1974) and this system is no different. However, the TOADY system has many advantages. The system consists of affordable hydrophone elements and is easy to install in any small boat. The localisation program allows visual selection of the best sections of the whistle, easy to use filters and the scanning depth function which helps to combat the problem of using a 2-dimensional array in a 3-dimensional environment. Additionally, analysis of 6 hydrophone pairs gives a much more reliable estimation of caller position as can be seen by the results when only 1 pair is considered.

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CHAPTER THREE

ABUNDANCE OF BOTTLENOSE DOLPHINS OFF NORTH-EAST SCOTLAND, A COMPARISON OF FREQUENTIST AND BAYESIAN ESTIMATION METHODS

ABSTRACT

A number of capture-recapture methods exist for abundance estimation. This study presents a comparison of two frequentist methods based on point estimation and associated confidence intervals and one Bayesian framework computing probability distributions and credible intervals. All methods were applied to the same photo-identification data using sighting histories of marked individual bottlenose dolphins (*Tursiops truncatus*). The two frequentist methods computed in programs MARK and CAPTURE produced lower estimates of abundance than the Bayesian model run in WINBUGS. The frequentist models also had much narrower confidence intervals suggesting they may be more precise in their estimation but may not account for all the variability in the data. The Bayesian model had greater resolution in incorporating information on numbers of animals with no marks so although not as precise, may be more accurate due to accounting for more variation through higher parameterisation. Taking a highly conservative view and combining the lowest and highest ranges of the frequentist and Bayesian 95% CI estimates, 81-142 dolphins were estimated to be using the study area.

INTRODUCTION

Estimating population size for cetaceans holds many problems. The animals are generally wide-ranging, dispersed over large sometimes inaccessible areas and spend much of their time below the water's surface. However many techniques have been developed to try and combat these problems including counts of animals from shore, boats or planes and mark-recapture of animals identified from individuals' markings. Simple counts of animals from shore can be used to provide minimum estimates of animals within a given area (Hammond and Thompson 1991) but will not provide information on individuals or the extent to which animals may move throughout the area. Boat or plane based counts in the form of sighting surveys often utilise line transect techniques where animal density along transects is estimated and then extrapolated to a population estimate (Hammond 1986) but again do not provide information on individuals.

Mark-recapture analysis using photographs of long-lasting natural marks on cetaceans has substantially increased biologists' abilities to monitor movement patterns and population changes for many species (for examples see Hammond *et al.* 1990). Photo-identification of bottlenose dolphins has occurred since the 1970's (Würsig and Würsig 1977) and has been used on populations throughout the world (e.g. Lusseau 2003, Parsons *et al.* 2003, Smolker *et al.* 1993, Wells and Scott 1990, Wilson *et al.* 1997a). Bottlenose dolphins show less variable pigmentation over their body surfaces than do species such as grey (*Eschrichtius robustus*) or killer whales (*Orcinus orca*) so nicks, scratches and irregularities of the dorsal fin are used for the purpose of matching. Many marks such as large nicks, areas of white pigmentation and deformities in fin shape provide long-lasting reference points for matching that enable correlation of individuals between years and less permanent marks such as scratches or skin lesions provide the possibility to match within years (Williams *et al.* 1993, Wilson *et al.* 1999b). Additionally, many well studied bottlenose dolphin populations (e.g. Wells and Scott 1990, Wilson *et al.* 1997a) are shown to exhibit some form of residency in geographical areas with the same individuals being re-sighted within a geographical range. This enables the use of photographic mark-recapture of individuals without full knowledge of the entire geographical range.

Generally in the determination of population estimates and distribution patterns, dedicated field effort (e.g. Williams *et al.* 1993, Wilson *et al.* 1999b) is undertaken in order to minimise biases such as uneven distribution of survey effort or heterogeneity of capture probability due to movement of individuals beyond the study area as a consequence of differences in individuals' ranging patterns. However, due to logistic reasons such as weather constraints, cost of boat time and limited availability of experienced observers, many studies of cetaceans often couple together a number of scientific studies within one fieldwork day. Photo-identification of individuals is one methodology that can be completed simultaneously with other field techniques such as acoustic recording or surface behavioural observations as long as care is taken when approaching animals and limitations due to potential bias are considered.

The aim of this study was to provide an estimate of abundance for the bottlenose dolphins using the St Andrews Bay area in the summer and to compare this to estimates of total population size. The use of different modelling techniques will allow comparison of estimates between different methodologies.

METHODS

Data collection

This study draws on photo-identification data taken during 35 separate days from July to September in 2003 and 2004. A further 7 trips were undertaken in this time period with no sightings of dolphins. During 28 of these 35 days, focal follows employing concurrent acoustic and non acoustic sampling were conducted. During the remaining 7 days, (16, 21, 24, 32, 33, 34, 35) no other field techniques were employed and dolphins were opportunistically photographed when encountered. On all but 2 days (33 and 34) the same photographer was used. Trips were conducted off the east coast of Scotland between Arbroath and Fife Ness (Figure 1 A and B), from a small boat when sea state was Beaufort 3 or less and weather was dry (Boat a, June-August 2003: 5.75m, 2 x 60 Hp 4 stroke outboard engines. Boat b, August-September 2003: 6.25m, 120 Hp diesel inboard engine. Boat c, June-September 2004: 5.70m, 1 x 90 Hp outboard engine). In instances where weather conditions changed during trips, data collection was aborted, until weather improved, or the trip was abandoned. For the duration of each trip, a Lowrance Global Nav 310 GPS recorded boat position every minute (Figure 1 A and B). Trips did not follow a pre-defined route (Figure 1 A & B) for two main reasons. Firstly, limited surveys had been carried out in the area prior to this study (Wilson *et al.* 2004), so regular presence of animals had not been determined and hence baseline information on broad distribution through the area had to be established. Secondly, the photo-identification was coupled with focal follow studies which predetermined the movement of the boat in association with the focal animal.

During each focal follow the focal animal and its close associates were photographed. During other trips, any animal encountered close enough to the boat was photographed. Photographs of dorsal fin marks (Würsig and Jefferson 1990) were taken with a Canon Digital D30 SLR camera with a Sigma 100-300 mm APO lens set on auto-focus. Pictures of animals' dorsal fins and backs were taken from at least one side when animals surfaced next to the research boat. It was attempted to photograph animals when perpendicular to the boat and close enough to obtain a photo with a 300mm lens. The water conditions did not permit identification shots to be taken whilst animals were underwater. Unlike a dedicated photo-identification survey, no attempt was made to photograph every individual present or from each side as boat movements were dictated by the movement of the focal individual. The subject animals were individuals of a bottlenose dolphin population numbering approximately 130 individuals (Wilson *et al.* 1999b) and known to travel large distances around the north-east Scotland coast from the Moray Firth to St Andrews Bay (Wilson *et al.* 2004). During each focal follow, estimates of group size, positions of animals relative to the boat, (direction based on a standard clock face and distance), and behavioural observations were recorded by observers. During non focal follow trips, information on group size and GPS positions were recorded.

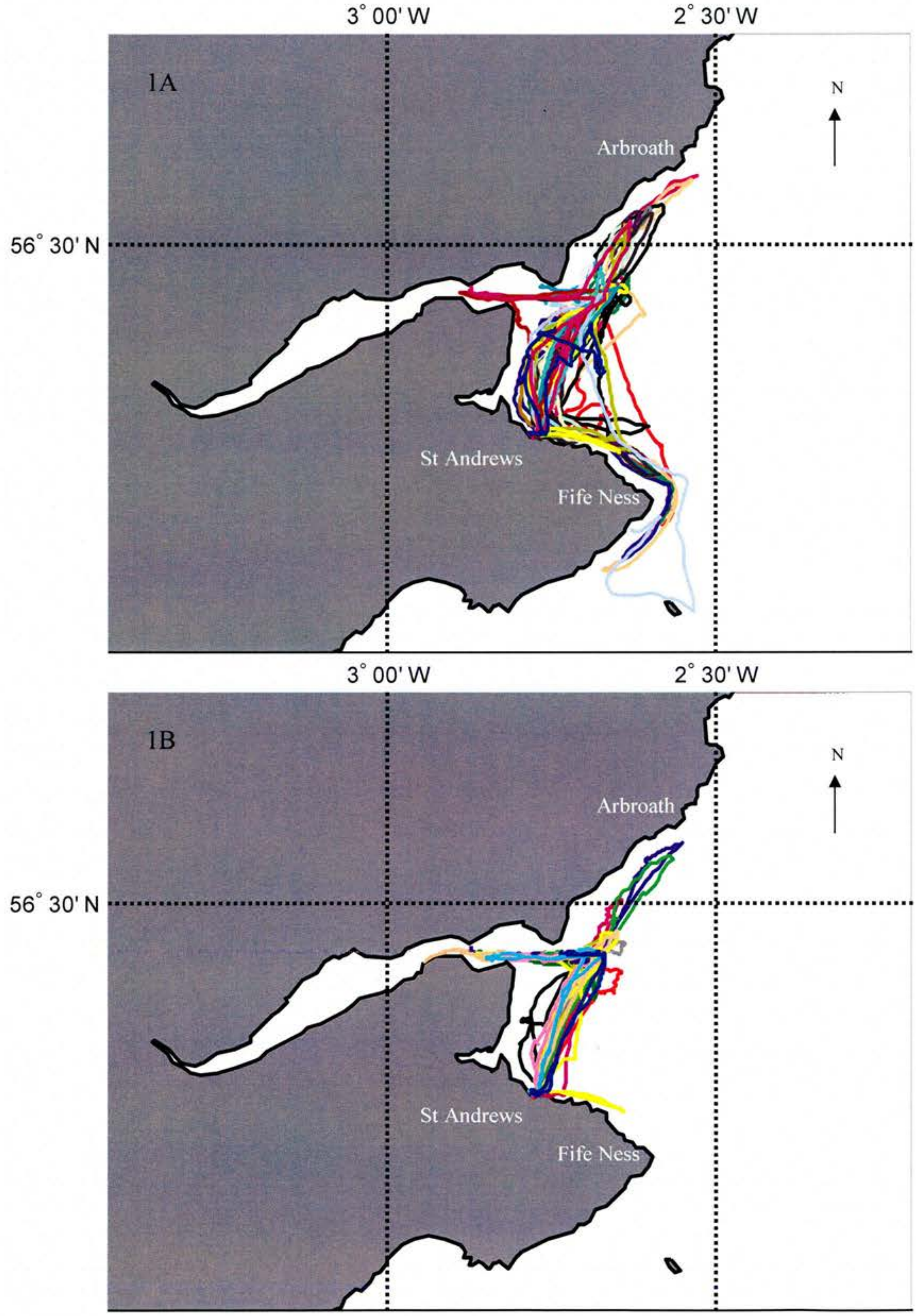

Figure 1 A: Survey effort (all trips) from June to September 2003 (n = 29). **B**: Survey effort (all trips) from July to September 2004 (n = 13)

Data Analysis

GPS data

On return from the trips, GPS positions were downloaded to excel files and imported into Matlab software version 6.5.1, for display of survey effort (Figure 1 A and B).

Identification of individuals

Photographs were downloaded using Canon ZoomBrowser EX and renamed to identify date, trip number and frame number (Appendix 1) with RedRename software (free internet download http://www.hostatelier.com/cracks/download-redrename.html). An access database was established detailing each individual picture (Appendix 1). Each photo was then graded (Appendix 2) based on the system used previously on this dolphin population (Wilson *et al.* 1999b). A modification was introduced in that some pictures were given the grade of Q4 which were photos where animals were identifiable as having some marks but not necessarily individually identifiable. This outlined a better idea of group size for reference purposes only but none of these pictures were used in any of the mark-recapture analysis.

Only picture quality 3 images were used for matching. Animals were matched primarily on 3 types of long-lasting marks previously identified in this population and shown to last for at least 3 years (Wilson 1995, Wilson *et al.* 1999b). These marks were fin nicks, unusual fin shapes and deformities. For animals without one of these three marks, matches were then considered using white-fin fringes and areas of scratching all of which are visible to differing degrees and lasted for variable lengths of time. In the case of animals where minimal marks were present i.e. minor scratches, presence of lesions or completely clean fins, animals were assigned a clean category. This was based on the matchers' ability to match between days. If this was considered impossible due to the potential of marks disappearing quickly, animals were assigned as clean. It has been previously shown that animals can be matched through skin lesions (Wilson *et al.* 1997b, Wilson *et al.* 1999a), but as the prevalence of lesions and potentially their rates of change have been shown to be variable in different habitats (Wilson *et al.* 2000) they were not used during this study due to lack of data on rates of change for this area. If possible, animals were matched to the existing lighthouse field station, University of Aberdeen (AU) photo-id catalogue, (to check if this was the same population) but, if not, animals were assigned a number with the prefix SA. For all analysis animals are not linked to the existing AU catalogue and are given sequential numbers beginning at 1 to avoid any confusion through potential false matches to the catalogue.

Mark-recapture assumptions

Mark-recapture analysis is a commonly used tool for estimating populations of wild animals. However many different models exist (see Chao 2001 and Schwarz and Seber 1999 for reviews) that rely on certain assumptions to be valid. For the population of bottlenose dolphins off the north-east Scottish coast a previous study by Wilson *et al.* (1999b) gave an estimation of population size for the inner and outer Moray Firth areas. Additionally a study by Durban *et al.* (2005) used a Bayesian approach to estimate population size using photo-identification data from three sites throughout the population's range.

For this study both a Bayesian method giving probability distributions and point estimation, giving a population number with associated confidence limits will be considered. However before these techniques can be applied, validation of model assumptions must be addressed.

The main assumptions for closed population capture-recapture methods are

1. The animals have long-lasting marks that are recognisable between sampling occasions.
2. The population is closed to births, deaths and permanent immigration and emigration during the length of the study.
3. The animals show no heterogeneity of capture probability.
4. The animals do not show behavioural responses to being marked / captured.

The animals have long-lasting marks that are recognisable between sampling occasions

Previous studies have shown that eight different types of natural marks occur in this population (Wilson 1995, Wilson *et al.* 1999b). Fin nicks (pieces of tissue missing from the trailing edge of the fin) have been shown to persist for multiple years (e.g. Wilson 1995, Würsig and Würsig 1977) and have been used in many studies for identifying individuals. Unusual fin shapes and deformities are often hard to quantify but are good identifiers of individuals and can be used for matching. All these three marks have been shown to persist for at least 3 years in this population (Wilson 1995) so are considered permanent for the course of this study. Additionally, white fin fringes also remain for at least two years (personal observation) so were also considered permanent. Due to potential difficulties in matching photographs of left and right hand sides of fins, separate estimates for the left and right side were made.

The population is closed to births, death and inward and outward migration

Closed population models require the population to be closed to births, death and inward and outward migration during the study period. For this population the assumption that closure exists has been validated through production of discovery curves based on photo-identification data (Wilson *et al.* 1999b) and also through genetic studies (Parsons *et al.* 2002). However due to a lack of dedicated photo-identification studies in this study area the rate of movement of animals in and out of this area is unknown. Therefore a discovery curve plotting the cumulative number of identifiable animals or the rate of discovery over the temporal length of the study was constructed.

The animals show no heterogeneity of capture

A traditional assumption of capture-recapture models is that all members of a population show equal capture probability during a sampling occasion (White *et al.* 1982). This can be difficult to determine if no information about the entire distribution or level of mixing in the population is known and it is common that this assumption is not met (Otis *et al.* 1978). It is known that the north-east Scotland population of dolphins range over large distances (Durban *et al.* 2005, Wilson *et al.* 2004) so it is likely that differences in capture probabilities with time and individual animal exist. Differences in capture probabilities may be obviously attributable to things like age or sex or may be more complex depending on social associations or movement throughout the population's range governed by factors such as prey availability. Additionally individuals are unlikely to have equal probability of sighting during this study due to no attempt being made to systematically sample the entire study area (Figures 1A and 1B). Also each individual is unlikely to have the same probability of occurring at any given location within the study area due to social and behavioural differences between individuals and groups. All these effects will violate the assumption of no heterogeneity of capture (Hammond 1986). Furthermore, on encounter with the animals each individual is likely to show differences in behaviour, such as variations in reaction to boats that will affect the ability to photograph marks (personal observation). If some individuals are more difficult to photograph than others or are not captured in a quality three photograph the resulting heterogeneity in capture probabilities will give an under-estimation of population size (Hammond 1986). A further issue is that a small proportion of well marked animals, designated as focal, was actively sought and photographed thus introducing a small level of bias from the outset. To allow for this, models incorporating heterogeneity in capture probabilities are needed.

The animals do not show behavioural responses to being marked

For mark-recapture studies using natural marks no behavioural effects should be evident, as animals are not physically captured or handled. There is a chance that animals may be attracted too or dispersed by the research vessel. However, these differences are accounted for when considering heterogeneity of capture.

Proportion of clean animals

Because population estimates rely on matching individuals between sampling occasions, only well marked animals were used in this study. Therefore the mark-recapture estimate is not of the population but of the population of well marked individuals using the area. To determine population size for all individuals therefore, it is necessary to determine the proportion of unmarked animals in the sample. To do this, quality 3 photographs for each of the 35 sampling days were analysed to determine the number of unmarked individuals present. An average was then taken for each month in 2003 and 2004, by combining all trips within each month, as each month was considered one sampling occasion. Then assuming that marked and unmarked individuals are no more likely to be photographed, the number of unmarked individuals can be divided by the total number of individuals for each survey day to obtain a proportion of the unmarked individuals present on any one day. This proportion can then be used to scale up to a total population size (N_t) using equation 1 below with its corresponding variance (Equation 2) (Williams *et al.* 1993, Wilson *et al.* 1999b). For the Bayesian estimate, the proportion of marked and unmarked animals is incorporated into the programming code using mark rate at the resolution of each day.

$$N_t = \frac{\hat{N}}{1 - proportion\ of\ unmarked\ \ individuals} \qquad \text{(Equation 1)}$$

$$\text{var}\,iance\ N_t = N_t^{\,2}\left(\frac{\text{var}\,\hat{N}}{\hat{N}^2} + \frac{1-\theta}{n\theta}\right) \qquad \text{(Equation 2)}$$

Where N_t = total population size, $\hat{N}$ = estimate of marked individuals, θ = proportion of animals with permanent marks, n = number of photographs from which θ was obtained.

Log-normal 95% confidence intervals can then be obtained using equation 3 Where scaling factor c is calculated (Where *CV* is the coefficient of variation of N_t) and confidence intervals correspond to N_t/c for lower estimate and N_t*c for upper estimate. This formula is after Burnham *et al.*, (1987) who state that standard confidence intervals can result in an unrealistic lower limit of zero.

$$c = \exp\left[1.96\sqrt{\ln\left(1 + CV(N_t)^2\right)}\right] \qquad \text{(Equation 3)}$$

Model options

Sighting histories for each marked individual were constructed on a monthly basis (i.e. all trips within 1 month were considered as one sampling occasion). In total 6 months (3 from 2003 and 3 from 2004) were used and the distribution of trips within months was 8, 7, 6, 7, 4, 3, with the first three months in 2003 and the last three months in 2004. For the estimation of the number of animals using the study area, two approaches were considered. The first was using the mark-recapture models available in Program MARK and Program CAPTURE within MARK. Program CAPTURE uses a series of pre-defined models based on a binary mark-recapture matrix of captures over different sampling occasions incorporating variations in capture probabilities (see Otis *et al.* 1978 for detailed explanation). Program MARK also uses a binary mark-recapture matrix but allows different levels of parameterisation and hence variability in capture probabilities to be built into the model by the user. These methods compute a single optimum or maximum likelihood estimate with associated confidence intervals. The exact models to be used were determined after validation of the mark-recapture assumptions. The second approach was using a Bayesian method involving mark-recapture with occasion and individual effects, where abundance estimation is achieved through Bayesian model selection in a fixed dimensional parameter space (Durban and Elston 2005). This method involves fitting a continuous logistic-normal model to the data to yield a full probability distribution for the number of dolphins, which demonstrates both the extent and the shape of the uncertainty of the estimate. This estimate is achieved using Markov Chain Monte Carlo (MCMC) simulation methods that involve sampling from, rather than maximising the likelihood and are run within the program WINBUGS. The idea of this sampling method is that the resulting sample converges to the posterior distribution of interest. The model incorporates a matrix of capture histories for marked individuals and also a matrix of 0's for animals not captured. The aim of the model is to estimate how many rows of 0's there should be (Durban and Elston 2005). This model assumes that the capture probabilities vary both across survey occasion and among individuals. For this model, prior information on population size (Wilson *et al.* 1999b) was used to set the upper bound of unobserved individuals to 200. Therefore a prior distribution was formulated using M = 200 potentially unseen individuals so that the prior density for the abundance estimate was distributed between the number of observed individuals (56 for right hand side and 58 for left hand side) at the lower bound and the number of observed individuals + M at the upper bound. A relatively uninformative prior formulation of df = 0.5 for both survey and occasion effects was used. For left and right hand side data, 3 chains were run simultaneously and each chain was specified a different initial value to assist with spotting convergence.

RESULTS

Mark-recapture assumptions

The animals have long-lasting marks that are recognisable between sampling occasions

In total 76 individual animals had sufficient marks to be identified from quality three photographs between surveys. No attempt was made to match animals with minor scratches or skin lesions in this study. 11 of these animals were matched through major scratches only and even though 9 of these were re-sighted between sampling occasions (Figure 2) they were not used in further analysis due to a lack of a permanent mark type. By deleting these animals from the analysis any chance of overestimating the population due to marks not being recognisable in later samples (equivalent to tag loss) was minimised. 65 animals were therefore used in the analysis for population estimates (Table 1 and Figure 2).

Table 1: Total number of animals identified (permanent marks = nicks, deformities, unusual fin shapes and white fringes) from left and right side pictures during each study year and both years combined. N_f = total number of fieldwork trips.

Year	N_f	Right (marked animals)	Left (marked animals)	Total number of animals identified with permanent marks	Number of permanently marked animals re-sighted	Total number of animals identified (all marks)
2003	29	45	44	52		60
2004	13	35	34	43	30	50
Both years	42	56	58	65		76

Thirty marked animals were sighted in both 2003 and 2004 (Figure 2).Individuals were sighted between 1 and 9 times during the study with 13 (20%) marked animals sighted only once (Figure 3). The re-sight rate of 58% suggests that some individuals may use this area regularly or be partly resident during the summer months.

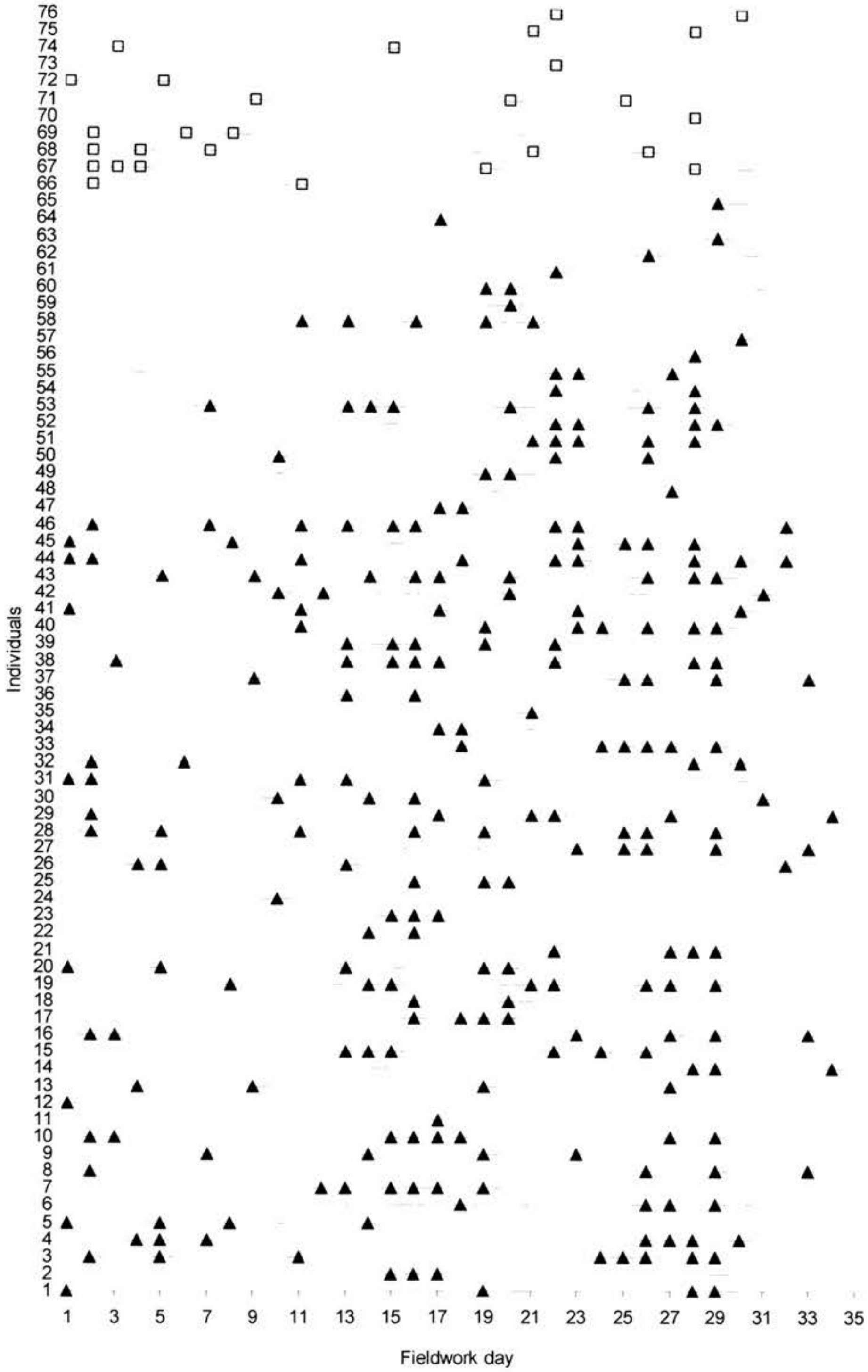

Figure 2: Sightings of individuals throughout the study. Triangles show sightings of animals with permanent marks, open squares show sightings of individuals with non permanent marks. Days 1-21 were in 2003 and 22-35 in 2004.

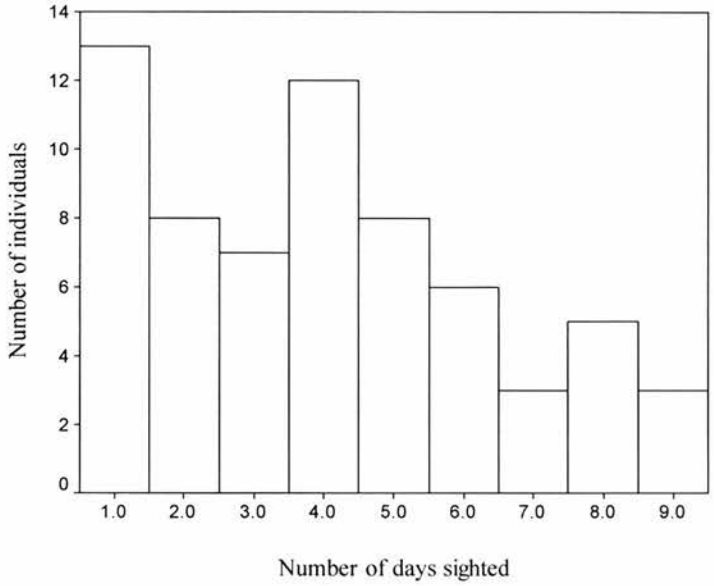

Figure 3: Frequency of sightings for the 65 marked individuals throughout the 35 sampling days in 2003 and 2004 (mean = 4, SD ± 2.4, N= 65)

The population is closed to births, death and inward and outward migration

Male and female bottlenose dolphins have been shown to exhibit different ranging patterns with males thought to range further than females (Wells 1991). These variations in ranging may have implications to sighting rates and hence model assumptions for capture-recapture analysis if only part of the population range is studied. Similarly, male animals in this population appear to have heavier body scarring and potentially be more marked than females (Wilson 1995), although this has only been confirmed for a small proportion of the animals due to limitations of observing genital areas in the wild. Therefore, by assessing the cumulative discovery of marked animals, it may not be possible to assess if the population is sufficiently geographically isolated to assume closure for capture-recapture assessment as the sample may be biased. However, a previous study on this population (Wilson *et al.* 1999b) produced a discovery curve for marked individuals giving an increase appropriate to recruitment of surviving calves. Similarly, Parsons *et al.* (2002) showed a degree of genetic isolation in this population, suggesting that large inward and outward migration does not occur. Data from this study back up these findings with a discovery curve for marked individuals showing a levelling off of new identifications after 30 field days (Figure 4) There is a steady increase during 2003 (field days 1-21) as different marked individuals are identified. However, the increase is reduced in 2004 (field days 22-35) with only 13 new individually marked animals being identified.

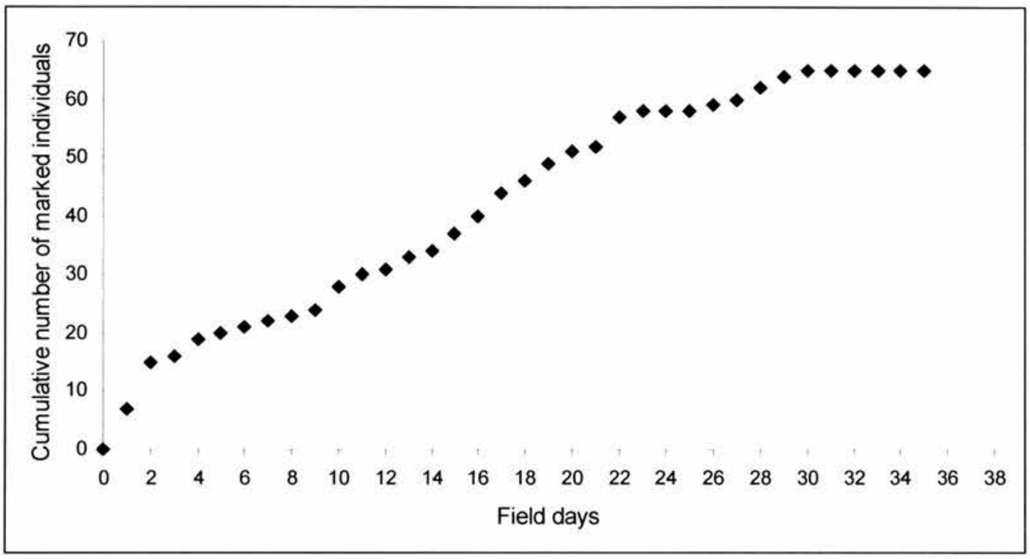

Figure 4: Discovery curve showing the cumulative number of marked animals against field days.

The animals show no heterogeneity of capture

This assumption is very likely to have been violated during the study, due to the primary focus of trips being focal follows, not photographing each individual and not following a systematic trip design. Similarly nothing is known about how animals are mixing in this area so the horizontal stratification seen in the northern end of this population's range (Wilson *et al.* 1997a) may also exist in this study area. This would have implications to the capture probabilities because the entire area was not always surveyed (Figure 1).

Proportion of clean animals

The proportion of clean individuals was variable throughout the six sampling occasions (Figure 5), with a mean of 0.317 for 2003 and 0.127 in 2004. This change maybe due to clean animals in 2003 gaining marks in 2004, but with only 13 new marked individuals sighted in 2004 (Table 1) this would assume that the same animals came back to the same area during both years and that all the clean animals gained marks. Although this is possible, it is unproven and the variation may be due to heterogeneity in the behaviour of individuals, especially as the standard deviations of the two year averages overlap. For estimates of total population size, for MARK and CAPTURE, an average of the two years combined for left and right sides will be used.

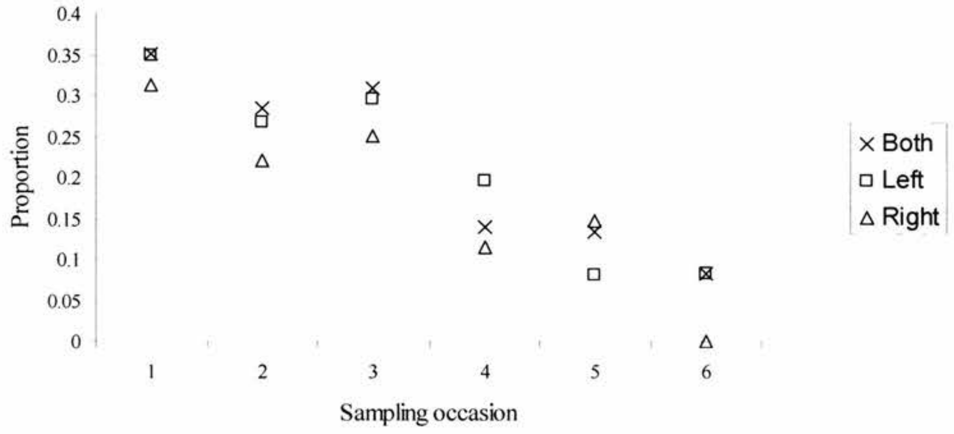

Figure 5: Proportion of clean animals for each sampling occasion for both sides combined and left and right sides separately. For combined data, mean values for 2003 (sampling occasions 1-3, mean=0.317, SD ±0.104) and 2004 (mean = 0.127, SD ± 0.133 sampling occasions 4-6). All sampling occasions both sides combined mean = 0.241, SD ± 0.149. For left side mean = 0.212, SD ± 0.112, for right side, mean = 0.174, SD ± 0.111 (all occasions combined).

Model selection

With reference to the validation of assumptions, population models assuming the following were used:

1. Well marked animals retained their marks and could be recognised between sampling occasions.
2. The population was closed over the sampling period due to a decrease in discovery of new marked individuals.
3. Heterogeneity in capture probabilities is likely to exist either over time, individual or both.
4. No behavioural effects of marking are present.

Program MARK

Within the program MARK, the closed population estimates all consist of the basic parameters[1]: p_c - probability of initial capture, c - probability of recapture given that the animal has been previously captured, and pi_m - proportion of the population with a specified mixture of p_c and c, (White 2004), hence allowing heterogeneity in the sighting histories of individuals. In total 7 closed capture models with different specifications of parameters p_c, c and pi_m were run in Program MARK for both left and right sides. Model 1 termed {p_c=c all}, has no heterogeneity and the probability of initial capture (p_c) was equal to the probability of recapture (c) across all 6 sampling occasions. As a result, this was the simplest model with only 2 parameters. Model 2 termed {p_c equal, c equal}, has no heterogeneity and the probability of initial capture and the probability of recapture were specified as constant across all 6 sampling occasions but were different to each other, i.e. the probability of capture did not equal the probability of recapture within one sampling occasion, but the probability of initial capture or recapture were the same from one sampling occasion to the next. Model 3 termed {pi_m (p_c diff, no c)}, incorporates heterogeneity, so specifies 2 different groups within the data and allows a different initial capture probability (p_c) of the two groups, that is constant across all sampling occasions but doesn't include any probabilities for recapture (c) in the model. Model 4 termed {p_c=c each occasion}, has no heterogeneity and the probability of initial capture (p_c) was specified as equal to the probability of recapture (c) within each sampling occasion, but these probabilities were specified to be different between each of the 6 sampling occasions. Model 5 termed {pi_m (p_c=c for each occasion)}, incorporates heterogeneity again specifying 2 different groups in the data. This model incorporated completely different probabilities of p_c and c for the 2 groups. However, within the two groups the probability of initial capture (p_c) and recapture (c) was equal within each of the 6 sampling occasions, but different between them. Therefore both groups had parameters p_c and c defined as equal within each sampling occasion, but different across them and different to each other. Model 6 termed {p_c equal, 4c equal, 1c not}, was run to test for bias in the final sampling occasion as the number of dolphin sightings in the last three

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[1] p_c and pi_m refer to p and pi respectively in the MARK notation given in the program. Extra subscripts were added here to prevent confusion with similar notation in the Bayesian model.

trips of the study was small (Figure 2). No heterogeneity was included and the probability of initial capture (p_c) was set as equal across all 6 sampling occasions. The probability of recapture (c) was set as equal for all but the last sampling occasion which was specified a different probability. Finally model 7 termed {pi_m (p_c and c diff)} incorporated heterogeneity and the probability of initial capture (p_c) and the probability of recapture (c) were specified as different for all groups both within and between the 6 sampling occasions and between groups. The results of the 7 models for left and right side are given in Tables 2 A & B. For model 7 {pi_m (p_c and c diff)}, the initial estimation had the best AICc and deviance value for all models. (AIC refers to the Akaike's information criterion, which is used for selecting the most appropriate model with respect to the data. AICc is based on the same measure, but accounts for sample size and parameterisation (see Burnham and Anderson 2002)). It also gave $\hat{N}$ estimates for right hand side of fins (RHS) of 56 (CI 56-56, SE 0.149E-04) and left hand side of fins (LHS) of 58 (CI 58-58, SE 0.684E-05). This appeared somewhat suspect and on initial computation when this model was placed with the lowest AICc, the number of parameters in the model was set to 20 rather than 24. Program MARK is unable to correctly determine the number of parameters (K) in closed captures models when the population size, N_t, is estimated close to the number of animals encountered (White 2004).This problem causes the AICc to be computed incorrectly and the number of parameters must be manually adjusted to match the initial parameters set. This problem did not occur with any other models and is likely to be caused by some of the probability estimates for the parameters being very small due to sparse data during some sampling occasions.

Tables 2 A and B: Result summaries for the 7 models run in Program MARK for left and right side photographs.

2A: Model summary for left hand side (LHS) photographs

Model (model id number)	AICc	Delta AICc	AICc Weight	Model Likelihood	Number of parameters	Deviance
Model 5	57.528	0.000	0.412	1.000	14	41.137
Model 6	58.232	0.704	0.290	0.703	4	62.985
Model 7	59.059	1.530	0.192	0.465	24	20.213
Model 4	60.220	2.692	0.107	0.260	7	58.760
Model 1	82.211	24.683	0.000	0.000	2	91.046
Model 2	83.797	26.269	0.000	0.000	3	90.597
Model 3	84.959	27.431	0.000	0.000	4	89.712

2B: Model summary for right hand side (RHS) photographs

Model (model id number)	AICc	Delta AICc	AICc Weight	Model Likelihood	Number of parameters	Deviance
Model 5	45.583	0.000	0.651	1.000	14	47.237
Model 4	47.613	2.030	0.236	0.362	7	64.234
Model 7	49.239	3.656	0.105	0.161	24	28.342
Model 6	54.176	8.593	0.010	0.014	4	77.017
Model 1	94.058	48.475	0.000	0.000	2	120.984
Model 3	94.934	49.352	0.000	0.000	4	117.776
Model 2	95.959	50.376	0.000	0.000	3	120.849

For both left and right sides the best model given by MARK was model 5, {pi_m (p_c=c for each occasion)}, with a mixture of 2 (pi_m) for individual heterogeneity synonymous with animals having different capture probabilities and with different capture and recapture probabilities between but not within each sampling occasion. This is based on the AICc value that shows this model is better supported by the data than any other model. It is clear from the tables that the models used showed great variation in number of parameters specified to explain the data. The more parameters there are in the model, the smaller the deviance and the better the fit of the model. This is because the more parameters that are used in the model the more flexibility the model has, hence the better the fit to the data e.g. model 7 {pi_m (p_c and c diff)} (Cooch and White 2005). However, the more parameters that are used the more the precision of the model estimates are reduced. So a payoff between the best fit and the best precision is needed. This is gained through the calculation of AICc which is corrected for low sample sizes

$AICc = -2\log Likelihood + 2K + 2K(K + 1)/(n\text{-}ess - K - 1)$ (Equation 4)

K = number of parameters and n-ess is the effective sample size. (Equation 4 reproduced from White 2004).

Therefore, models with the lowest AICc values give the best fit when the number of parameters and sample size have been taken into account, indicating that for both left and right hand side photographs, model 5, {pi_m (p_c=c for each occasion)} is most appropriate.

Program CAPTURE

With reference to the validation of assumptions and the program MARK results, only two models were run in CAPTURE, Model M(t) and M(th) based on Chao *et al.* (1992). Model M(t) assumes all individuals have the same probability of capture on any particular trapping occasion, but heterogeneity in capture probabilities from one occasion to the next exists (Otis *et al.* 1978). Model M(th) assumes the same heterogeneity in probability of capture between occasions as model M(t) but also includes heterogeneity among the capture probabilities of individuals. The results of the best model from program MARK and the two models in Capture are shown below (Table 3).

Table 3: Results of model estimates: (side = side of fin, $\hat{N}$ = estimate of number of animals with permanent marks. $SE(\hat{N})$ = standard error of $\hat{N}$. 95% CI = 95% confidence interval. p_o = proportion of clean animals in the sample. N_t = total population estimate. CV = coefficient of variation.

Model	Side	$\hat{N}$	$SE(\hat{N})$	95% CI ($\hat{N}$)	p_o	N_t	95% CI (N_t)	CV
{pi_m(p_c=c for each occ)} (MARK)	Left	62	3.413	59-75	0.212	79	73-85	0.059
	Right	72	10.721	61-109	0.174	87	72-105	0.151
M(t) (CAPTURE)	Left	67	5.191	61-83	0.212	85	77-94	0.081
	Right	65	5.521	60-83	0.174	79	71-88	0.087
M(th) (CAPTURE)	Left	72	7.495	64-95	0.212	91	79-104	0.107
	Right	72	7.831	53-95	0.174	87	75-100	0.111

For the models from CAPTURE the estimates from model M(th) give the highest abundance estimates and hence suggest there is heterogeneity in capture probabilities of both individuals and sampling occasions. This is also supported by the results from

Program MARK, where model 5 incorporated heterogeneity both within individuals and between sampling occasions. Model M(th) is therefore the most appropriate model from CAPTURE.

Bayesian Model

30,000 iterations were run for both left and right side data (models took between 40450-110461 seconds depending on computer used). The value was established after multiple short runs (200-20,000 iterations) to try and determine model convergence. The model was assumed to have converged after 5000 iterations for both LHS and RHS estimates (Figure 6). Satisfactory convergence of Markov chain simulation is reached when inferences for quantities of interest are not dependent on the starting point of the simulations (Brooks and Gelman 1998) so for each of the 3 chains a different over-dispersed starting point with respect to the target distribution was used. The basis of this is that all the chains should behave in the same way and that the variance within the chains is the same as the variance across the chains. The Gelman-Rubin (a.k.a. Brooks, Gelman-Rubin) diagnostic can be referenced for evidence of convergence. For each parameter of interest, this statistic assesses the variability within chains to the variability between them and if the ratio of between to within variability is close to 1 the model is judged to have converged (Figure 6) (Brooks and Gelman 1998, Gelman and Rubin 1992). Convergence can also be tested by other diagnostics such as time-series plots of parameter value against iteration number (Figure 7), the presence of multimodality in kernal density plots (Figure 8) or checking if autocorrelation is declining with increased iterations. Additionally, running means should not change greatly if more or less iterations are performed if the model is reasonably stable. Once enough draws have been taken to summarise the posterior distribution then if the model has converged, further samples from a parameters' posterior distribution should not influence the calculation of the mean. This is clearly the case for this model (Table 4) as the posterior mean and mode remain relatively stable regardless of burn-in time. In fact diagnostics with no burn-in time suggest stability of the posterior distribution prior to 5000 iterations. However, 95% credible intervals (Table 4) suggest more precision if a burn in time in included and so convergence was assumed after a burn-in time of 5000 iterations. Therefore all following results are calculated with this 5000 iteration burn-in time removed. For both left and right hand side data, 3 parameters were monitored. Parameter *N* is the abundance of reliably marked animals, *P* is the total abundance and *pi* is the estimated proportion of animals with reliable marks.

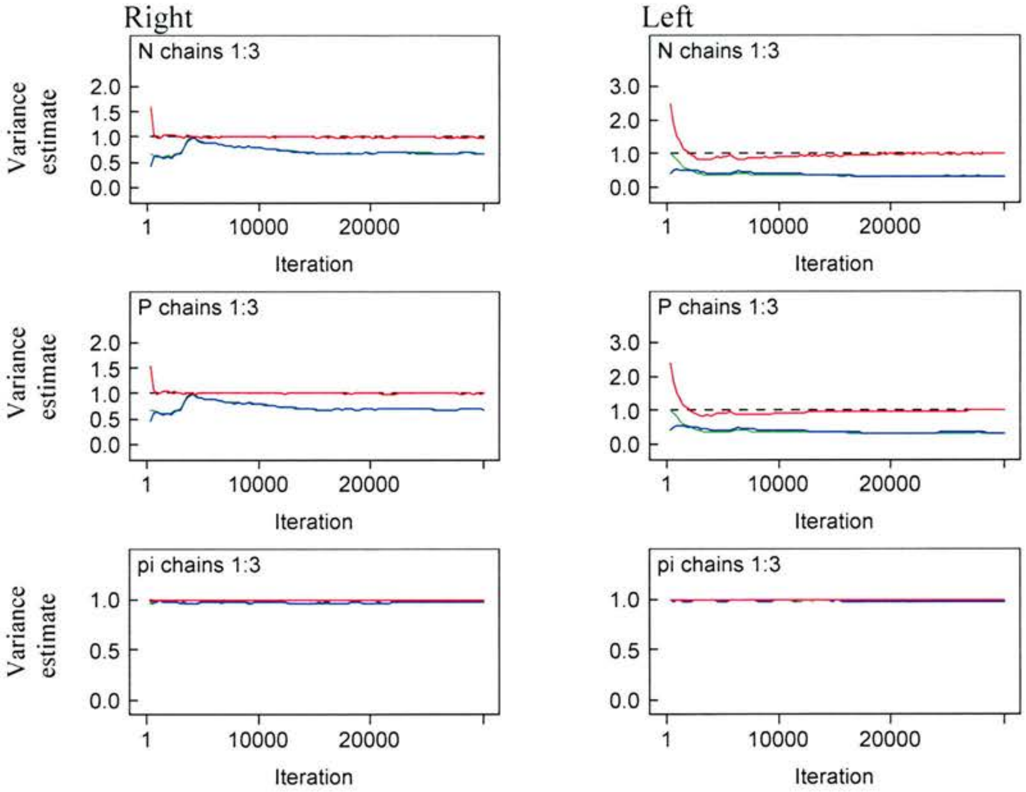

Figure 6: Gelman-Rubin plots for 30000 iterations for left and right hand side data. Green line is between chain variability, blue line is within chain variability, red line represents the ratio of within to between. Evidence for convergence is shown from the red line being close to 1 and the blue and green lines being horizontally stable across the plot. As a result convergence can be assumed at about 5000 iterations.

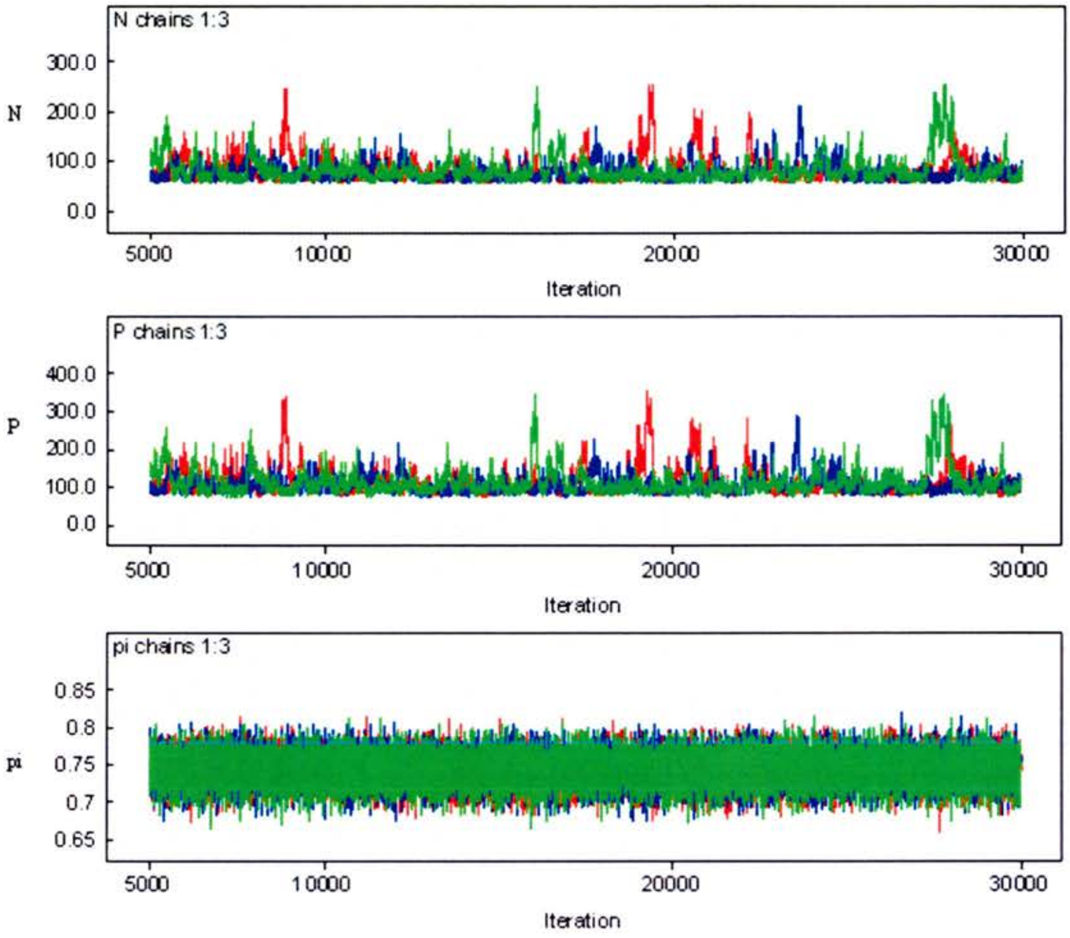

Figure 7: Example of time-series plots of each parameter against iteration for RHS data only. (Note initial burn-in phase of 5000 iterations has been discarded). For all three parameters (N = number of reliably marked individuals, P = total abundance and pi = estimated proportion of animals with reliable marks) all chains are overlapping suggesting convergence to the same mean and variance (each colour represents 1 chain). Evidence of peaks indicates model sampling at the extremes of the distribution but shows all chains tending back to similar values.

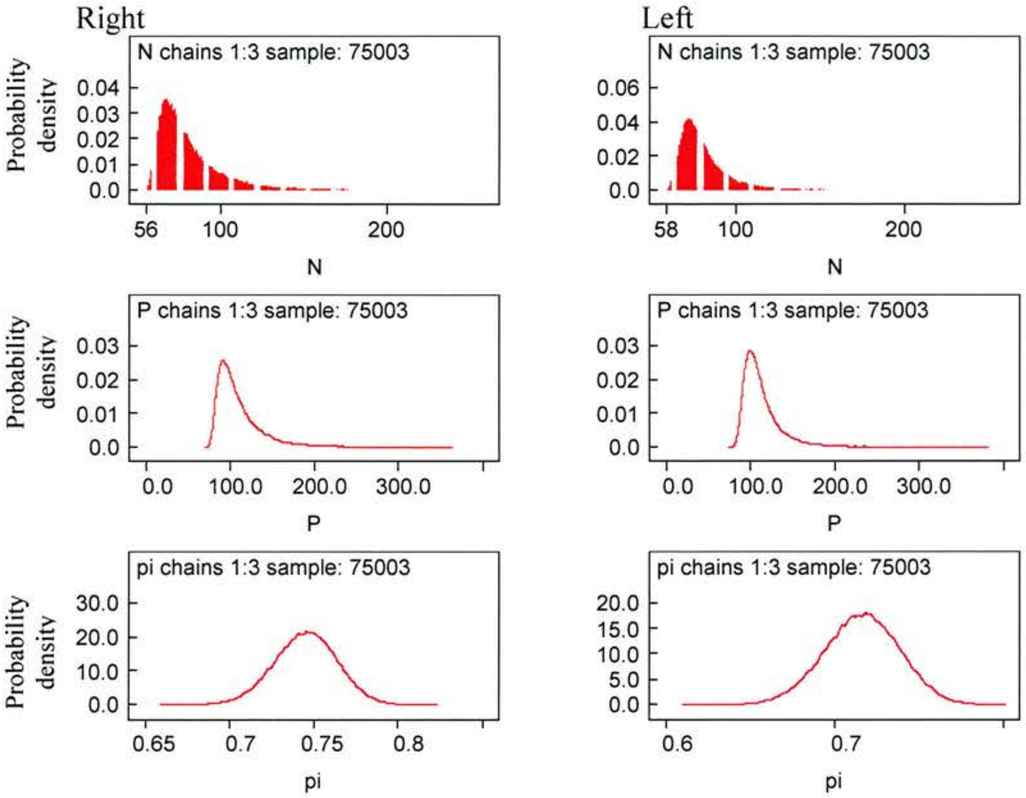

Figure 8: Kernel density plots for right and left data for all 3 parameters. Unimodal distributions indicate good convergence of chains. Skewed distributions for *N* and *P* reflect the level of prior knowledge about the lower bound of the distribution.

Table 4: Examples of running mean, standard deviation (SD), median and 95% credible intervals for different burn-in periods for both left and right hand data for parameter *P*.

Iterations	Mean	SD	Median	2.5%	97.5%
Right					
1-30000	112	32.95	102	80.44	206.0
5000-30000	111	31.06	102	80.45	197.6
10000-30000	110	30.97	101	80.28	199.6
15000-30000	111	33.73	101	80.42	212.7
20000-30000	111	33.38	101	80.41	213.7
25000-30000	110	35.68	99	80.06	223.3
Left					
1-30000	115	28.05	107	87.12	191.6
5000-30000	114	27.45	107	87.06	187.7
10000-30000	113	25.83	106	86.81	182.4
15000-30000	113	25.99	107	86.82	178.7
20000-30000	116	28.04	108	87.09	185.5
25000-30000	113	21.14	107	87.16	166.4

The summary statistics for the model were estimated for the posterior distribution for each parameter of interest. The population was estimated to have a posterior mean of 111 animals for right hand side data and 114 for left hand side data with credibility intervals of 81-198 for right and 87-188 for left (Table 5).

Table 5: Summary statistics of each parameter for right and left hand side data. Table shows mean, Standard deviation (SD), mc error (how well the mean of the posterior has been estimated from the number of samples), median and the 95% credible intervals (i.e. there is a 0.95 probability that the interval contains the mean).

Side	Parameter	Mean	SD	MC error	2.5%	Median	97.5%
Right	N	82.6	23.01	0.895	60.0	76.0	147.0
	P	110.9	31.06	1.202	80.5	102.0	197.6
	pi	0.7449	0.01859	7.013E-5	0.7076	0.74.53	0.7804
Left	N	81.65	19.47	0.7204	63.0	76.0	134.0
	P	114.1	27.45	1.006	87.06	107.0	187.7
	pi	0.7161	0.02241	8.387E-5	0.6711	0.7164	0.7591

Abundance estimates from all models

Estimates of left and right sides were combined using inverse variance weighted average using the coefficient of variation and log-normal confidence intervals as described in Equation 3. The results are given in Table 6.

Table 6: Left, right and combined estimates for each of the three models (note for models 1 and 2, 95% CI refers to confidence intervals, but for model 3 it refers to credible intervals).

Model No.	Model	Side	Abundance estimate (N_t)	95% CI
1	$\{pi_m\ (p_c=c \text{ for each occ.})\}$	Left	79	73-85
	(MARK)	Right	87	72-105
		Combined	**80**	**75-86**
2	M(th) (CAPTURE)	Left	91	79-104
		Right	87	75-100
		Combined	**89**	**81-98**
3	Bayesian estimate	Left	114	87-187
	(WINBUGS)	Right	111	81-108
		Combined	**112**	**89-142**

DISCUSSION

Program MARK and CAPTURE have been used for abundance estimation in a number of studies (e.g. Baker 2004, Gormley *et al.* 2005, Williams *et al.* 1993, Wilson *et al.* 1999b). The Bayesian approach to abundance estimation, used in this study is relatively new, but Bayesian models are gaining support as an alternative way to analyse data, especially with questions pertaining to conservation and environmental biology (e.g. Ellison 1996, Wade 2000). This is due to the ability to provide a probability distribution of possible outcomes given the data (Figure 8) alongside a mean abundance estimate (Table 6) and corresponding credible intervals i.e. there is a probability of 0.95 that the interval contains the mean. MARK and CAPTURE methods, however compute a point estimate of abundance and corresponding log-normal confidence intervals where 95% of such intervals contain the mean. The choice of the best model will come down to the suitability of the model assumptions given the data and it is clear in this study that the validation of the assumptions was key to model selection. These validations indicate that the requirement for variability in capture probabilities both across survey occasions and among individuals was justified (Figures 2 and 3) This is not surprising due to variation in capture effort across surveys due to focal follow procedure, not taking photographs of all animals present and the presence of individual heterogeneity in capture between individuals (Figure 2). Similarly, it has been shown that these animals travel large distances (Wilson *et al.* 2004) and hence it is likely that individuals have home-ranges which only partially overlap that of the geographic area covered and individual ranging patterns may not be fully covered in only 2 years of study.

The precision of the MARK and CAPTURE estimates were higher than that of the Bayesian estimate as shown by the low CV values (Table 3) and the CI range (Mark = 80, 95% CI 75-86, Capture = 89, 95% CI 81-98, Bayesian 112, 95% CI 89-142). However the posterior mean estimate of N_t was noticeably greater ($N_t = 112$ as opposed to $N_t = 80$ or 89) for the Bayesian method. However it is unclear if the more frequentist MARK and CAPTURE models are an underestimation of the abundance or if the Bayesian model is an overestimation. There were high sighting and re-sighting rates of marked animals during this study (Figure 2) so the probability of detecting each individual was high and the proportion of marked individuals was also high (Figure 5). Hence the confidence intervals should be relatively narrow as there is much less uncertainty about N_t through the estimation of unmarked animals. However due to the heterogeneity in the data, the accuracy of the Bayesian model is likely to be higher due to the incorporation of the clean proportion data at a finer resolution giving the model a higher degree of parameterisation. For example by taking an average of the clean proportion, only one value was used to scale up the N_t estimate for mark rate in the MARK and CAPTURE models. These values (Left = 0.212, Right = 0.174) are significantly lower than the estimates of Wilson *et al.* (1999b) for the same population (Left = 0.43, Right = 0.39). There is the chance that this clean proportion has decreased due to animals gaining long-lasting marks, but over the course of Wilson *et al's* (1999b) three year study the mark rate remained almost constant between years. It is therefore more likely that the data collection method of following marked animals and not photographing all animals has negatively biased the clean proportion calculation. Additionally, bottlenose dolphins have been shown to form sub-adult groups (Reynolds *et al.* 2000), which contain younger individuals, that may not yet have permanent marks. For the focal follows, these whole groups may have been avoided as they didn't contain well marked individuals and hence it seems that this may be a better explanation for the lower mark rate. For the Bayesian estimation, the proportion of marked to unmarked individuals was incorporated over the 35 individual sampling days. On some of these days the proportion of clean animals was equal or greater to that of the Wilson *et al.* (1999b) estimate of 0.4. By incorporation of this variability and hence uncertainty in the clean proportion into the Bayesian estimate, it may be that this is a more accurate reflection of the number of animals using the study area. This is shown in the kernel density plots of the posterior distribution of *pi* (Figure 8). The distributions have lower modal values than given by the average method used for MARK and CAPTURE so would explain the higher estimation of N_t.

Convergence of the chains within the Bayesian method determines if the model has reached a stationary distribution but this does not mean it is a good model for these data. However, the Bayesian code is for communicating uncertainty where heterogeneity in capture probabilities varies across individuals and occasions (Durban and Elston 2005). The data presented here have been shown to contain this heterogeneity due to sampling methods and variability in individual sighting histories. Similarly the best fitting frequentist MARK and CAPTURE methods also incorporate some level of heterogeneity so the difference in final abundance estimation may be a parameterisation issue based on resolution of mark rate data, or may be due to some of the assumptions for the models not being met. The MARK model was built based on subjective views of heterogeneity and hence may have underestimated abundance as it is not complex enough to account for the variation present. A previous study (Baker 2004) found mark-recapture models run in program MARK frequently underestimated true abundance of Hawaiian monk seals, determined from census. Additionally, in about half of the MARK models the upper 95% CI for total abundance was lower than the known minimum estimate (Baker 2004), making this quite a substantial under estimation. Baker (2004) found program CAPTURE models to be less negatively biased, but still had occasions where it estimated total population below the minimum estimate. Although the MARK models used by Baker (2004) are not directly comparable to the model used here due to different model construction, the CAPTURE M(th) model based on Chao *et al.* (1992) is the same. Hence it may be that in this study some of the assumptions needed to run these models were not met. It may be that the use of closed population models was incorrect, even though the discovery curve (Figure 4) suggests this is valid. However, if the assumption of closure was violated, then the estimation of total abundance should be an overestimation (Otis *et al.* 1978), which appears not to be the case for the MARK and CAPTURE estimates. Therefore, it is more likely that some form of heterogeneity has not been accounted for in the model construction. These may be subtle effects such as attraction or dispersion to or by the research boat, or use of different areas by different individuals based on social or ecological reasons.

Both frequentist and Bayesian methods have pros and cons argued by staunch supporters. However, in this study even if the lowest and highest limits of the three estimates are taken (Table 6), then between 75-142 dolphins were using the study area during the summer months of 2003 and 2004. For a population estimated to be 129, 95% CI 110-174

(Wilson *et al.* 1999b) this is a significant proportion. However, at least 76 animals were identified during this study (Figure 2) and this did not include any calves (at least 2 sighted each year) or any unmarked animals (variable numbers sighted each day, personal observation). Therefore, taking the 81-142 limits of the CAPTURE and Bayesian models may be a closer estimation for this area.

This study highlights the differences in abundance estimation that can be obtained from published mark-recapture methods and suggests that care be taken when choosing appropriate models. For this study, where the population in question is considered small and isolated and is hence of conservation concern, it may be considered appropriate to use the Bayesian model. This is because the probability distributions allow a more precautionary approach, giving associated probabilities at different values of N_t.

From a conservation and management standpoint, the estimation of at least 81 individuals from a bottlenose dolphin population identified in the European Unions Habitat directive (92/43/EEC) as endangered (Scottish Natural Heritage 1995) in an area, many hundreds of kilometres from their supposed resident area is important. The Moray Firth has been established as a special area of conservation (SAC) designated specifically to protect this population. However, with over half the population being repeatedly sighted in the St Andrews bay area, revision of the boundaries of this SAC should be considered if effective management of this entire population is to be achieved.

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APPENDICES

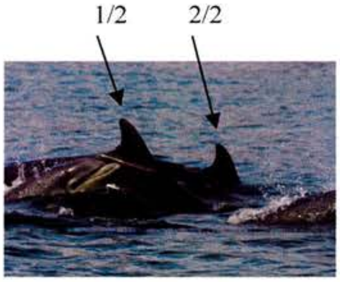
Appendix 1

Example of database set up used for recording picture information

Trip No	Follow No	Picture No	No of fins	Fin position	Side	Quality Grade	Initial ID
EXAMPLE DATA							
001	FW001	010104_001_001	1	1/1	L	2	

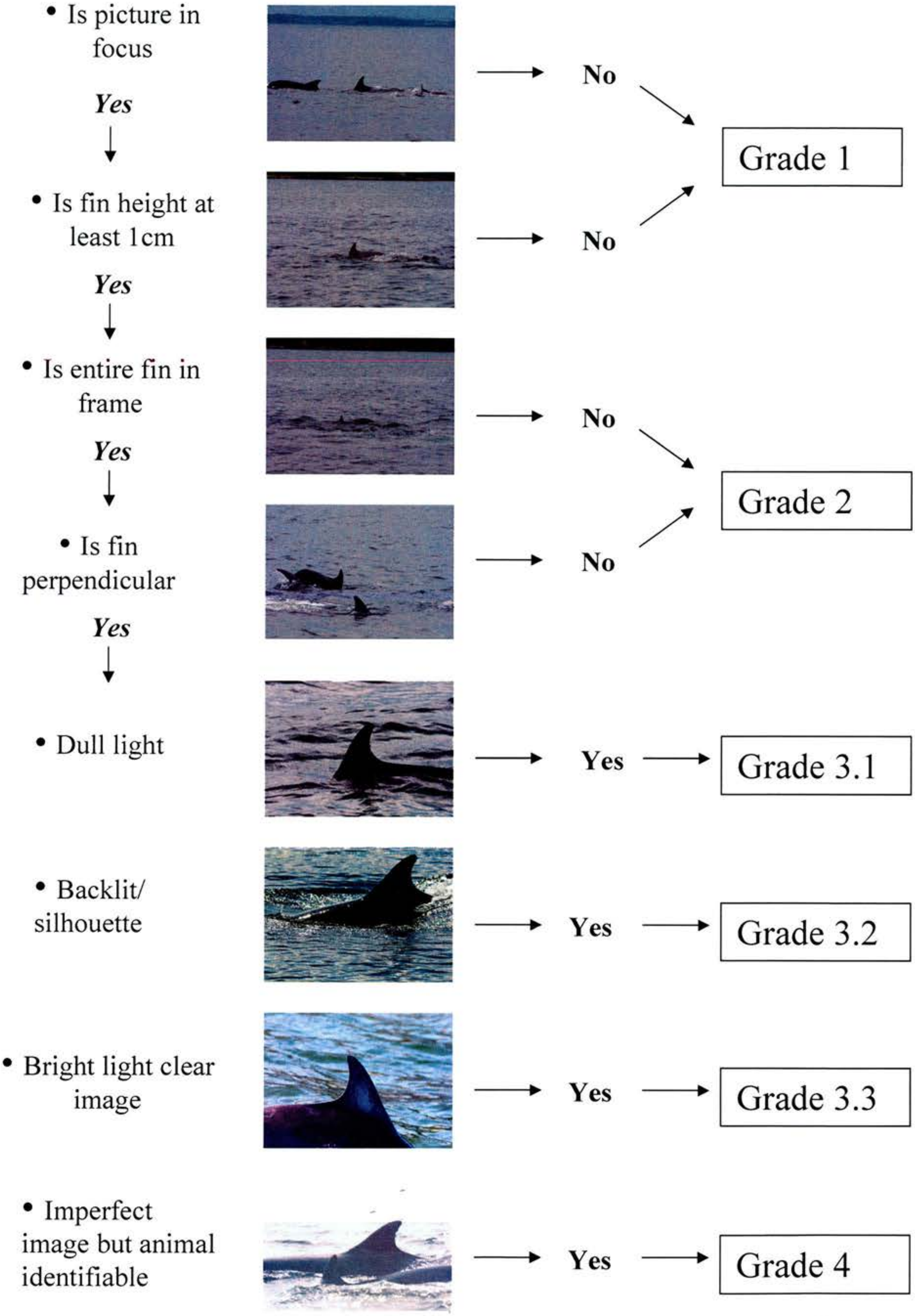
Date/Trip/Frame

Trip number: These will be assigned on a daily basis each time the research vessel leaves the shore.
Follow number: These will be assigned each time a focal follow is completed in a sequential order (prefix FW)
Picture number: A record of the date the picture was taken, the trip number used and the frame number.
Number of Fins: Number of dolphin fins captured in the frame
Fin Position: Working from left to right across each individual frame each fin is recorded on a separate line in the database (see example figure below)



Side: Is the photograph of the left or right hand side of the fin
Quality Grade: Grade of picture quality (see appendix 2)
Initial Id: Identification number of animal taken from existing or new catalogue. (Existing catalogue is that based at the Lighthouse filed station, University of Aberdeen and id numbers take the form of individual numbers. The new catalogue is animals not identified in the existing catalogue and id numbers take the prefix SA).

Appendix 2: Picture quality grading system used for photographs



CHAPTER FOUR

THE CATEGORISATION OF WHISTLE CONTOURS INTO TYPES: VIGILANCE LEVELS AND SIMILARITY

ABSTRACT

Separating calls of animals into like categories is difficult. Different methods yield contrasting opinions about how calls are categorised and how relevant these categories are to the animals. The ARTwarp automated classification system incorporates an adaptive resonance theory neural network and dynamic time warping to categorise calls based on a vigilance factor. This study uses two recordings of wild bottlenose dolphin (*Tursiops truncatus*) whistles to assess how categorisation changes with changing vigilance factor. For both recordings, the highest variance ratio values corresponded to a vigilance level giving similar classification of the whistles as a human observer, however this vigilance level was less than the 96% previously reported for categorising signature whistles of captive dolphins. This suggests that a deflated vigilance factor of 91% to 92% may be more appropriate for determining signature whistles in wild bottlenose dolphins.

INTRODUCTION

The classification of dolphin whistles into like categories can cause debate. Different methods used by different groups yield contrasting opinions about how whistles are categorised and how relevant these categories are to the animals (Janik 1999, McCowan, 1995, McCowan and Reiss 2001). For studies of dolphin whistles and other animal calls, two approaches are generally used. The first is to use the pattern recognition abilities of humans to assign calls (either spectrograms or frequency contours) to like categories by eye, and has been used in a number of studies (Janik 1999, Janik and Slater 1998, Nowicki and Nelson 1990, Rendell and Whitehead 2003, Sayigh *et al.* 1995, Tyack 1986). However due to individual variation in judging different patterns some discrepancies may exist (Jones *et al.* 2001) and this process may be very time consuming making it unviable if data sets are large. The second method is to use computer based automated approaches. These approaches include cluster analysis, where like calls cluster together (Hammerschmidt *et al.* 2000, Wood *et al.* 2005), time dilation of the contour to compare structure (Buck and Tyack 1993) or neural network techniques where new calls are categorised based on their similarity to a given reference (Deecke *et al.* 1999, Parsons and Jones 2000, Reby *et al.* 1997). These methods have yielded differences in results (Janik 1999) due primarily to differences in methodology especially when defining parameters for testing. Additionally, it has recently been argued, (Deecke and Janik 2006) that two factors of standardising for time and accounting for exponential perception of frequency are not always incorporated into programs and may account for some of the failure in existing computer based methods. A further problem with classifying signature whistles of bottlenose dolphins are loops. Loops were termed by Caldwell *et al.* (1990) and refer to repeated contours of signature whistles. Different numbers of loops may be repeated each time a signature whistle is made and decisions about whether these are one or many different whistles is subjective. In past studies, signature whistles with repeated loop structures were differentiated based on the detailed structure of the loops and as such, whistles with considerable variations in the number of loops or deletions of segments, are still considered signature whistles (Caldwell *et al.* 1990, Tyack 1986, 1997).

The ARTwarp automated classification system (Deecke and Janik 2006) incorporates an adaptive resonance theory (ART) neural network and dynamic time warping to categorise contours based on a certain degree of similarity or vigilance factor (Deecke and Janik 2006). The program uses an unsupervised learning algorithm, where new patterns are compared to reference patterns based on the vigilance factor. If the degree of similarity to a reference pattern is met, the new pattern is assigned to the category and the reference pattern is then updated with the new pattern. If the level of similarity is not met then a new category is formed (see Deecke and Janik 2006 for full details). This differs from supervised neural networks where classification is based on information from a training set of patterns. Dynamic time warping is included to allow compression and expansion of the time axis, by a factor of three, to maximise frequency overlap between the new and reference signals (Deecke and Janik 2006).The program allows vigilance factor to be set by the user, allowing manipulation of the categorisation, depending on levels required. The vigilance level, or how fine the categories are, gives a quantitative measure not achieved in human classification, where individual variation, depending on how precise the judge is, i.e. whether they judge a whistle to be similar enough if it looks about 80% the same or whether they go for a complete match, synonymous to a 100% match, creates human bias. Additionally, ARTwarp allows the maximum number of iterations taken by the program to be set, and the program will complete the number of iterations required until the same classification of contours to categories occurs twice.

Initial tests show ARTwarp is capable of correctly classifying known signature whistles of bottlenose dolphins into distinct categories (Deecke and Janik 2006). However, for populations where the signature whistles of the individuals are unknown, it is unclear which vigilance level is needed for categorisation.

METHODS

Data collection

This study uses two recordings taken on the 16/08/03 (recording 1) and 26/07/04 (recording 2) during focal follows on individuals from the bottlenose dolphin population from the north-east coast of Scotland. Recordings were made on a 4 element distributed array consisting of three HTI-94-SSQ hydrophones and one HTI-96-MIN hydrophone, all with a frequency response of 2 Hz to 30 kHz ± 1 dB, directly onto a Fostex D824, 8 multitrack digital recorder during 2003 (sampling frequency 48kHz, 24 bit) and an Alesis adat HD24 multitrack digital recorder during 2004 (sampling frequency 48kHz, 32 bit) (change due to replacement of damaged equipment). A sequence of two stereotyped whistles, previously classified by a human observer, (classified as types A to D given in Figure 1) were visually extracted from each recording. Recording 1 contained 14 whistles, 6 of type A (single and multi-loop type A whistles were classified as the same type) and 8 of type B. Recording 2 contained 21 whistles, 11 of type C (single and multi-loop type C whistles were classified as the same type) and 10 of type D. Whistle types A and C are multi-loop whistles (Figure 1) and appeared with different loop numbers throughout the recording.

Contour extraction

Frequency contours of each of the whistles were extracted in Matlab version 6.5.1. Spectrograms of each whistle were produced (FFT 2048, frame length 512, overlap between frames 87.5%, Hanning window, time resolution 1.333ms) and automated contour extraction, using a peak algorithm, was performed. A maximum of 10 edits were used depending on the signal quality. Editing allowed the initial extraction to be improved by adjusting the extraction line produced by Matlab, to better fit the underlying whistle. Each contour file was down-sampled to a time resolution of 10 ms and converted to a text file. Contours were down-sampled after the extraction so as not to affect the extraction process. If extraction was completed at a time resolution of 10 ms, large errors in the automated contour extraction occurred.

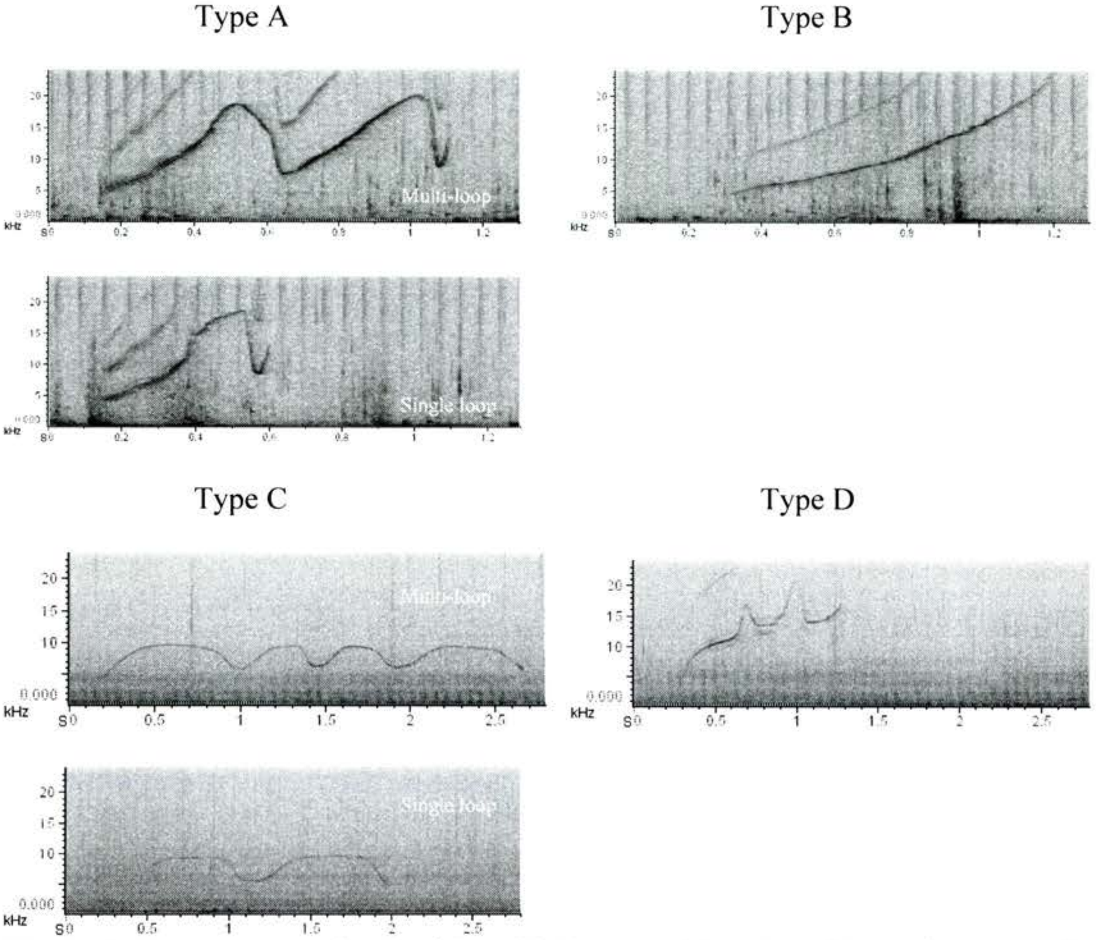


Figure 1: Spectrograms of each of the whistle types. (Type A and B are from recording 1 and type C and D from recording 2). For the multi-loop whistle types A and C, examples of the multi-loop and single whistles are given.

ARTwarp analysis

The text files for each of the two recordings were run through ARTwarp. The vigilance factor was initially set at zero and then increased by increments of 2%. The learning rate of the algorithm was set to 10%, the maximum number of iterations to 10 and the maximum categories to 14 (recording 1) and 21 (recording 2). Once the categorisation was complete, the resulting data files were run through a Matlab routine (art_var_ratio) to determine the within and between category variation and calculate the corresponding ratio for each vigilance level. To do this, art_var_ratio constructs a similarity matrix for all the frequency contours. The average similarity of all the contours in the same category and in different categories can then be compared for each categorisation at each vigilance level. When the within categories to between categories variation is highest, then an increase in vigilance level does not help to explain any more of the variation between the contours. This is a way of determining which vigilance level is the most appropriate for categorisation of the data. A further test was also completed where contours from both recordings were mixed together and run at 96% vigilance. This allowed categorisation with a higher sample size of more contour types, as a comparison between the critical vigilance factor previously reported in Deecke and Janik (2006) for signature whistle identification. For this test the learning rate remained at 10% and the maximum iterations at 10. However the maximum categories value was increased to 35.

RESULTS

Recording 1

The results of increasing the vigilance level on categorisation are shown in Figure 2A. It can be seen that the similarity of the whistles, means only one category is present up to 90% vigilance. At 90%, 2 categories are produced after which increasing vigilance leads to a dramatic increase in category number until 14 categories at 100%. Figure 2B shows the variance ratio of within to between category variations. The highest ratio is given at 92%. However, there is variation within each vigilance level as shown by the other symbols on graph 2B. These extra symbols show the results when the categorisation is repeated and different categories arise. The highest variance ratio corresponds to 3 categories and is shown by the black diamond in Figure 2B and illustrated in Figure 5.

The differences in categorisation within one vigilance level, (92%) are demonstrated in Table 1. For a vigilance of 92%, ARTwarp was run 20 times and the resulting number of categories recorded. This variation in categorisation is due to the random number generation used by ARTwarp to decide which order the contours are input to the program. This input order has a marked affect on both the number of categories produced (Table 1) and the variance ratio (Figure 2B). An example of two different classifications of the contours of recording 1 is shown in Figure 3. These two runs both produced two categories but contours were assigned differently depending on the initial reference contour and the following order of input into ARTwarp. The difference in the variance ratios were 1.0598 for run 1 and 1.0928 for run 2.

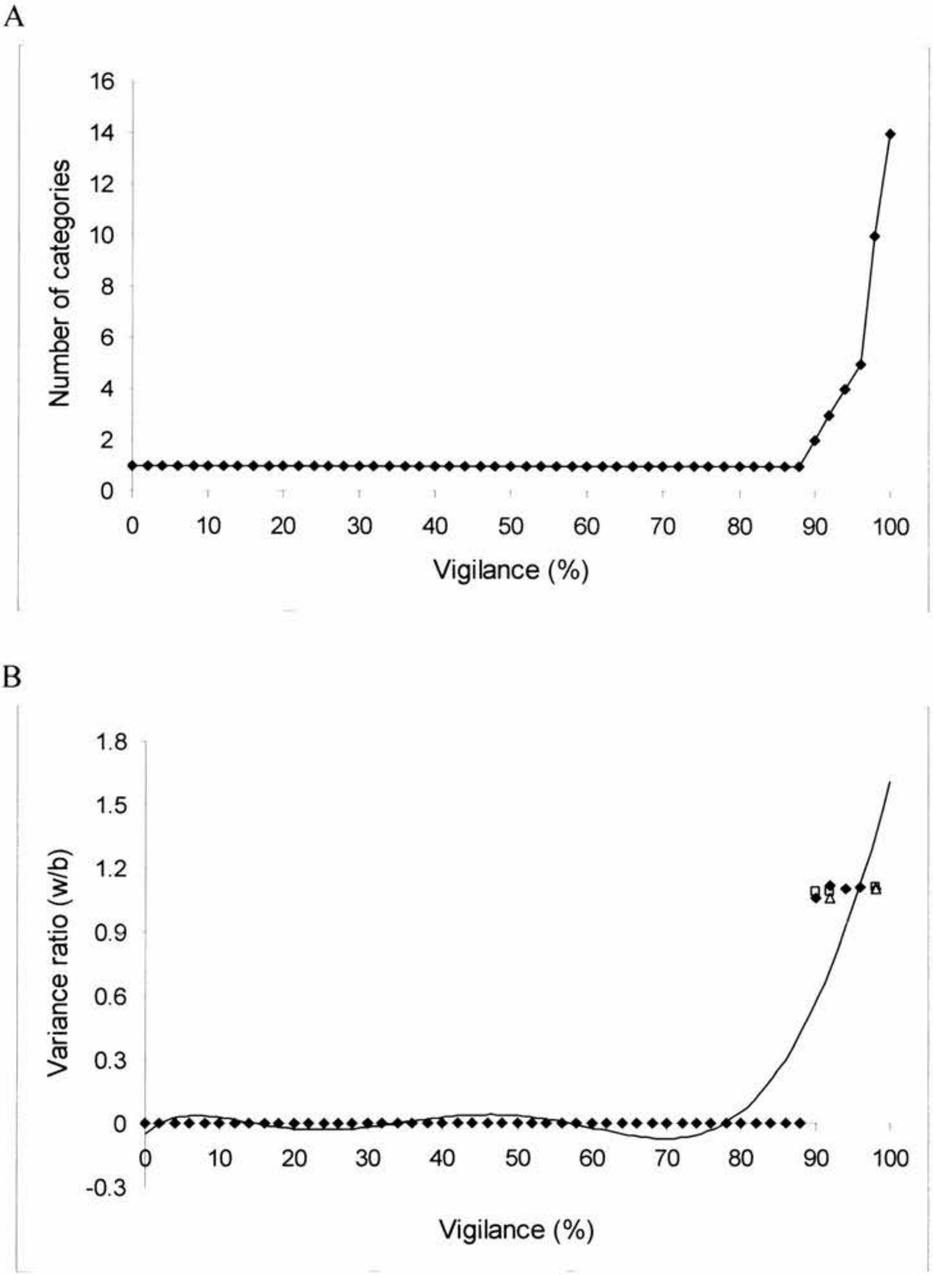


Figure 2: Recording 1: The effect of increasing vigilance on categorisation is shown in graph A. Graph B shows the change in variance ratio with increasing vigilance. Different symbols for 90%, 92% and 98% highlight variation in the ratio value depending on the categorisation as a result of the randomisation of contour input into ARTwarp.

Table 1: Results of 20 runs at 92% vigilance for recording 1 (Mean = 2.3, SD = ± 0.657)

Run	*No. of iterations*	*No. of categories*
1	2	3
2	3	2
3	2	2
4	2	3
5	2	3
6	2	2
7	2	2
8	2	2
9	3	3
10	2	2
11	2	3
12	2	1
13	2	2
14	2	2
15	2	2
16	2	2
17	2	2
18	2	4
19	2	2
20	3	2

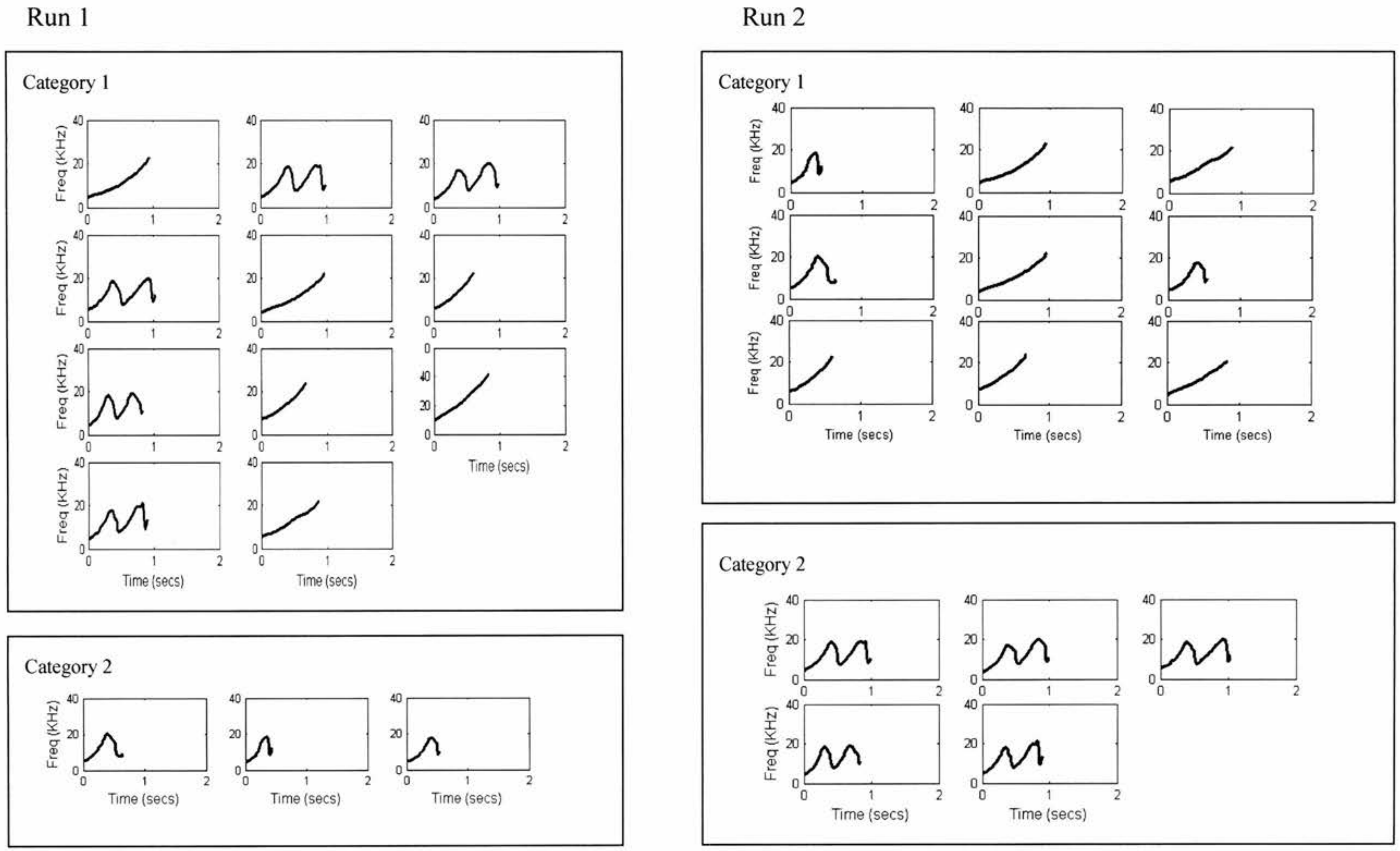


Figure 3: Categorisation results of two separate runs at 92% vigilance for recording 1. In run 1, types are mixed and only the 3 single loop sections of whistle type A are classified separately. However for run 2, these first loops are mixed with all the type B whistles.

Recording 2

The results of increasing the vigilance level on categorisation are shown in Figure 4A. The similarity of the two whistle types is less in recording 2 than recording 1, with generally one category being present until 65%. Instances of ARTwarp producing two categories at vigilances less than 65% did occur. Table 2 shows the frequency with which 2 categories are produced, during 20 runs at these lower vigilance levels. For 8 of the 20 runs 2 categories were produced (Table 2). Two categories are always present until 91% vigilance, after which the two types are split into more categories, until 21 categories are reached at 100%. Figure 4B shows the variance ratio of within to between category variations. The highest ratio is given from 65-91% corresponding with the 2 category classification. After this, increasing vigilance does not help to explain any more of the variation in the whistles. The difference in categorisations seen at high vigilance levels in recording 1 was not evident in recording 2 due to the differences in contour shape between whistle types C and D (Figure 1).

Overall categorisation for separate recordings

For both recordings the categorisation corresponding to the vigilance level at the highest variance ratio is shown in Figure 5. For recording 1, this was at a vigilance level of 92% and for recording 2 at a vigilance level of 91%. In this categorisation, contours were assigned almost identically to the assignment by a human observer. The main difference is that for recording 1 the best variance ratio is given when the single loop, type A whistles, are categorised separately to the multi-loop type A whistles.

Both recordings mixed together

Results of the categorisation of all contours mixed together from both recordings at 96% vigilance returned 11 categories after 2 or 3 iterations in 4 runs and 9 categories after 3 iterations in one run. In none of the categorisations were any of the 4 whistle types (A, B, C, D) mixed together. However for the four runs that produced 11 categories none of the runs placed the exact same contours in the exact same categories. This again highlights how the initial reference contour affects the final placement of contours into categories.

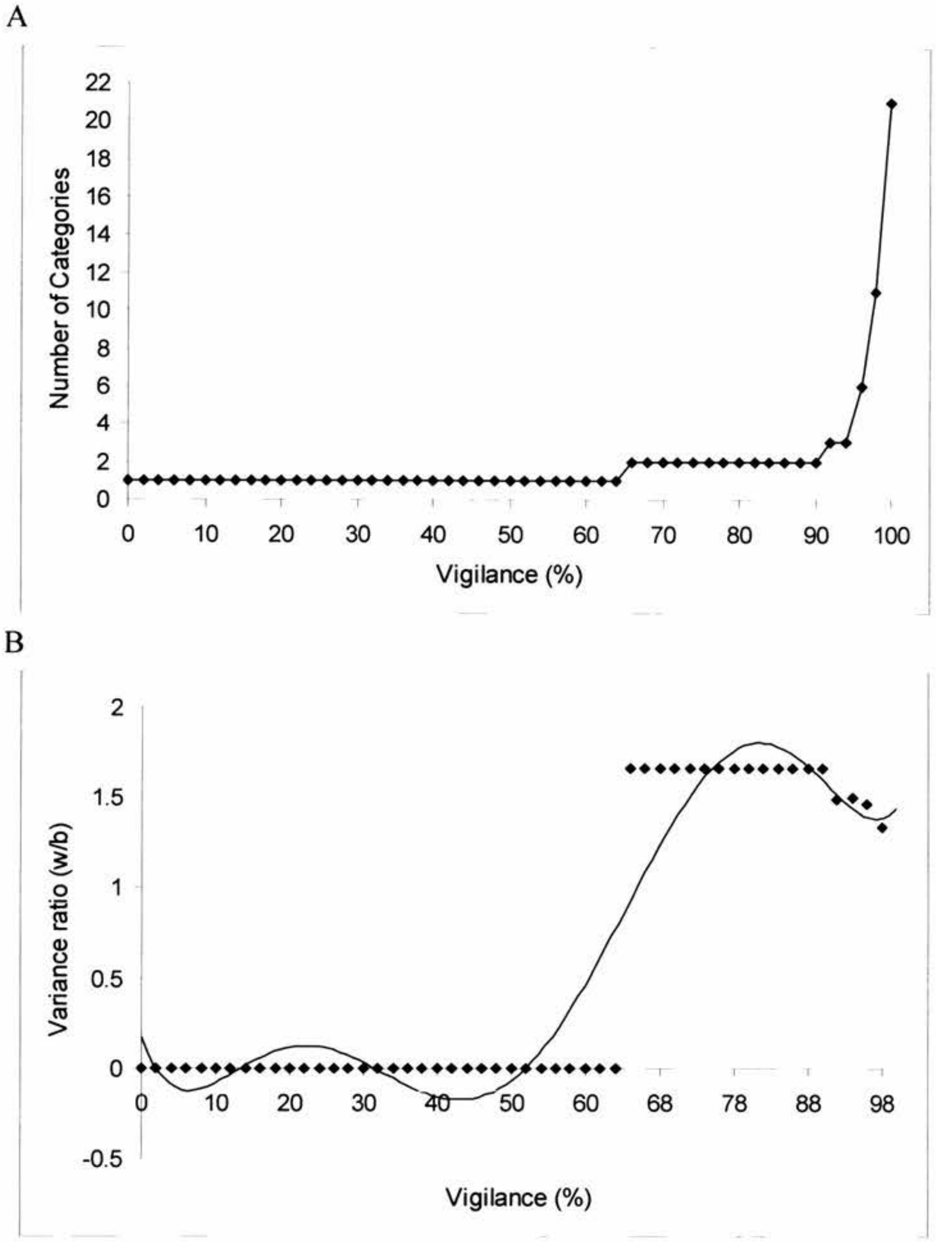


Figure 4: Recording 2: The effect of increasing vigilance on categorisation is shown in graph A. Graph B shows the change in variance ratio with increasing vigilance.

Table 2: Results of 20 runs at vigilance levels less than 65% for recording 2. Number of zero similarities refers to the number of times the dynamic time warping failed during categorisation.

Run	*No. of iterations*	*No. of categories*	*No. of zero similarities*
1	3	2	5
2	3	2	6
3	2	1	0
4	2	1	0
5	3	2	11
6	2	1	0
7	2	1	0
8	3	2	7
9	2	1	0
10	2	1	0
11	3	2	8
12	2	1	0
13	2	1	0
14	2	1	0
15	3	2	8
16	3	2	8
17	2	1	0
18	2	1	0
19	3	2	7
20	2	1	0

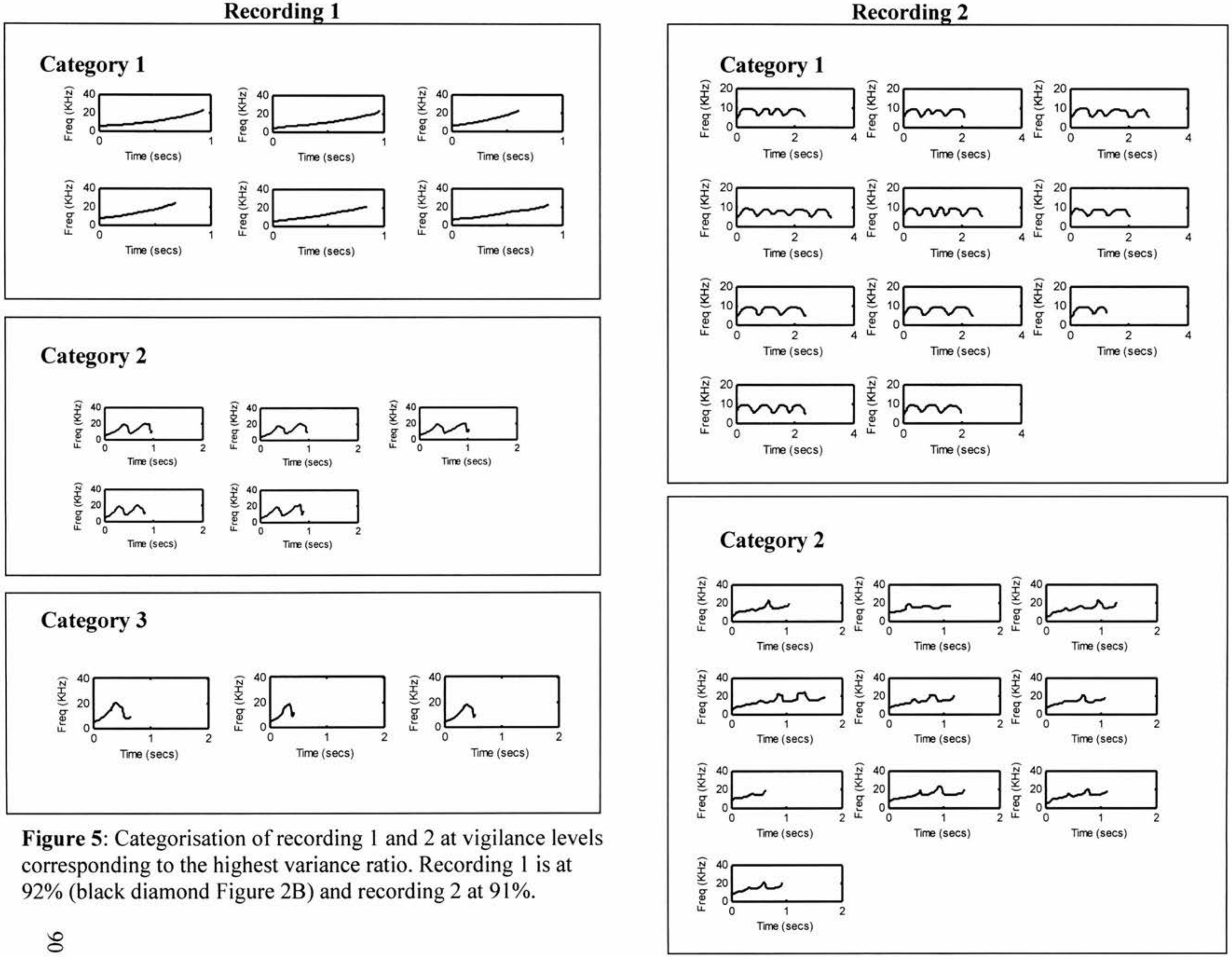


Figure 5: Categorisation of recording 1 and 2 at vigilance levels corresponding to the highest variance ratio. Recording 1 is at 92% (black diamond Figure 2B) and recording 2 at 91%.

DISCUSSION

For both recordings the highest variance ratio values (Figure 2B, Figure 4B and Figure 5) corresponded to a similar classification of the whistles as a human observer (Figure 1). For recording 1, the two whistle types were classified separately from each other, but there was a discrepancy, with ARTwarp segregating the single and multi-loop, type A whistles into two categories (Figure 5). For recording 2, the two whistle types C and D were all categorised separately from each other into 2 categories that matched the categorisation of the human observer (Figure 1 and Figure 5).

A previous study has shown that ARTwarp correctly classified known signature whistles of bottlenose dolphins at 96% vigilance (Deecke and Janik 2006). At this vigilance the program performed marginally better than human observers, but did make a couple of mistakes (Deecke and Janik 2006). These mistakes were due primarily to the duration constraint during the time-warping phase. The dynamic time warping algorithm used in the ARTwarp code allows horizontal and vertical jumps of three elements in the input contour, relative to the reference contour. In instances when the input contour is three times shorter or longer in time duration or frequency content than the reference contour, the code will return a zero similarity and not complete the time warping section of the algorithm. This results in the automatic formation of a new category and hence a new reference contour for matching. This was noticeable in this study, where it was shown in recording 2 at vigilances less than 65% (Table 2), that if the input contour was three times shorter or longer than the reference contour, then the time-warping failed and a zero similarity was returned. This is an issue when dealing with single and multi-loop whistles, if the multi-loop whistle is long in duration with respect to other whistles. In recording 2, one type D whistle in particular, (Figure 5, recording 2, category 2, column 1, row 3), was very short with respect to the multi-loop whistles of type C (Figure 5, recording 2, category 1, column 1, row 2). This whistle was the primary cause of zero similarity matches and the production of a new category. If the original reference contour was type D, input of more whistles caused a flattening out of the reference contour and a shortening of duration. Then if the shorter type D whistle was compared prior to the incorporation of the longest multi-loop whistles of type C, 1 category was produced. However, if the reference contour was type C and was maintained as modal with a longer duration, due to the incorporation of the longer multi-loop type C whistles, prior to the input of the short type D whistle, two categories were produced. Although this variation is interesting, it is not in fact such a big problem. In studies of signature whistles of dolphins, the aim is to determine stereotypy of whistles. Therefore because the whistle types were different enough to be separated at higher vigilances, due to their fundamental differences (65% in this example), the fact that there are discrepancies at lower vigilances will not affect investigations of stereotypy or the effectiveness of the ARTwarp program. However this does highlight a weakness in the program when whistles are of differing lengths, but may be similar. This is because the time warping will not be carried out due to the code restriction and therefore caution should be exercised if categorisation is based at vigilance levels lower than the highest variance ratio. The time warping factor can be changed by the user if deemed necessary. However, caution should be taken with this, as it would be possible to significantly bias the categorisation if whistle duration information was not included. It is clear from the Type C whistles that much variation occurs in the duration of this one whistle type. This is not uncommon for signature whistles, as previous work has shown many signature whistles contain multiple loops and hence could vary in duration (Tyack 1997). Therefore, although it is easy to assume that the human categorisation where the single and multi-loop whistles are placed together is correct, this may not be the case. It is possible that the single and multi-loop whistles are perceived as different types by the dolphins and as such it is difficult to know how these changes affect the information transfer between individuals. It has previously been hypothesised that these variations could transmit other information such as motivational state (Caldwell *et al.* 1990, Janik *et al.* 1994), so categorising single and multi-loop types together may in fact be incorrect.

The issue of zero similarity and variation in categorisation depending on input order is more of a problem, if it occurs at higher vigilances. This is the situation with recording 1. Here zero similarity was not a problem, but the random order of contour input caused variation in the assignment of contours to categories (Figure 3). This was especially evident with the presence of single loops of whistle type A. Through the time warping procedure, the single loops of whistle type A were very similar in duration and frequency upsweep to whistle type B. However depending on the order that the contours were presented, very different categorisation resulted (Figure 3). At high vigilance levels it was more likely that the two types would be mixed. The highest variance ratio for 92% vigilance for recording 1 was when 3 categories (Figure 5) were produced (black diamond, Figure 2B). However the mean after 20 runs at 92% vigilance was actually 2.3, SD ± 0.657 (Table 1) suggesting a degree of instability in the categorisation at this vigilance level. This problem disappears at vigilance levels of 88% and lower, when the whistles are similar enough to be consistently placed together in 1 category, but this only gives a very small window of a few percent to categorise the whistles if they are in fact of two types. At the previously identified critical vigilance of 96%, (Deecke and Janik 2006), recording 1 yielded five categories and recording 2 yielded six. For both these categorisations, none of the types were mixed together, suggesting the whistles do possess a high degree of stereotypy. However, the presence of single loop whistles of much shorter duration increases the chances of more categories being produced, due to the zero similarity restriction in the code. This was the case when all four types were mixed together and categorised at 96% vigilance. In 4 out of 5 runs, 11 categories were produced. In none of the categorisations were any of the four types mixed together, but the same categorisation never occurred twice.

The five signature whistle types used by Deecke and Janik (2006) were all less than 1 second in duration (see Janik 1999) and all recorded in a captive environment without interference from background noise. For this study, both recordings were made on a distributed mobile array, from a small moving boat in the open sea, and whistle duration ranged from less than a second to over 3 seconds (Figure 5). It is likely that the four whistle types in this study are signature whistles of individuals, due to their stereotypic nature and their use in a social event (see chapter 5). However, this is difficult to establish with any degree of certainty as it is difficult to isolate individuals or determine which individual is calling in the wild. This is however, a common feature in many studies, unless water clarity or individual behaviour allows the researcher to isolate an individual and then record its vocalisations. As a result, the 96% vigilance level set for categorising biologically important signature whistles may be most effective in captive situations and it may be more viable to reduce this level for wild studies. However, 96% could still be used to isolate signature whistles in wild recordings, if the researcher was interested in separating types from a large data set. This in some ways may be a more conservative approach, synonymous with splitting the data initially, with the option of lumping later on. However, the results of this experiment suggest that a deflated vigilance factor of 91% to 92% may be just as useful for determining signature whistles in wild bottlenose dolphins. This is still higher than the categorisation of 50 frequency contours of wild transient killer whales, which suggested a vigilance factor of 81.24% (Deecke and Janik 2006) for the most effective categorisation. At 81% vigilance levels in this study, recording 1 placed all whistles together in 1 category, but recording 2 effectively separated the two types into two categories. Therefore in some examples even a vigilance level of around 90% may be too high when nothing is known about the whistle origin or context. It would therefore be wise to test more than two different stereotyped whistle types from wild recordings, and determine the variance ratio, to see how comparable this is to both the 96% and 81% levels reported in Deecke and Janik (2006) and the 91-92% level reported here.

It is clear that ARTwarp is effective at categorising stereotyped bottlenose dolphin whistles at high vigilance levels (Figure 5). However, there are limitations when single and multi-loop whistles are included, as the random input order may affect the overall categorisation if marked differences in duration, (recording 2), or frequency (not seen in this study) exist. It may therefore be prudent to repeat categorisation a number of times to assess any differences in categorisation or consider single loops of multi-loop whistles to be different whistle types. Or it may be most prudent to check the variance ratio for the contours at a number of vigilance levels. This approach was possible in this study due to the small sample size, but would not be possible in samples of hundreds of whistles. Therefore, for large data sets it may be better to categorise at 96% vigilance and look for instances of mixing between types.

This study highlights the difficulties in quantitative categorisation of call types in wild cetaceans. However, ARTwarp does give the user the ability to change parameters depending on the question under investigation and is a repeatable methodology applicable across species.

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CHAPTER FIVE

STEREOTYPED WHISTLE EXCHANGES BETWEEN WILD BOTTLENOSE DOLPHINS

ABSTRACT

This study investigated the behavioural context of stereotypic whistle exchanges in wild bottlenose dolphins off north-east Scotland to infer function from whistle usage. Concurrent acoustic and non-acoustic behavioural data sampling were conducted during focal follows. Passive acoustic localisation using a four-element distributed array was used to identify vocal exchanges (i.e. whistles from different individuals within 3 seconds of each other). Vocal exchanges of stereotypic (2 whistle types produced repeatedly by at least 2 animals) nature occurred during 12 focal follows from 10 separate days containing 108 whistles that could be localised. Exact randomisation tests (10000 iterations) using whistles from exchange and non-exchange periods within each follow, showed that the observed number of exchanges (i.e. whistles produced by different individuals within 5 seconds of each other) was significantly different to the value that resulted from randomisation. Vocal exchanges occurred prior to dolphin subgroups joining in 9 out of 10 observed joins. Only 2 of 11 vocal exchanges were not followed by a join. Vocal exchanges of stereotyped whistles between individuals appear to be important in coordinating joins in wild dolphin groups. Categorisation analysis of exchange whistles showed that their degree of stereotypy equalled that found in signature whistles.

INTRODUCTION

Communication within a social group depends on the exchange of signals between individuals to convey information from one member to another. These signals may be acoustic, visual or olfactory but for any communication system to function it is reasonable to suspect that signals vary with context, and the need for information varies with situation.

Vocal exchanges can be described as any situation where a caller produces a signal and the receiver responds to that signal through production of its own signal, within a brief time interval. Matching of vocal signals, where animals produce the same call type in response to a call, has been demonstrated in many social animals including songbirds (Anderson *et al.* 2005, Burt *et al.* 2001, Krebs *et al.* 1981), bottlenose dolphins (Janik 2000b), killer whales (Miller *et al.* 2004), monkeys (Sugiura 1993), and elephants (Soltis *et al.* 2005). This process of acoustically matching a caller's signal may be aggressive or affiliative depending on social status and context. However for many wild studies especially of cetaceans the function of this calling behaviour remains unclear and very little information exists on vocal exchanges where different stereotyped calls are exchanged.

Bottlenose dolphins have a large repertoire of sounds including pulsed, broad-band sounds of short duration used in echolocation, (see Au 1993 for review), less distinct pulsed sounds such as cries, grunts, brays and barks (see: Connor and Smolker 1996, Janik 2000a, Overstrom 1983 for examples) and tonal whistles which are frequency modulated narrow-band sounds (e.g. Caldwell and Caldwell 1965, Janik and Slater 1998, Sayigh *et al.* 1990, 1995). Tonal whistles have been the focus of many studies and the tendency of individual bottlenose dolphins to emit a stereotyped whistle contour or signature whistle has been shown in captive, temporarily restrained and free-ranging animals (Caldwell and Caldwell 1965, Sayigh *et al.* 1990, 1999; Smolker *et al.* 1993; Janik and Slater 1998; Cook *et al.* 2004; Watwood *et al.* 2005). Caldwell and Caldwell (1965, 1968) first hypothesised that the identity of the caller was encoded in the stereotyped contour of the signature whistle, and Janik and Slater (1998) demonstrated that undisturbed captive bottlenose dolphins primarily used signature whistles during voluntary separations, and almost only used non-signature whistles when all in the same pool. Similarly, Smolker *et al.* (1993) and Watwood *et al.* (2005) have demonstrated increase signature whistle use during separations of mums and calves and allied males respectively. This tendency of whistle use by the animals suggests that signature whistles may function as cohesion calls (Janik and Slater 1998, Watwood *et al.* 2005), and explains the increased use of these whistles in isolation context where a social animal would need to convey its position to close associates. Bottlenose dolphins have been shown to live in a fission-fusion grouping pattern (Wells 1991; Connor *et al.* 2000), where social groups frequently split into sub groups and then fuse again. These changes in composition vary in temporal scale and are likely to be strongly influenced by the pressures exerted by the distribution of resources and the risk of predation, as has been suggested in other groups such as primates (Clutton-Brock and Harvey 1977). However, vocal exchanges between members of the group and behavioural context may also play a role in the temporal change of group composition.

There are many potential reasons why individuals may emit calls prior to forming a pair or group. The call may be given in ownership of a territory, such as in bird song, where the male's song advertises his ability to defend territory (for review see Catchpole and Slater 1995). Or calls may be used as a mechanism for maintaining contact when individuals are out of visual range. The term "contact call" covers a wide range of signals that have been demonstrated to maintain contact between different social units. The social units may be pairs such as mothers and young, where individuality in calls facilitates reunion (e.g. Collins *et al.* 2005, Illmann *et al.* 2002). Or the units may be groups, where contact calls are recognised by individuals within the same social group (e.g. McComb *et al.* 2000, Ramos-Fernández 2005). Because dolphins have been shown to possess a signature whistle for individual identity (Sayigh *et al.* 1999), it would be expected that if stereotyped signature whistles are used as cohesion calls or individual identifiers, then animals may emit their signature whistles prior to a group fusion to broadcast their identity to an associate. This study explores the production of stereotyped whistle contours in free-ranging bottlenose dolphins in St Andrews bay, Scotland.

METHODS

Data collection

This study was conducted off the north-east coast of Scotland between Arbroath and Fife Ness (Figure 1) from July to September in 2003 and 2004. The subject animals were individuals of the bottlenose dolphin population numbering approximately 130 individuals (Wilson *et al.* 1999), and known to travel large distances around the north-east Scotland coast from the Moray Firth to St Andrews bay (Wilson *et al.* 2004). Focal follows (Altmann 1974), employing concurrent acoustic recordings on a 4 element distributed array and non acoustic, behavioural continuous sampling with 2 minute summaries, and standard photo-identification techniques were undertaken from a small boat when sea state was Beaufort 3 or less and weather was dry: (Boat a, June-August 2003: 5.75m, 2 x 60 Hp 4 stroke outboard engines. Boat b, August-September 2003: 6.25m, 120 Hp diesel inboard engine. Boat c, June-September 2004: 5.70m, 1 x 90 Hp outboard engine).

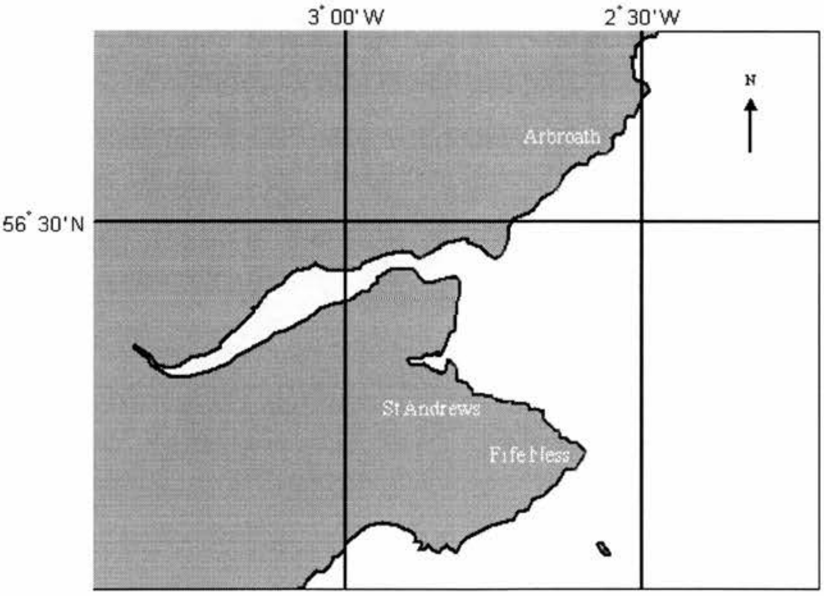


Figure 1: Map showing location of study area between the extremes of Arbroath to the north and Fife Ness to the south.

The distributed array consisted of three HTI-94-SSQ hydrophones and one HTI-96-MIN hydrophone all with a frequency response of 2 Hz to 30 kHz ± 1 dB, attached to tensioned 2 meter pieces of chain, with waterproof tape. The four elements were then distributed around the boat in a box array to allow passive acoustic localisation. Hydrophones were positioned at 2m depth and were placed between 160 cm and 280 cm apart depending on vessel used. Recordings were made onto a Fostex D824 multi-track digital recorder during 2003 and an Alesis adat HD24 multi-track digital recorder during 2004 (sampling frequency 48 kHz, 24 bit for the Fostex, 32 bit for the Alesis. Change due to replacement of damaged equipment). Spoken tracks of two observers, one detailing the surface behaviour of the focal animal and its associates and one the positions and behaviour of the non focal animals were also synchronised to the multi-track recorder. These observations included descriptions of group composition and size, distance and direction of groups from the boat (based on a standard clock face with the bow being 12 o'clock) and group activity (see Table 1, Chapter 6), Focal observations were spoken into a head-microphone and received on a Yaesu FRG-9600 receiver and non focal observations on a hand held microphone connected directly to the multi-track recorder. Dorsal fin photo-identification of the focal and its associates was completed using a Canon Digital D30 SLR camera with a Sigma 100-300 mm APO lens.

Data analysis

In total, 72 focal follows were conducted over 28 separate days, totalling 48 hours of recordings. For each follow the same hydrophone track was scanned to visually pick out instances of stereotyped and repeated whistle vocalisations. This method was used as a primary way to sort the data, as human observers have been shown to be efficient in determining stereotyped vocalisations (Janik 1999). The scanning was completed without any knowledge of the group composition, behaviour sampling or recording history in order to minimise contextual bias. The stereotyped and repeated whistles (Figure 2) were defined as any occurrence of at least two different whistle types each repeated at least twice, and separated in time by 3 seconds or less (The 3 second period was measured from the end of one whistle to the start of the next). When multiple sections were within the same recording, sections had to be at least 2 minutes apart to be used. Instances of engine noise were also catalogued and graded. Engine noise level 1 referred to times when dolphin signals would be masked. This occurred whenever the engine exceeded 2000 rpm. Engine noise 2 referred to times when dolphin signals could be reliably seen through the background noise, this was at times when the engine was running at below 2000 rpm. There were also times when only minimal or no engine noise was present as the engine would be out of gear or off. Any sections of recordings containing level 1 engine noise were discarded from the analysis.

Localisation of whistle types

Onset time of each whistle event was logged and candidate sections were formatted for localisation analysis in the Matlab based TOADY program (see chapter 2). Toady uses the method of cross-correlation of time of arrival differences between hydrophone pairs to determine signal source, a method possible when delays are preserved on a multi-track recorder. For this study, 6 hydrophone pairs were present as four receivers were in use. Therefore for each whistle 6 hyperbolas were plotted to determine signal source (see figure 3 for example). In total 18 separate whistle sections from 12 separate follows from 10 separate days were identified as examples of a candidate for stereotyped exchanges. From these 18 sections, 2 were discarded due to not meeting the time criteria of whistles being less than 3 seconds apart or within 2 minutes of another section. From the remaining 16 sections, 432 individual whistles were identified and run through the localisation system. Whistles were discarded if: 1. The signal was too weak to appear on all four hydrophone recordings. 2. Large portions of the whistles overlapped so that it was difficult to distinguish between them or filter out the overlapping whistle. 3. Three or more hyperbolas did not converge on the same caller position. 4. Source location was given behind the boat in the engine position. 5. Categorisation of calls, via computer matching did not occur at a high similarity value. In all instances, localisation of all pairs was completed without reference to the position of the hyperbolas of previously localised pairs or the visual observations of dolphin positions.

Considering all these factors, 11 separate sections totalling 108 whistles, from 8 separate follows on 7 separate days, were of sufficient quality for localisation and further analysis was only conducted on these whistles.

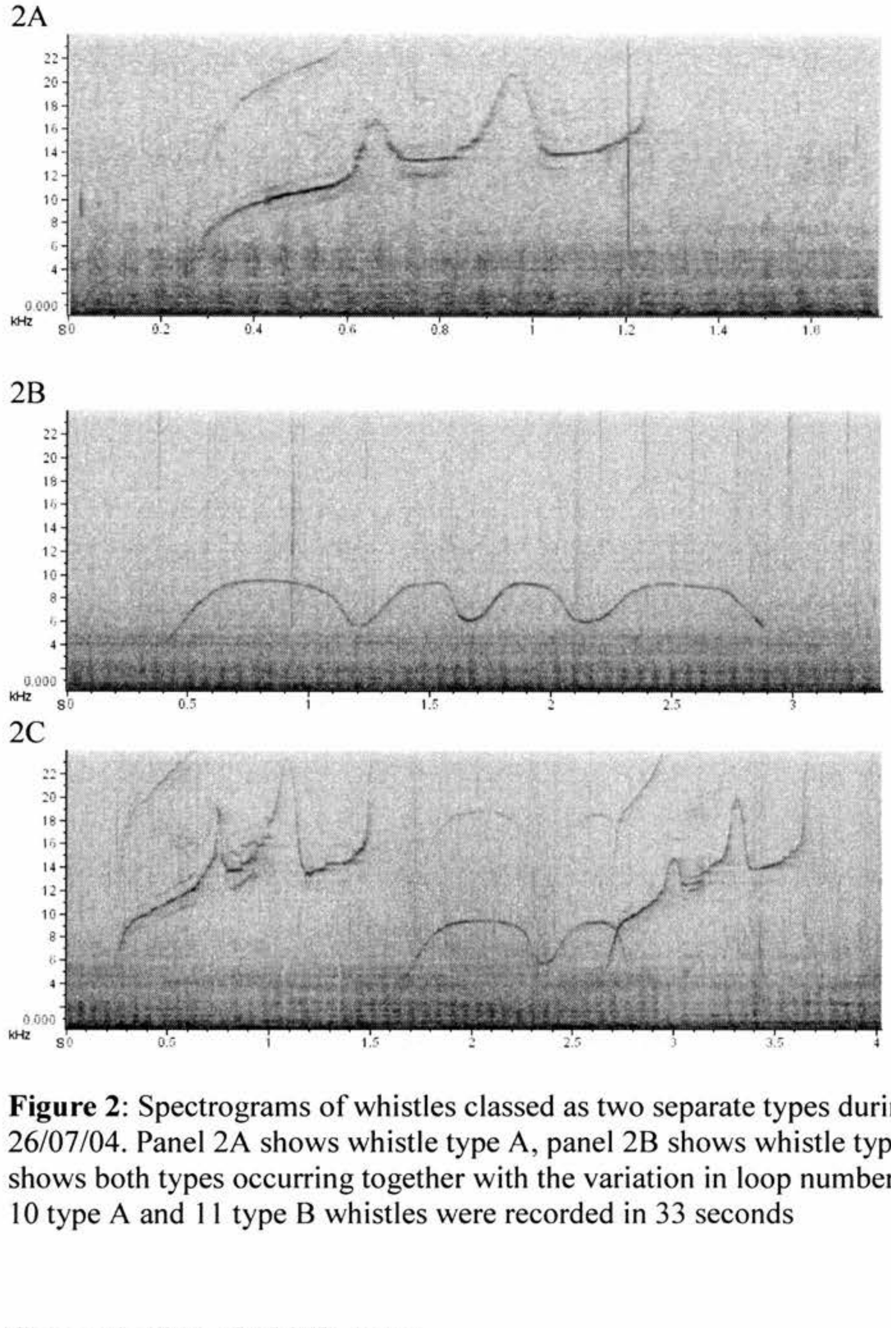


Figure 2: Spectrograms of whistles classed as two separate types during the event on 26/07/04. Panel 2A shows whistle type A, panel 2B shows whistle type B and panel 2C shows both types occurring together with the variation in loop number for type B. In total 10 type A and 11 type B whistles were recorded in 33 seconds

Categorisation of whistle types

Categorisation tests for each of the 11 exchange events was undertaken to test if whistles classed as the same type by initial human judgement, were also classed together by ARTwarp, a neural network program (Deecke and Janik 2006). Firstly, frequency contours of each of the 108 whistles were extracted in Matlab version 6.5.1. For this, spectrograms of each whistle were produced (FFT 2048, frame length 512, overlap between frames 87.5%, Hanning window, time resolution 1.333 ms) and automated contour extraction, using a peak algorithm, was performed. A maximum of 10 edits were used depending on the signal quality. Editing allowed the initial extraction to be improved by adjusting the extraction line produced by Matlab, to better fit the underlying whistle. Each contour file was down-sampled to a time resolution of 10 ms and converted to a text file. The text files for each of the 11 separate sections were run through the ARTwarp automated classification system (Deecke and Janik 2006). This system uses an adaptive resonance theory (ART) neural network and dynamic time warping to categorise contours based on a certain degree of similarity or vigilance factor. The vigilance factor was initially set to 96%, based on the critical vigilance factor determined by Deecke and Janik (2006) during the categorisation of known stereotyped signature whistles. 96% vigilance refers to the fineness of categorisation, i.e. for two whistles to be in the same category they must have a 96% similarity. To test the influence of the vigilance parameter, if categorisation held at 96%, the vigilance was increased until contours of the same type were split, thus recording a maximum vigilance level. Vigilance was then decreased by 1% increments until the categorisation broke down and mixed the whistle types together. Down-sampling was a practical necessity to decrease the time taken by the ARTwarp software. Categorisation run at a time resolution of 1 ms, took at least 10 times as long to complete compared to a time resolution of 10 ms, showing the method to be impractical for analysis. For control, contours from one event were categorized at a time resolution of 1.3 ms (time resolution at initial extraction) and 10 ms (time resolution after down sampling) and both yielded equal results when categorised in ARTwarp at 96% vigilance. Contours were down-sampled after the extraction so as not to affect the extraction process. If extraction was completed at a time resolution of 10 ms, large errors in the automated extraction occurred.

Randomisation test

When a number of animals were sighted around the boat, it would be expected that a number of whistles may be within three seconds of each other by chance alone without an exchange taking place. Therefore a randomisation test was performed to determine if the observations of stereotyped whistles within three seconds of each other could be explained by a chance occurrence. For each follow from which the exchange sequences were taken, one minute intervals where the background noise was equal to or lower than that observed during the exchange were identified. The occurrence of each of the whistle types present in the exchange was then noted over the entire follow. The number of times the start of the first type of whistle was within five seconds of the start of the second type was recorded for each follow. Five seconds was used to allow for duration of the whistles, because for the exchange events the 3 second period was measured from the end of one whistle to the start of the next. The locations of each whistle type were then randomised 10,000 times to observe the number of times the pairs were within five seconds of each other by chance and this value compared to the actual observations (see Appendix 1 for code).

Behavioural context

The tracks detailing surface behaviour of the focal and non focal animals were scribed to a database. Times of each exchange event were compared to the synchronised time in each spoken track. In order to standardise the two sets of observations, details of group locations and behaviour during the two minute behavioural sample after the exchange event had ceased, were considered (Table 1). In the one instance, where the event appeared to continue after the last call was localised (event 10, table 1), observations were considered after the last non localised call.

RESULTS

11 separate sections, totalling 108 whistles, were identified as vocal exchanges. The number of whistles in the 11 events was variable (Table 1) ranging from 4-23 (mean 9.8 SE ± 2.02). 10 of the 11 events consisted of two whistle types and 1 event had 5 whistle types (Table 1).

Localisation of whistle types

Localisation was effective for all 108 whistles identified in the exchanges. In line with the calibration of this system (Chapter 2) only direction from the array and depth of the calls was considered when assigning caller position. Callers' position for each whistle is shown in Table 1, and an example of the localisation using the first 10 whistles from event 8 are shown in Figure 3. For all 108 whistles, localisations corresponded to behavioural observations of groups, indicating that dolphins were in fact present at the positions given by the localisation. Dolphins routinely cruise at speeds of 1.4 to 3.1 meters per second (Reynolds *et al.* 2000), so in 3 seconds individuals could have travelled up to 9 meters. However, throughout the continuous sampling at no time were individual animals observed to be continually switching between subgroups at each surfacing. Additionally, during the exchange events, individuals were not observed to cross from one whistle location to another, making it unlikely that one animal was responsible for all call types within any event.

Categorisation of whistle types

For events 1-10, ARTwarp categorised whistles into the same two categories as the human observer at vigilance levels over 90% (Figure 4). For 4 of the events, (3, 4, 5, 6) categorisation was at the same or higher vigilance level as the critical vigilance factor of 96% given by Deecke & Janik (2006) for the classification of signature whistles. For the remaining event, which involved 5 whistle types, 3 of the types categorised into 3 separate categories at a vigilance level of 92%. The remaining 2 types were so similar that at 92% vigilance they were categorised together. At vigilance levels higher than 92% these 2 types were mixed and an example of this is given in Appendix 2. The subtle differences seen between these two types, questions the importance of differences observed by humans to the animals. These two types are very similar and may be classified by the animals as one type. This high similarity is generally in line with that seen when signature whistles have been classified with ARTwarp (Deecke and Janik 2006).

Randomisation test

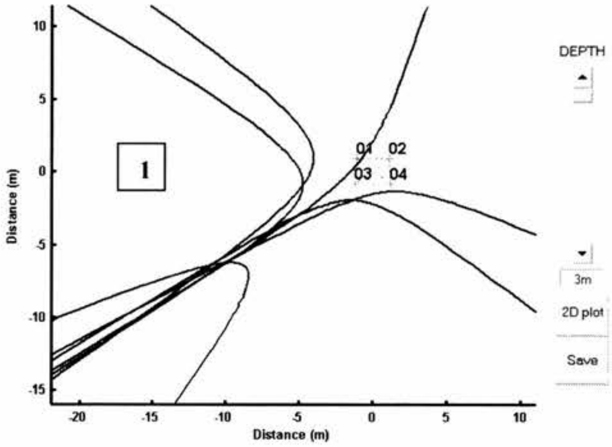
Randomisation showed that the observed occurrence of whistle types (either A-B or B-A) within 5 seconds of each other was unlikely to have occurred by chance (Table 2). For 8 of the 11 events, 100% of randomisation runs produced less than the number of whistle proximities in the actual data. For the remaining 3 events 72, 78 and 98 percent of runs produced less than the observed number of whistle proximities. Two of these events (72% and 98%) contained only 1 and 2 actual whistle proximities and were short sequences. The remaining event contained the five whistle types and hence some types were never within 5 seconds of other types, resulting in some pairs having zero proximity in the actual data.

Behavioural context

From convergence of caller position through localisation, and behavioural observations of surface group positions, results showed that 9 of the 11 instances of vocal exchanges were followed by sub-groups joining (Table 1). For the remaining 2 events, (3 and 5) surface observations did not conclusively point to groups joining, and caller positions did not converge during the localisation. Only 1 other instance of a join, in the 170 minutes of recording where the background noise levels would have allowed whistles to be visible, was seen during the follows containing the exchange events. This join was not preceded by an exchange.

Table 1: Summary of all 11 events, including localised positions of whistles and behavioural outcome. Lower case letters indicate part of sequence too faint for localisation. ub indicates under boat (Types A and B are not the same in all follows).

Event	Whistle sequence	Type A localised position (o'clock)	Type B localised position (o'clock)	Behavioural observation in 2 minute sample period after event	Outcome (Identification method)
1	AABBAB	7, 8, 11.30	10, 10.30, 12	Sub group 1: Splashing and socialising at 10 o'clock (40m away) Sub group 2: mum and calf pair at 9 (10m away)	Came together (localisation)
2	ABAABAb	10,10, 10, 5.30	10, 8	Animals joined to form 1 large group from 10.30-3 : leaping, splashing and surfacing	Came together (visual)
3	BABAAAAA	5.30, 5.30, 6.30, 6.30, 6.30, 7	4, 4	Socialising and bellies out by big group ranging from 1-3, and Small sub group at 3.30 surfacing	Not together (localisation and visual)
4	AABB	11.30, 12	1, 12	Sub group 1: surfacing at 10 (<30m away) Sub group 2: surfacing at 12 (<30m away) Subgroup 3: surfacing at 1.30 (<30m away)	Came together (localisation)
5	aABBAA	5.30, 6.30	5.30, 5.30, 5	Sub group 1: surfacing at 3 (20m away Sub group 2: heading away at 4 (20m away)	Not together (localisation and visual)
6	ABAB	4, 5	3.30, 7(ub)	All animals jumping and chin slapping at 9-10	Came together (visual)
7	ABAABABBAB	11, 9, 7, 7, 6.30	1(ub), 1, 6.30, 5.30, 5.30, 6.30	3 animals have joined at 12.30 Sub group behind have been lost	Came together (localisation)
8	ABABAABABA ABAB	7 (all)	5 (all)	Animals joined to form one large group at 4: aerial behaviour, heads out and bellies up	Came together (visual)
9	aaABABABA	11 (>30m away)	11 (5m away)	Subgroups joined at 9-10: are synchronously diving	Came together (visual)
10	ABABABABBB AABABABBAA B bbbbbbbbaba	3 (all)	1 (all)	Animals joined to form 1 large group from 1-4. Closest animals at 2 (15-20m away): aerial behaviour, splashing, side, head and chin slaps.	Came together (visual)
11	ABBACBBBCB DBCBDBCCAE CDE	All types localise to 9, 10 and 11		Animals joined to form 1 large group at 10-1: changing direction, splashing and tail slapping	Came together (localisation and visual)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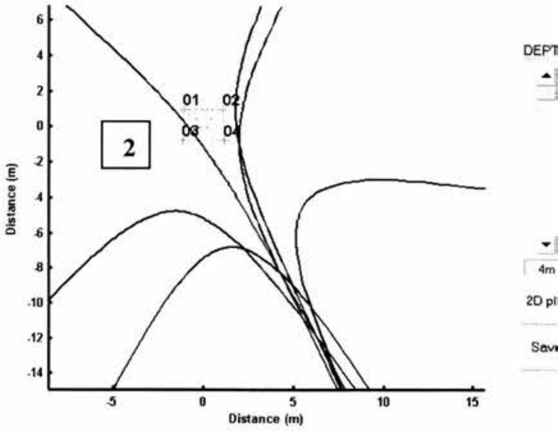
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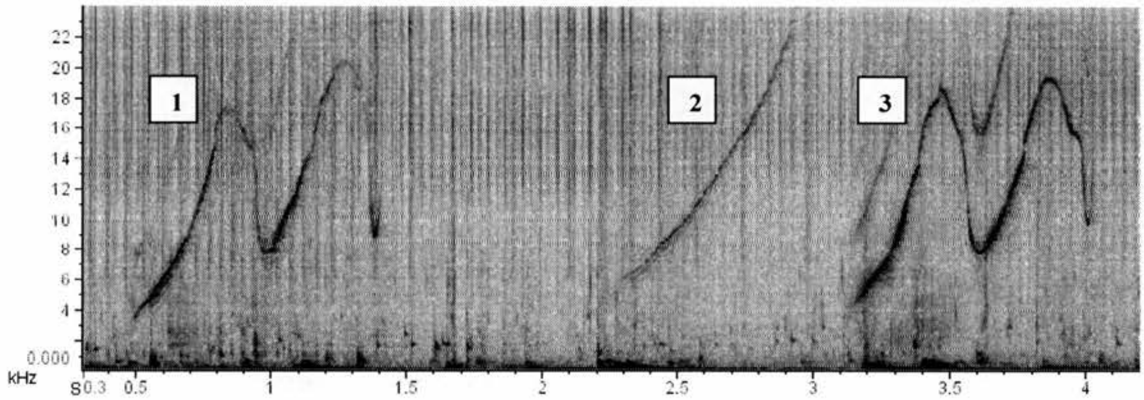
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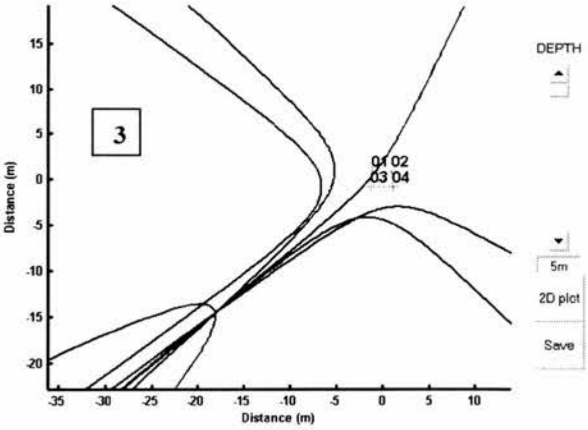
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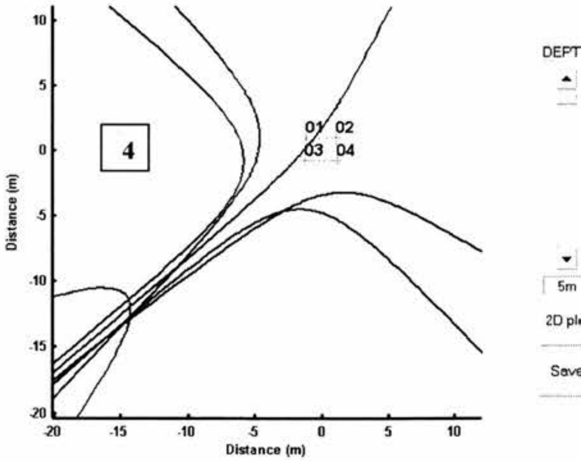
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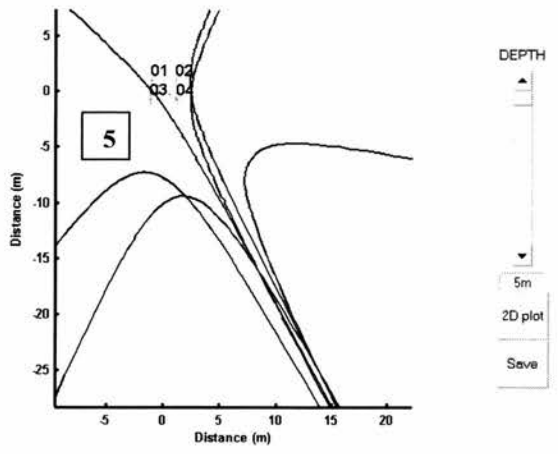
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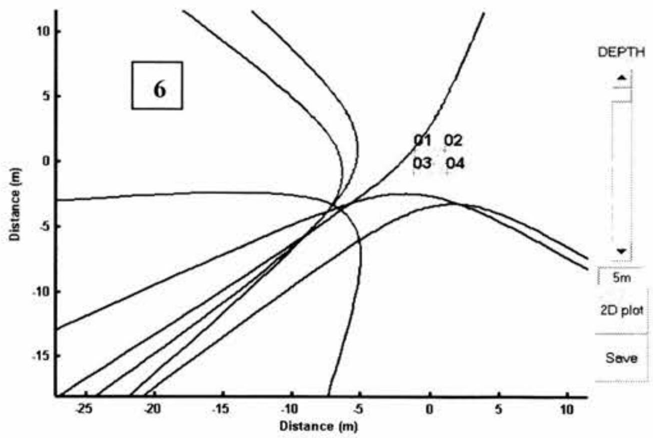
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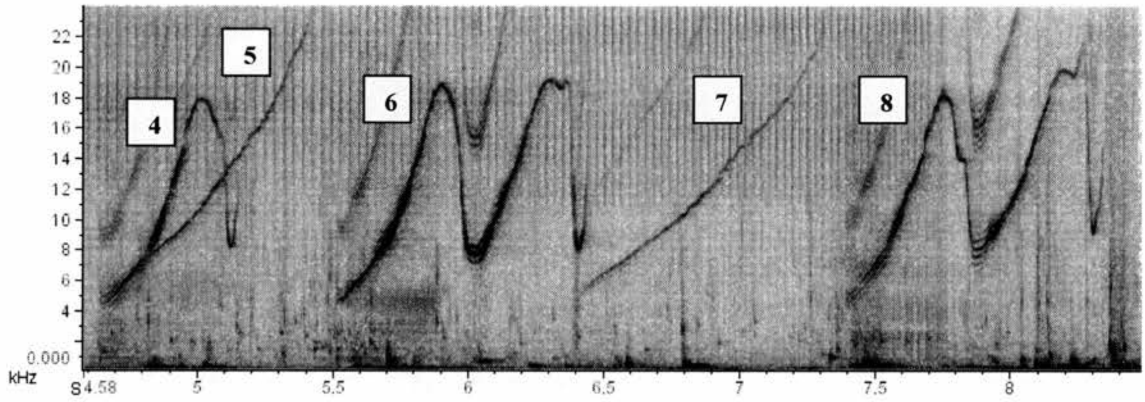
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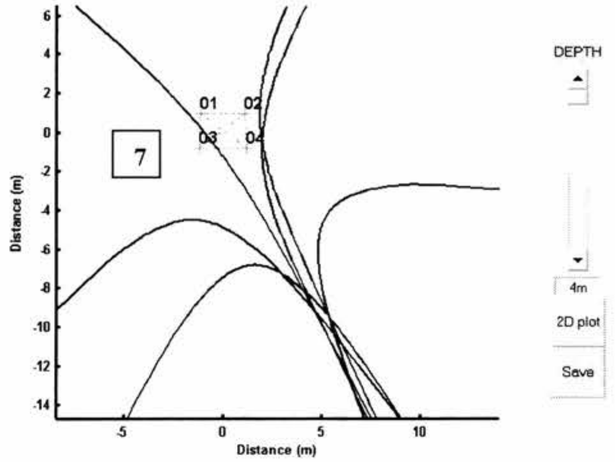
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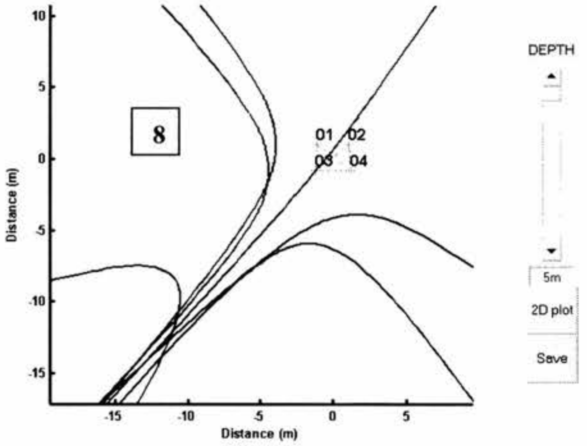
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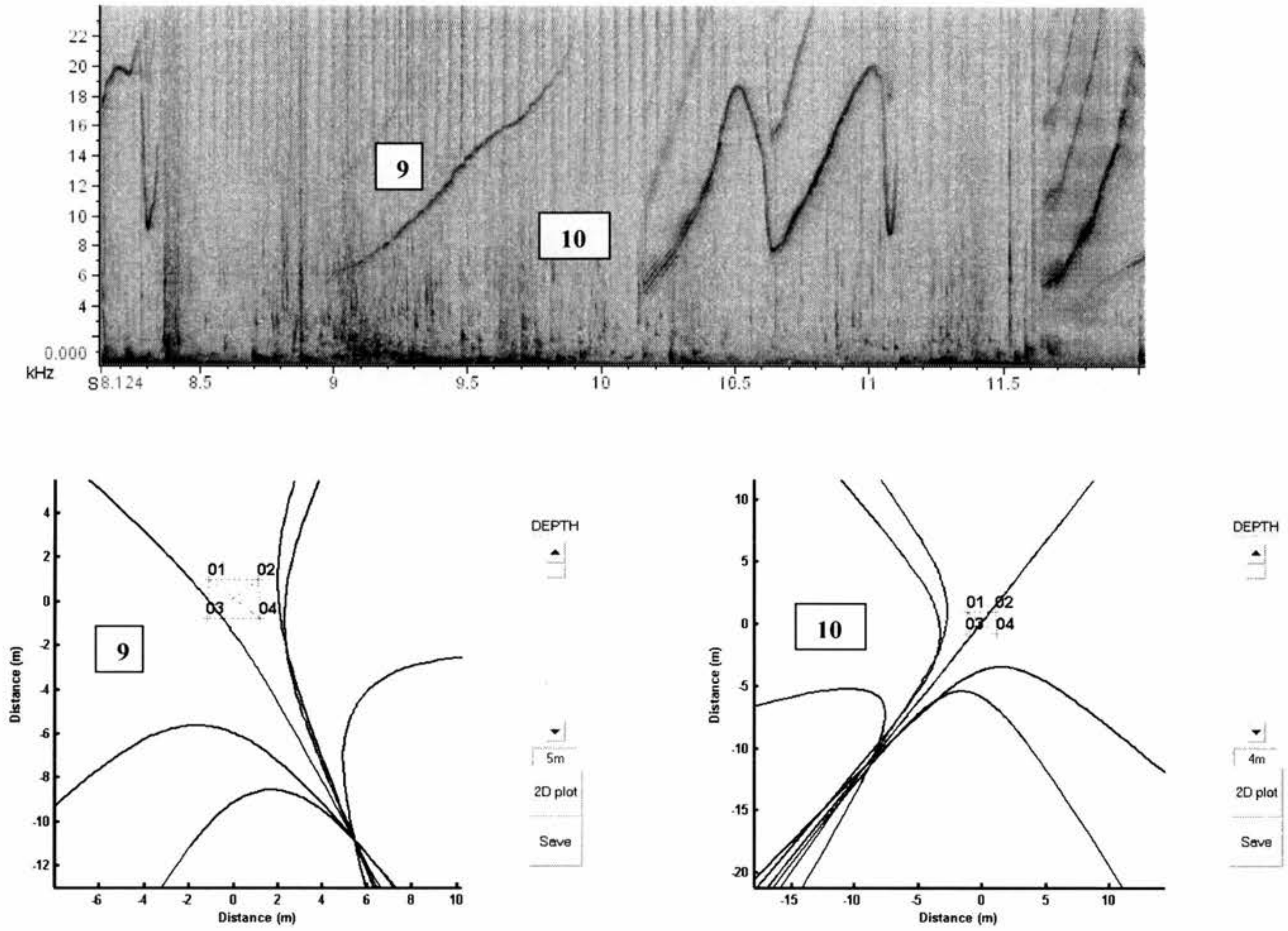

Figure 3: Spectrogram of an exchange event. Numbers on spectrogram indicate which whistle is localised on the corresponding numbered localisation plot. The intercept of lines on the localisation plots show position of calling dolphin. Whistle type A (numbers 1, 3, 4, 6, 8, 10) all localise to a position of 7 o'clock from the boat and whistle type B (numbers 2, 5, 7, 9) all localise to a position at 5 o'clock from the boat

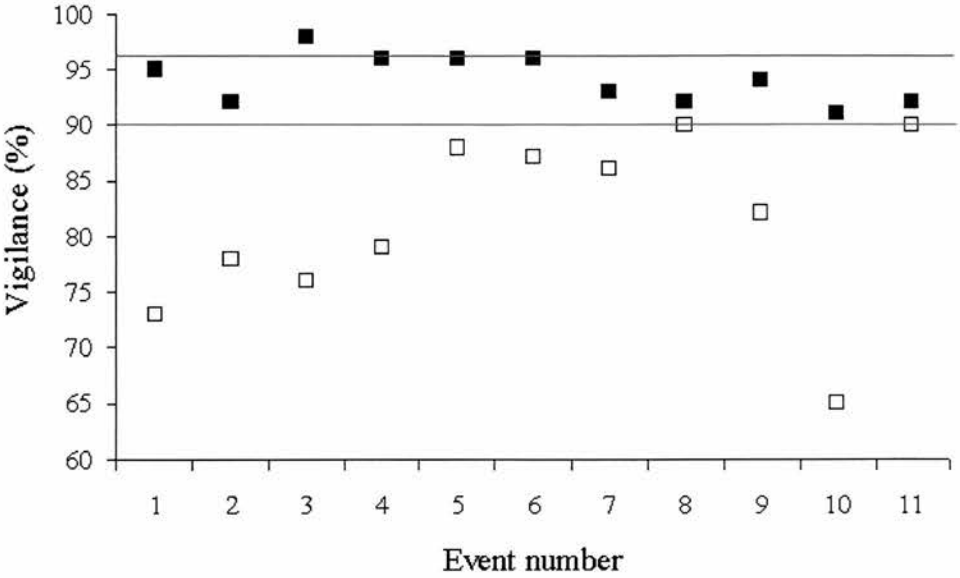

Figure 4: Vigilance range for events 1-10. Closed squares indicate highest vigilance level for assignment of 2 categories (events 1-10) and 4 categories (event 11). Open squares represent lowest vigilance level at which the 2 categories remained stable. Blue line represents the 96% critical vigilance level identified by Deecke and Janik (2006). Red line represents 90% vigilance at which all the events categorised above.

Table 2: Results of the randomisation tests, showing percentage of runs in which the randomised values were lower than values observed in the data (10,000 randomisations). For event 11 instances of pairs for all 5 types were considered and then summed.

Event Number	Percentage of runs producing less than observed number of whistle proximities
1	100
2	100
3	100
4	72
5	98
6	100
7	100
8	100
9	100
10	100
11	78 (mean, se ± 9.8)

DISCUSSION

This study shows that when sequences of at least two stereotyped whistles are observed, within a 3 second temporal proximity, a fusion of dolphin groups occurred 82% of the time (9 out of 11 events). Also only 1 other instance of a join was seen during the follows containing the exchange events and this join was not preceded by an exchange. This shows that individual dolphins exchanged stereotyped whistles prior to groups joining in 90% of joins (9 out of 10 observed joins). Localisation analysis confirmed that whistle types within each exchange came from different locations and behavioural observations confirm that the two types were not emitted by the same individual. However, it is not possible to conclude if the production of one call type directly caused the production of the other call type, or if all instances of each type within one exchange were made by the same individual. The issue here is firstly if the calls are actually an exchange event and secondly whether two individuals or two groups are producing the calls.

The randomisation test effectively showed that the call types were unlikely to occur together by chance alone, suggesting that they may be associated with a specific context. However, the test only randomised the timing of the events within the sequence, which may bias towards finding a dependency if calls only occur in bouts. The presence of many single whistles during the recordings suggests that not all whistles occur within bouts. Analysis of call rates with behaviour and group size (chapter 6) indicate that whistle production varies depending on a number of factors including spacing of individuals and activity, making the presence of bouts difficult to tease apart. Further evidence of the events being an exchange can be seen from the categorisation tests and the behavioural observations. The level of whistle stereotypy, shown by the categorisation, matches that seen in signature whistles (Deecke and Janik 2006) and suggests that the call types used during exchanges may be signature whistles of individuals. The theory that signature whistles function to convey individual identity of the caller to members of its social group, was first hypothesised in the 1960's (Caldwell and Caldwell 1965, 1968). Since then a number of studies have demonstrated that signature whistles do convey individual information and are used as cohesion calls (Cook *et al.* 2004, Janik *et al.* 1994, Janik and Slater 1998, Sayigh *et al.* 1999, Watwood *et al.* 2005). If the whistles seen in the exchanges are signature whistles, then it follows that the caller will be emitting this whistle to supply individual information to another dolphin and maintain contact. Additionally, with 82% of the exchanges shown to precede a join of groups, both visually and via localisation in the cases where caller's position converged, it can be reasoned that these exchanges are used to convey identity between two individuals as a precursor to associates joining. This may also explain the reason why two of the exchanges were not followed by a join. In these cases it may be that the association or social circumstance of the individuals was not such as to cause a join. In squirrel monkeys (*Saimiri sciureus*) mutually preferred partners were shown to exchange chuck vocalisations more frequently and with shorter response latencies (Biben *et al.* 1986). Additionally, in a sequence of chucks, the identity of successive vocalisers was not random, suggesting the order in which chucks calls are made depends on recognition of individual's chucks (Symmes and Biben 1988). For individuals to discriminate between chucks they must have some familiarity with the individual they are exchanging with. The correlation of chuck calls with an affiliative context is similar to the mechanism of dolphins broadcasting their identity to close associates with signature whistles. Maintaining contact with preferred associates in this way is advantageous in highly mobile species like dolphins or troops of monkeys that may lose sight of each other in murky environments or dense vegetation.

There is a possibility that the calls were in response to some other stimulus that was not detected during the recording. If some other acoustic stimulus was produced then it should have been received on the hydrophones. Or the stimulus could have been visual and produced by another animal within the callers group. This is difficult to completely rule out, as underwater observations are impossible due to the poor water clarity. However, this poor water clarity also exists for the dolphins, and during the exchange events the animals were often more than 10 meters apart, suggesting they are more likely to use acoustic rather than visual stimuli to elicit a response from others. Additionally the Scottish population of dolphins appear to vocalise considerably more than bottlenose dolphins from some tropical regions (V Janik pers comm), suggesting the environment may not be sufficient for keeping visual contact.

The question of whether two individuals or two groups are producing the calls is problematic without knowledge of each individual's signature whistle or how dolphin groups communicate in the wild. The fission-fusion society and lack of long-term associations seen in this population (Wilson 1995) suggest that the distinctive repertoires' seen in stable matrilineal groups such as killer whales (Ford 1991) is unlikely. Stable groups of killer whales have been shown to exchange the same call type between matrilineal groups suggesting that these exchanges are important in intragroup calling (Miller *et al.* 2004). Similarly, bottlenose dolphins in Monkey Mia, Western Australia have shown whistle convergence between males within an alliance (Smolker and Pepper 1999). In this instance all three male dolphins converged on a set of closely related whistle types and it appears that this convergence functions in the context of alliance formation and herding of females. This convergence can than be seen as an alliance signature, synonymous with a group call to signify alliance membership. However, as signature whistles have been shown to remain stable for up to 12 years (Sayigh *et al.* 1990), it is likely that these alliance members also have individual signature whistles. Therefore the alliance whistle is probably a convergence of non-signature whistle types, which is used to reinforce alliance membership but not convey individual identity. In other animals, group call types are associated in fission-fusion living and do serve to maintain association with conspecifics in a variety of context and social units (e.g. Japanese macaques; Sugiura 1993: Spider monkeys; Ramos-Fernández 2005: African elephants; McComb *et al.* 2000, Poole *et al.* 1988: Greater spear-nosed bats; Boughman & Wilkinson: Golden brown mouse lemur; Braune *et al.* 2005: Mexican jays; Hopp *et al.* 2001). An example of this is seen in cotton-top tamarins (*Saguinus oedipus oedipus*), that have a repertoire based on a few simple elements that are varied and combined for use in different contexts (Cleveland and Snowdon 1982). For intragroup cohesion when animals are closely located, the quiet long call with lower amplitude and shorter duration is used. In contrast when intergroup cohesion is needed the normal long call with higher amplitude and longer syllables is used. A further combination long call is used when individuals are isolated. The variations in the parameters of these calls allow different levels of localisation which allow cohesion to be maintained. A similar situation exists in white-faced capuchin monkeys (*Cebus capucinus*) where initiation and cohesion in troop movement is maintained by a trill vocalisation given by troop members (Boinski 1993). Similarly in the mangabey, *Cercocebus albigena,* the whoopgobble vocalisation appears to increases cohesion and influences the direction of movement within a group (Waser 1977). In baboons, (*Papio cynocephalus ursinus*) contact barks are given at higher rates when an individual or sub-group has lost contact with the main group (Cheney *et al.* 1996), and a marked temporal clumping of contact barks from females suggests that females may exchange calls with one another. Female baboons are more likely to give answering contact barks when they hear a bark from a relative when they themselves are lagging behind in the group. Hence, giving barks is primarily with reference to their own position. Individual attributes in contact barks may allow baboons to exchange calls selectively with certain individuals, explaining why barks can be given when females are in close proximity to other individuals. In these cases barks may be directed to a close relative or infant that may be out of sight. Although contact barks may ultimately function to allow individuals to avoid separation they appear to serve the primary function of reflecting the signaller's attempts to maintain contact with certain conspecifics (Cheney *et al.* 1996). This appears to be a similar system to that used by dolphins, with the main difference being an individual call as opposed to a group call. However in the marine environment where the depth of the caller will affect sound production, it appears more functional to have an individualised rather than group call where contour structure, which is not changed at depth, is the primary identifier. Additionally, if a group call type was used to elicit joins, then it would be expected that each of the observed exchange sequences, that preceded a join, would have contained a similarly contoured whistle, identifiable across the population as is seen in the group calls used for cohesion in other species.

The presence of individual signature whistles rather than group specific calls to maintain group cohesion (Janik and Slater 1998, Watwood *et al.* 2005) adds more support to one rather than many individuals producing each call. However, there is the possibility that different individuals are mimicking each others whistles, again resulting in a different individual producing each call. Bottlenose dolphins are capable of mimicking both novel sounds (Reiss and McCowan 1993, Richards *et al.* 1984) and each others signature whistles (Tyack 1986), but it is unknown when animals do this in the wild and what function it may serve. Matching of whistles has been shown in wild bottlenose dolphins (Janik 2000b) and may be an aggressive interaction or a way to maintain contact. An example of aggressive interactions occur during counter-singing in songbirds, where individuals use learned song-types in matching interactions during territorial disputes with unknown callers (Beecher *et al.* 2000, Burt *et al.* 2001, Krebs *et al.* 1981). However in killer whales (*Orcinus orca*), call-type matching has been shown between members of matrilineal groups travelling together (Miller *et al.* 2004), suggesting a more affiliative than aggressive function. Similarly, in northern cardinals (*Cardinalis cardinalis*) male birds are least likely to come to the nest when their mates match their calls suggesting matching is important in coordinating biparental care (Halkin 1997). However, if matching was occurring in this study it would not be expected for separate groups to join after the exchanges, but rather for groups to remain distinct as the same whistle type is emitted in the same location. However this was not observed. Additionally, copying of signature whistles in a group of captive dolphins was shown to be rare and to not initiate reunions or specific vocal responses (Janik and Slater 1998).

The final evidence to suggest these whistles may be from one individual comes from the literature on vocal learning. Bottlenose dolphins have been shown to be efficient vocal learners (for review see Janik and Slater 1997) with calves learning their signature whistles (Fripp *et al.* 2005, Tyack 1997). As a result of this learning ability, noticeable differences are present between signature whistle contours of individuals (see examples in: Caldwell and Caldwell 1965, Janik and Slater 1998, Smolker *et al.* 1993) and signature whistles make up a large proportion of an animal's daily repertoire (Cook *et al.* 2004). Therefore, the repeated production of such stereotyped whistles indicates that they are likely to be signature whistles of individuals. However, even if a different animal was emitting each call, the behaviour observations suggest that the function of producing stereotyped calls in these sequences still elicits a join of groups.

This study has demonstrated that Scottish bottlenose dolphins appear to use stereotyped whistles to broadcast identity to close associates and use these calls as precursors to social joins. This theory is in line with the fission-fusion living demonstrated for this species (Conner *et al*. 2000, Wells 1991) and the lack of stable alliances or close associations in this population (Wilson 1995), which suggests a need for animals to be able to determine which individuals are present in their environment. It is also consistent with the theory of signature whistles which have been shown to be individual identifiers and contact calls. Future analysis could concentrate on recording more instances when subgroups are present and hence likely to be involved in joining events. Similarly, analysis could focus on identifying other instances of stereotyped whistle production and trying to relate these to specific individuals or context. Trying to look at the levels of individual associations in this area may also provide some insight into whether certain animals join more frequently than others.

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APPENDICES

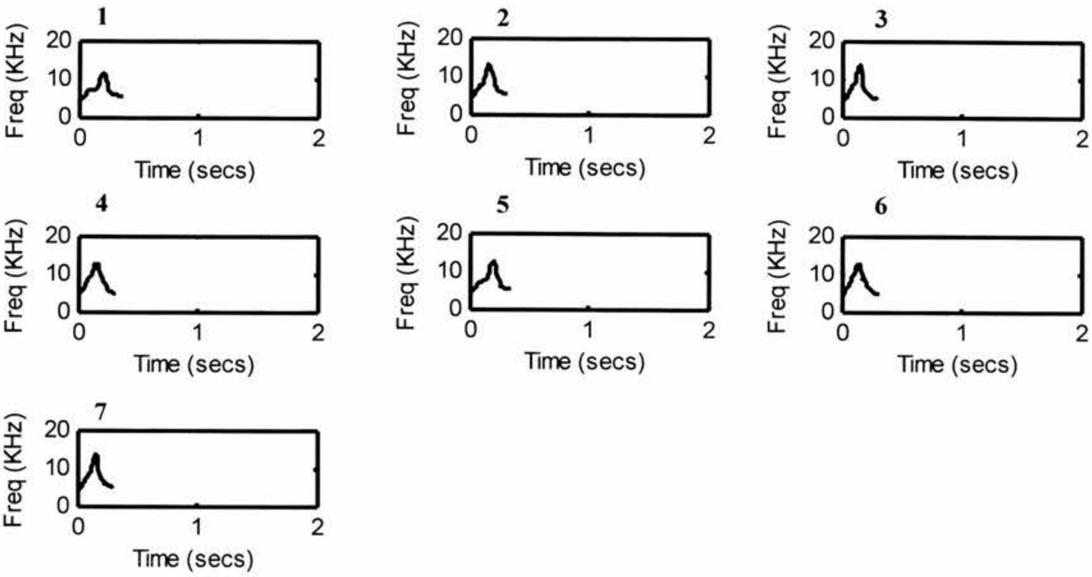
Appendix 1

The Matlab code used in the randomisation tests. Values in italics were changed depending on observations.

```
nrands = 10000;
ncloseobserved = 2;
minutesrecorded = 13;
secondsrec = minutesrecorded*60;

atimes = round(rand(7,nrands).*secondsrec);
btimes = round(rand(4,nrands).*secondsrec);

close = zeros(1,nrands);

for k = 1:nrands;
   disp(k);
   close(k) = sum(sum(abs(repmat(atimes(:,k),1,4) - repmat(btimes(:,k)',7,1))<5));
end

hist(close,[0:1:max(close)]);
%bar([0:1:max(close)+1],n,'histc');
hold on
plot([ncloseobserved ncloseobserved],[0 max(get(gca,'Ylim'))],'k-');
xupper = max([ncloseobserved+1 max(get(gca,'Xlim'))]);
set(gca,'Xlim',[-0.5 xupper],'Xtick',[0:xupper],'Xticklabel',num2str([0:xupper+1]'));

pl = round((sum(close<ncloseobserved) / nrands)*100);
disp('Percent runs producing less than observed number of whistle proximities:');
disp(pl);
```

Appendix 2

An example of an ARTwarp categorisation, at 96% vigilance, for 7 whistles for event 11. Note human observer classified 1 and 5 as different contours to others, based on flat section in initial upsweep.



CHAPTER SIX

WHISTLE RATES OF WILD BOTTLENOSE DOLPHINS: INFLUENCES OF GROUP SIZE AND BEHAVIOUR

ABSTRACT

This study investigated how whistle rate varies between behavioural activities in wild bottlenose dolphins. Previous studies have focused on how signature whistle production varies with context, but in populations where data on signature whistles are absent limited information exists on context specific whistle rates. Concurrent acoustic and non-acoustic behavioural data sampling was conducted during focal follows. Passive acoustic localisation using a four-element distributed array was used to localise whistles to observed surface behaviour. Whistle rates during direction changing and socialising were significantly higher than the whistle rates observed during surface travel. An increase in group size did not produce a significant linear effect on whistle rate across behaviours showing individuals must be whistling at a higher rate during direction changing and socialising compared to when they are engaged in surface travel. This study gives the first insight into context specific whistle rates localised to individual groups.

INTRODUCTION

Bottlenose dolphins are able to produce a variety of different vocal signals that can be classified into three main types. The first are pulsed, broad-band sounds of short duration used in echolocation, (see Au 1993 for review) the second are less distinct pulsed sounds such as cries, grunts, brays and barks (see: Connor and Smolker 1996, Janik 2000a, Overstrom 1983 for examples) and the third are the tonal whistles which are frequency modulated narrow-band sounds (e.g. Caldwell and Caldwell 1965, Janik and Slater 1998, Sayigh *et al.,* 1990, 1995). A number of studies have been able to assign context to specific vocalisations such as the bray call during feeding events (Janik 2000a) or the pop vocalisation as a threat during mating attempts (Connor and Smolker 1996). Additionally, the use of echolocation clicks for navigation and location of objects has been widely discussed (see Au 1993 for review). Whistles have been shown to serve the function of communicating information between individuals in a number of studies (e.g. Caldwell *et al.* 1990, Janik and Slater 1998, Sayigh *et al.* 1998, Tyack 1997). The tendency of each individual to emit the same basic whistle contour during a variety of circumstances, led to the hypothesis that the individually distinctive attributes of signature whistles function to broadcast the identity of the whistler (Caldwell and Caldwell 1965). Studies demonstrating increased use of these whistles during separation of individuals (Janik and Slater 1998, Smolker *et al.* 1993, Watwood *et al.* 2005) supports that these whistles act as contact calls. A number of studies have been able to assign individually distinct signature whistles to individuals and assess the use of these individual identifiers in the wild in different behavioural contexts and associations (Cook *et al.* 2004, Watwood *et al.* 2005). However, bottlenose dolphins produce a variety of whistle types and much still remains unknown about the specific contexts of signal use in wild unrestrained bottlenose dolphins, particularly where studies of functionality and variability in wild populations are sparse.

The rate of whistle production in a free-ranging dolphin is likely to be dependent on a number of factors. These may include environmental effects such as background noise and local topography or may be social factors such as behaviour state or presence of conspecifics. Previous studies have looked at rates of whistle production during different scenarios including mum-calf separations (Smolker *et al.* 1993) and male-male alliances (Watwood *et al.* 2005). These studies focused on signature whistles and found increased whistle rates during times of separations, adding to the evidence that signature whistles function as contact calls. Additionally, Cook *et al.* (2004) found significant differences in signature and non-signature whistle frequencies across activity types and with increasing group size. This finding suggests that during activities where groups may become more dispersed, animals may facilitate cohesion by emitting signature whistles more frequently. However, Cook *et al.* (2004) found signature and probable signature whistles made up 52% of all whistles produced, leaving a large number of non-signature whistles also in frequent use. Identifying signature whistles in the wild, is only possible in populations where individuals' signature whistles are known from capturing animals and in general this is not the case for many dolphin populations. A further problem in assigning calls to individuals, in populations where group sizes may be large and dispersed, is the need to determine caller position to prove whistles originate from the group displaying the observed activity. In the study by Cook *et al.* (2004) whistles were not localised to determine caller position. This was also the case in other studies looking at overall whistle rates across different contexts for bottlenose dolphins (Buckstaff 2004, Jones and Sayigh 2002) and Hawaiian spinner dolphins (Brownlee and Norris 1994). This potentially produces a problem when groups are dispersed and small subgroups are present as was often observed during time of socialising by Cook *et al.* (2004). Wild dolphins are able to quickly change position around a small vessel and also emit their whistles underwater out of sight of the observer. Similarly, the use of a towed array for localisation presents problems for localising individual dolphins. Watwood *et al.* (2005) used this system with wild dolphins, but experienced limitations when animals were located in close proximity to each other. Additionally, the left-right ambiguity of towed arrays also presents a problem. If large numbers of dolphins are present, subgroups may be situated on each side of the array, presenting potential problems in identifying the source. To reliably relate whistles to behaviour exhibited by specific groups, a towed distributed array is needed to pinpoint caller direction. This system allows whistles to be accurately assigned to a direction that can then be correlated with surface behaviour observations. This study looks at whistle rates across activity and with different group sizes for a population of wild bottlenose dolphins inhabiting the waters of north-east Scotland. The aim of this study was to determine whistle rates in relation to behaviour type and group size for wild dolphins. Through localisation of individual whistles to caller position, the average rates for localised and total whistles and how these relate to observed surface behaviour and group size can be studied.

METHODS

Data collection

This study was conducted off the north-east coast of Scotland between Arbroath and Fife Ness (see figure 1, chapter 5) from July to September in 2003 and 2004. The subject animals were individuals of the bottlenose dolphin population numbering approximately 130 individuals (Wilson *et al.* 1999), and known to travel large distances around the north-east Scotland coast from the Moray Firth to St Andrews Bay (Wilson *et al.* 2004). Focal follows (Altmann 1974), employing concurrent acoustic recordings on a 4 element distributed array and non acoustic, behavioural continuous sampling with 2 minute summaries, and standard photo-identification techniques were undertaken from a small boat when sea state was Beaufort 3 or less and weather was dry: (Boat a, June-August 2003: 5.75m, 2 x 60 Hp 4 stroke outboard engines. Boat b, August-September 2003: 6.25m, 120 Hp diesel inboard engine. Boat c, June-September 2004: 5.70m, 1 x 90 Hp outboard engine).

The distributed array consisted of three HTI-94-SSQ hydrophones and one HTI-96-MIN hydrophone all with a frequency response of 2 Hz to 30 kHz ± 1 dB, attached to tensioned 2 meter pieces of chain with waterproof tape. The four elements were then distributed around the boat in a box array to allow passive acoustic localisation. Hydrophones were positioned at 2m depth and were placed between 160 cm and 280 cm apart depending on vessel used. Recordings were made onto a Fostex D824 multi-track digital recorder during 2003 and an Alesis adat HD24 multi-track digital recorder during 2004 (sampling frequency 48 kHz, 24 bit for the Fostex, 32 bit for the Alesis. Change due to replacement of damaged equipment). Spoken tracks of two observers, one detailing the surface behaviour of the focal animal and its associates and one the positions and behaviour of the non focal animals were also synchronised to the multi-track recorder. These observations included descriptions of group composition and size, distance and direction of groups from the boat (based on a standard clock face with the bow being 12 o'clock) and group activity (Table 1), Focal observations were spoken into a head-mic and received on a Yaesu FRG-9600 receiver and non focal observations on a hand held microphone connected directly to the multi-track recorder. Dorsal fin photo-identification of the focal and its associates was completed using a Canon Digital D30 SLR camera with a Sigma 100-300 mm APO lens.

Table 1: Definitions of behavioural activities assigned to focal and other groups during behavioural sampling. All events are mutually exclusive.

Behaviour type	Definition
Surface travel	Animals all moving in the same direction, usually with some synchrony in surfacing and in close formation.
Direction changing	Animals exhibiting non-directional movements and all surfacing facing different directions. Overall distance travelled by group is minimal.
Socialising	Animals interacting with each other. Including rubbing together, rolling over, showing bellies, fins and heads out. This behaviour involves a number of animals in very close proximity.
Jumping / body slaps	Animals leave water to exhibit aerial behaviour, often causing splashing.
Porpoising	Animals leave water in low forward jumps creating white water in their wake and travelling in a definite direction.
Tail slaps	Animals slap tails on water surface.
Bow-riding	Animals positioned at bow of research or other vessel travelling along in the vessels bow wave.
Tail out dive	Animals dive with tails visible above water surface, often underwater for long periods.
Submerged	Animals under water surface, no animals visible.
Logging	Animals remain at surface with backs and fins visible above the water surface for long periods of time.
Feeding	Animals seen with fish in their mouths or tossing fish at the surface.
Join	Two or more subgroups join together so that one large group is formed.

Data analysis

For each follow, the focal and non-focal behavioural observations were played back through Cool Edit Pro LE and scribed to a spreadsheet. Times of any observed event was transcribed (decimal mm:ss.ddd) and actual time spoken at each two minute point sample was also transcribed. Any instance where recordings were not clear was also noted. The acoustic recordings were analysed using Cool Edit Pro LE through a spectrogram display (Hanning window, FFT 512) and the start and end time of each vocalisation event was transcribed (decimal: mm:ss.ddd) into a spreadsheet. The vocalisation events were described as in Table 2. Instances of engine noise were also catalogued and graded. Engine noise level 1 referred to times when dolphin signals would be masked, this occurred whenever the engine exceeded 2000 rpm. Engine noise 2 referred to times when dolphin signals could be reliably seen through the background noise, this was at times when the engine was running at below 2000 rpm. There were also times when only minimal or no engine noise was present as the engine would be out of gear or off.

Table 2: Definitions of vocalisation events recorded during the follows

Vocalisation event	Definition
Whistle	Tonal whistle – frequency modulated narrow band.
Possible whistle	Whistle sound seen in recording but not heard or whistle sound heard but not seen in standard analysis settings.
Clicks	Pulsed broad band sounds always in trains of more than one. (All single clicks were ignored as it was impossible to identify them).
Calls	Any pulsed sound of longer duration than a click.
Bray	Low frequency burst-pulsed sound.
Unidentified noise	Any sound not recognisable as a whistle, click or call, may or may not have been a dolphin sound.

For each two minute period the direction, distance and activity of the focal animal and its associates, (focal was never seen on its own), was recorded and then summarised. Definitions of dolphin groups can be very subjective and a large dispersed group of dolphins may consist of a number of smaller subgroups that to the observer appear separate, but may be within acoustic contact due to the active space of the whistles (Janik 2000b). The close associates of the focal were engaged in the same activity as the focal in times of surface travel, direction changing, jumping / body slaps and socialising. However, behaviours such as feeding or tail slapping were only exhibited by one individual, so were not included in this analysis. Additionally, for all behaviours other than surface travel, direction changing, jumping / body slaps and socialising sample sizes were too small to be included in analysis. The positions and behaviour of other sub groups was also summarised through analysis of the non-focal spoken recording.

For each two minute section, the acoustic recordings were checked to identify periods of level 1 engine noise. Any two minute sections containing any amount of level 1 noise were discarded. All whistle events were then assigned to the correct two minute section. Similarly, any sections where behavioural observations were incomplete, the focal animal was lost or focal animal was greater than 60m away were also discarded. 60m was chosen based on the calibration results (see chapter 2) indicating that signals are received and could be localised at this distance. For all follows the group size of the focal and its associates was estimated. If exact group number was unclear, a minimum number was established using the behavioural visual observations and the photo-identification of individuals within the group. An upper limit was set based on the visual observations recorded during the follow.

Onset time of each whistle event within the useable two minute sections were formatted for localisation analysis in the Matlab based TOADY program (see chapter 2 for program details). Any events noted as possible whistles (Table 2) were discarded. Toady uses the method of cross-correlation of time of arrival differences between hydrophone pairs to determine signal source, a method possible when delays are preserved on a multi-track recorder. Each whistle was localised in turn and the caller position noted if localisation was successful. If whistles could not be successfully localised the reason was recorded. Reasons for non-localisation ranged from the signal being too weak, to overlap from other signals, making the result uncertain, to caller position being given to the engine location at 6 o'clock. Once all whistles were localised, each caller position was compared to focal position and activity at the same time of the whistle event. For each follow the average whistle rate per 2 minute section was determined for localised whistles only and also for total whistles, (localised, not localised and localised to other groups), recorded in the sections. For whistle rates using localised whistles, the effect of group size was also considered by dividing the rate by the average group size, taken as the mid point between the lowest and highest group estimate, for each follow.

For statistical analysis, a general linear model was constructed based on a quasi-Poisson distribution. This model was chosen due to over-dispersion of the data (see Burnham and Anderson 2002 for details on over-dispersion and model choice). The presence of over-dispersion was determined by consideration of the dispersion parameter for the quasi-Poisson family being greater than 1 (Dispersion parameter =11.5246), suggesting that the sampling variance exceeded the model-based variance by 12 times and hence the data has variation that cannot be explored directly by the parameters given. Using whistle rate as the response variable, behaviour type was modelled as the categorical predictor variable and could take one of four values, surface travel, socialising, direction changing or jumping /body slaps. For each of these variables a mean whistling rate was calculated. The mean whistle rates for socialising, direction changing and jumping /body slaps were then modelled against the rate for surface travel. The log of average group size was modelled as a linear predictor variable and the log of duration (total number of usable minutes in each follow) was added as an offset due to increased listening times increasing the chance of hearing whistles. Logs of group size and duration were used to account for the quasi-Poisson model using a log link. Data were grouped by behaviour for each follow resulting in 43 different data points for the model. No interaction terms were considered due to small sample size. If interaction terms were considered, the chance of over parameterisation was high. Model fitting was completed in R software.

RESULTS

Identifying whistles

In total 26 follows from 13 separate days, totalling 13 hours and 52 minutes of recordings and 1783 whistles were analysed. A further 3 follows were discarded due to being incomplete either through missing observations or failure of the microphone or hydrophone. Of a possible 332 two minute sections, 161 were put through for further analysis with 171 being discarded. These sections were distributed throughout all the 26 follows in different numbers (Figure 1). Of the 1783 whistles identified, 954 (54%) were in the usable sections. The percentage of the total whistles in usable sections varied between follows (Figure 2) and ranged from 0-100%. Of these usable whistles, not all could be localised. In total, of the whistles in usable sections, 321 (34%) could be localised and 633 (66%) could not. This was also variable between follows (Figure 3). No follows had all usable whistles localised, but some had all usable whistles that could not be localised.

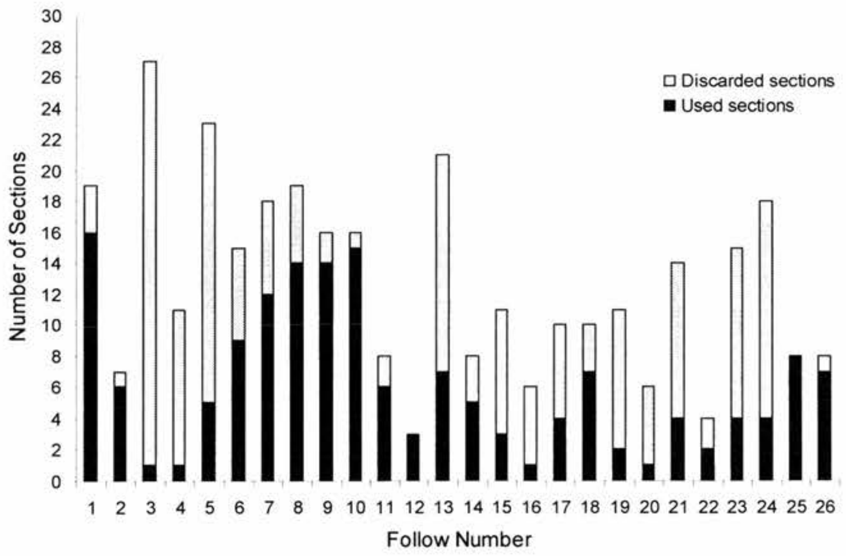


Figure 1: Number of two minute sections used and discarded throughout the 26 follows.

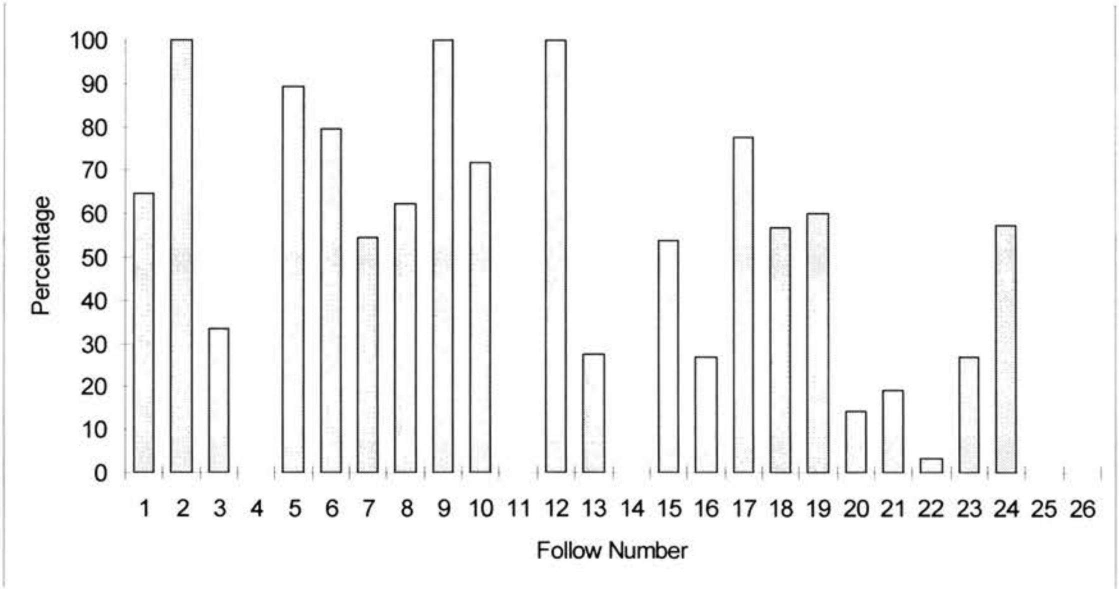


Figure 2: Percentage of whistles in usable sections in each follow as a percentage of the total whistles recorded in each follow. For follows 11, 14, 25 and 26 no whistles were identified at any time during the whole follow. For follow 4, all identified whistles were in discarded sections of the follow.

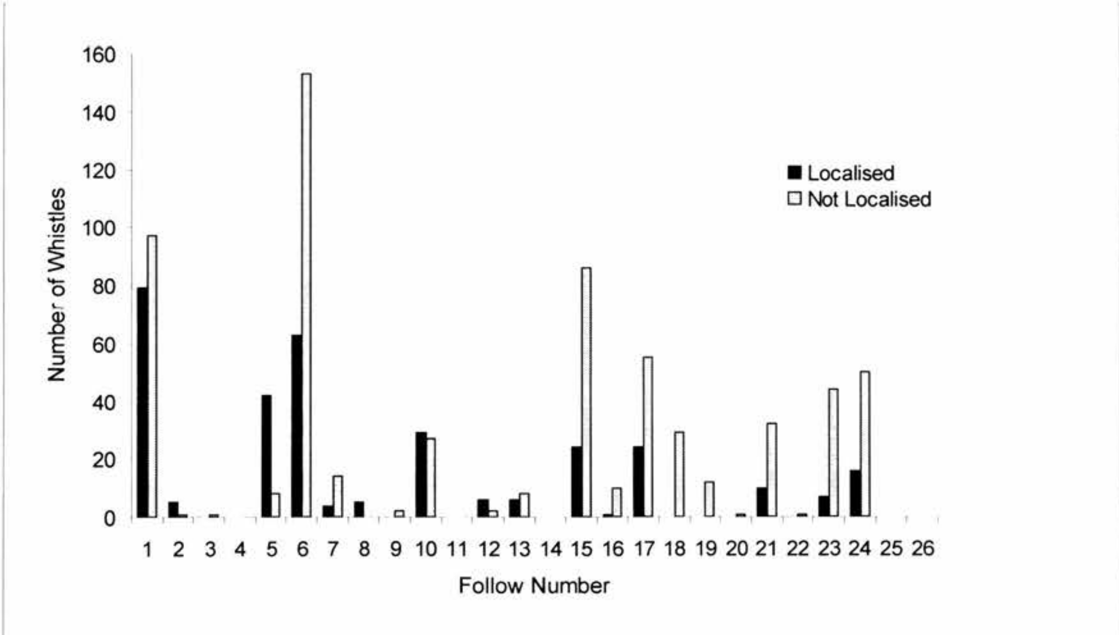


Figure 3: Number of whistles from usable sections localised and not localised for each follow. For all but 6 follows (3, 4, 19, 22, 25, 26) other subgroups were present.

Assigning whistles to behaviour types

For all but 3 of the 161 usable sections, the focal animal was engaged in one of four behaviour types, surface travel, direction changing, socialising or jumping / body slaps. Although all the other behaviour types described in Table 1 were observed during the follows, many were exhibited by individuals other than the focal or its associates, so occurred in sections excluded before the further analysis. Similarly others were observed during times when sections were masked by engine noise or when observations on the focal were incomplete. For the remaining 3 sections, all animals were submerged for the entirety of the 2 minutes. The number of whistles associated with each of the four behaviour types, in usable sections only, during each follow is shown in Figures 4a-d. Figures show the number of whistles localised, not localised and also localised to a position other than the focal and its associates.

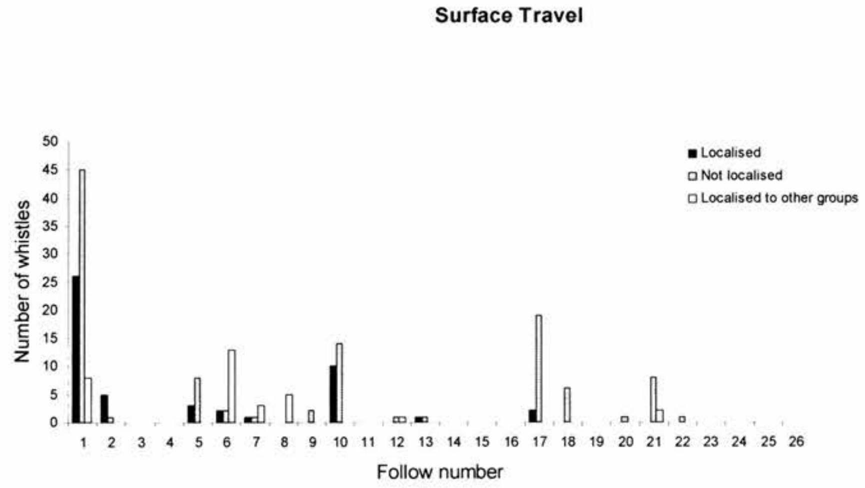


Figure 4a: Number of whistles during surface travel that were localised, not localised or localised to other groups.

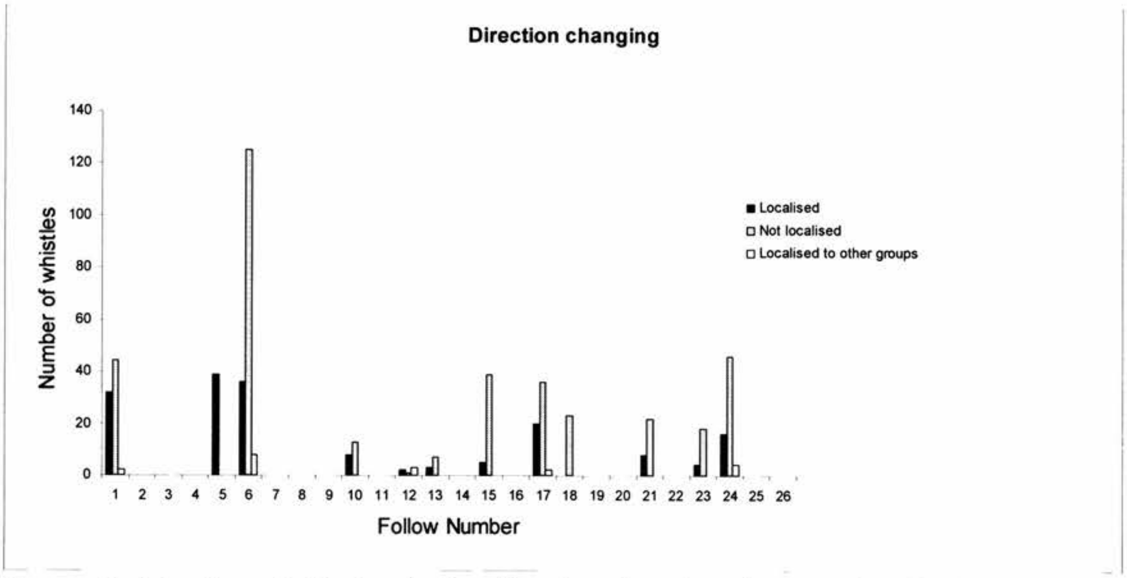


Figure 4b: Number of whistles during direction changing that were localised, not localised or localised to other groups.

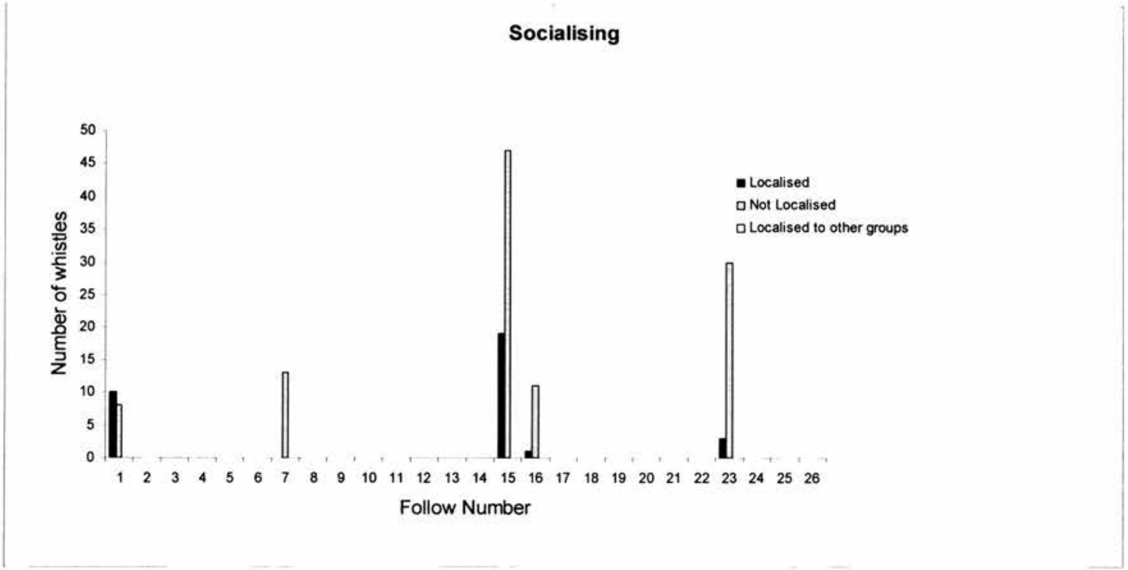


Figure 4c: Number of whistles during socialising that were localised, not localised or localised to other groups.

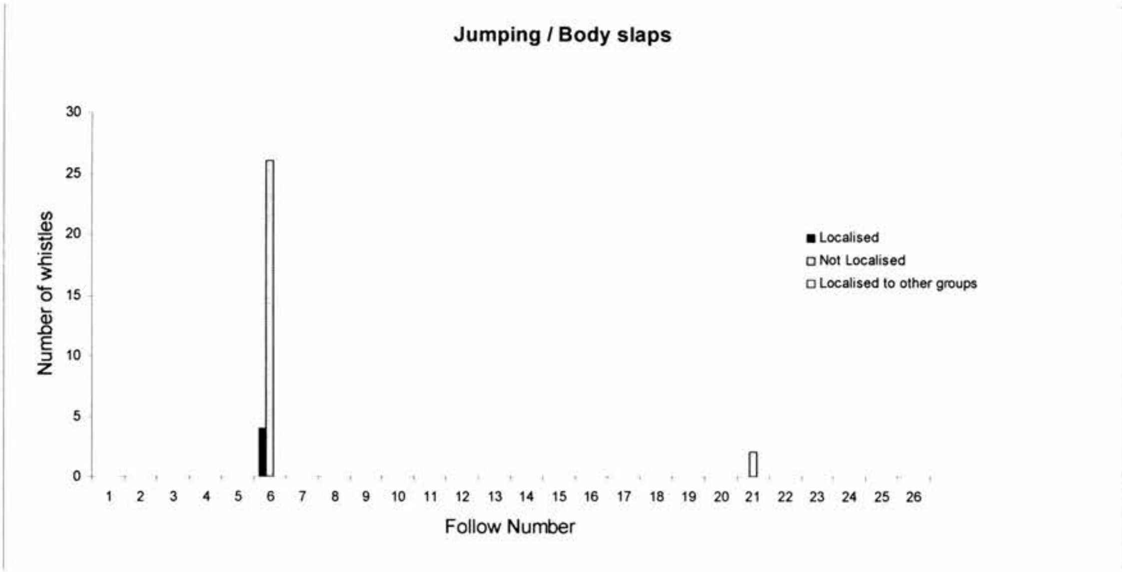


Figure 4d: Number of whistles during jumping / body slaps that were localised, not localised or localised to other groups.

Whistle rates with behaviour type

The whistle rate for each of the four behaviour types for localised whistles per 2 minute section was variable across follows (Figure 5, Table 3). In total, 14 of the follows included usable sections for two or more of the behaviour types (Table 3). 23 of the follows contained sections of surface travel, 13 contained sections of direction changing, 5 contained sections of socialising and only 2 contained sections of jumping / body slapping. There were marked differences in the mean whistle rates across all follows for the four behaviour types (Table 3, Figure 6), with surface travel exhibiting the lowest rate and direction changing the highest (Table 3).

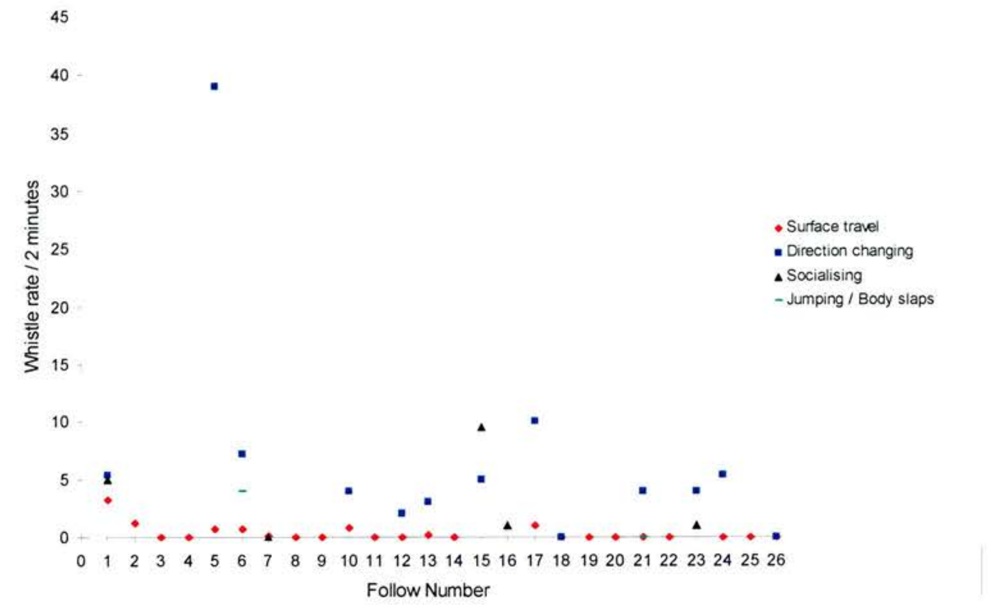


Figure 5: Whistle rate per 2 minutes for each behaviour type for each follow for localised whistles only.

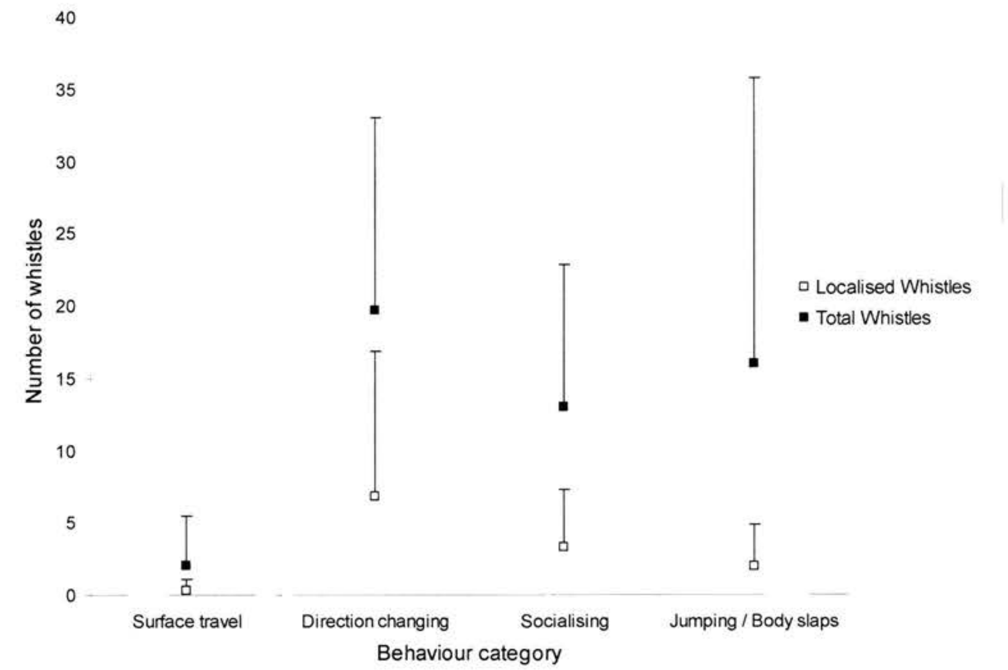


Figure 6: Mean whistle rate across all follows for the four behaviour types. Open squares show localised whistles only, Black squares show total whistles. Error bar shows positive standard deviation. (Negative error bars are omitted for clarity).

Table 3: Summary of whistle rates per 2 minutes, for localised (loc) and total (tot) number of whistles for each of the four behaviour types for all follows.

Follow Number	Group size	Surface travel			Direction changing			Socialising			Jumping / body slaps		
		rate/2 mins (loc)	rate/2 mins (tot)	No. of sections	rate/2 mins (loc)	rate/2 mins (tot)	No. of sections	rate/2 mins (loc)	rate/2 mins (tot)	No. of sections	rate/2 mins (loc)	rate/2 mins (tot)	No. of sections
1	20+	3.25	9.88	8	5.33	13	6	5	9	2			
2	10-15	1.25	1.50	4									
3	2	0	0	1									
4	2	0	0	1									
5	10-15	0.75	2.75	4	39	39	1						
6	15-20	0.67	5.67	3	7.2	33.8	5				4	30	1
7	10-15	0.09	0.45	11				0	13	1			
8	2	0	0.36	14									
9	20+	0	0.14	14									
10	40+	0.77	1.85	13	4	10.5	2						
11	40+	0	0	6									
12	15	0	1	2	2	6	1						
13	10-15	0.17	0.33	6	3	10	1						
14	8-10	0	0	4									
15	8-10				5	44	1	9.5	33	2			
16	30+							1	12	1			
17	30+	1	10.50	2	10	29	2						
18	12-15	0	1.20	5	0	11.5	2						
19	3	0	0	2									
20	12-15	0	1	1									
21	12-15	0	10.00	1	4	15	2				0	2	1
22	6	0	0.50	2									
23	30-40				4	22	1	1	11	3			
24	15-20	0	0	1	5.33	22	3						
25	15	0	0	8									
26	10-15	0	0	6	0		1						
Mean		0.35	2.05		6.84	19.68		3.3	13		2	16	
Stdev		0.74	3.44		10.03	13.38		3.96	9.84		2.83	19.80	

Whistle rate in relation to group size

Dividing whistle rate with mean group size for localised whistles shows that direction changing and socialising still exhibit consistently higher rates of whistle production than surface travel per 2 minutes (Figure 7). For all follows where surface travel and either direction changing or socialising are seen, the whistle rate when accounting for group size is higher within the follow, suggesting more whistles are produced during direction changing or socialising than during surface travel, regardless of group size.

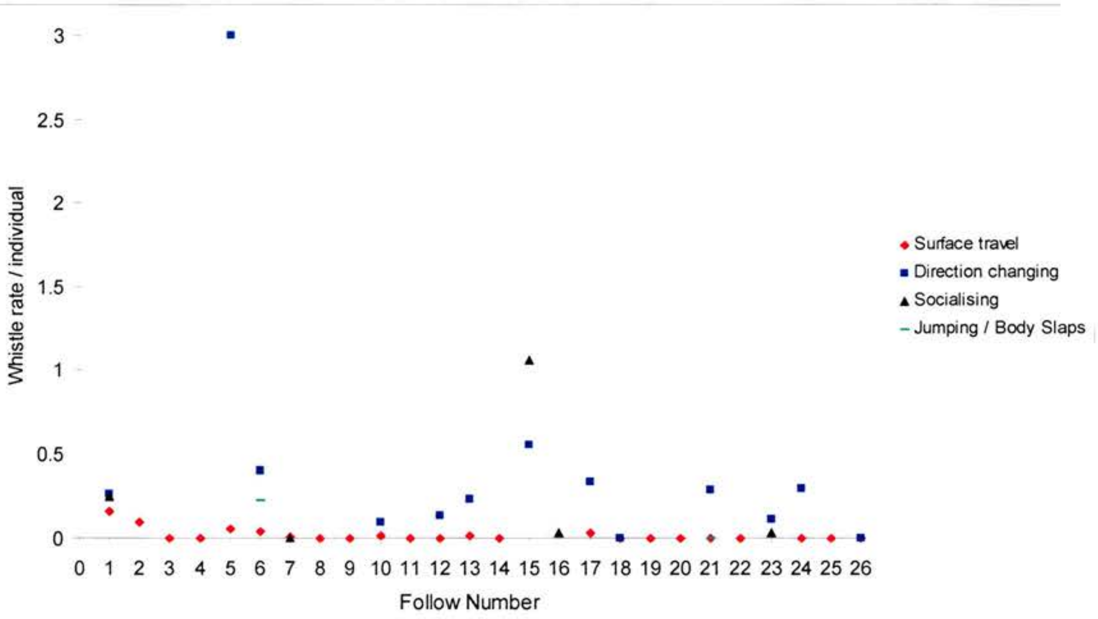


Figure 7: Whistle rate across follows for the four behaviour classes when scaled for group size.

The results of the general linear model are shown in Table 4. There were significant differences in whistle rates across behaviour types. The whistle rate during direction changing was the most significantly different to that during surface travel ($p<0.001$) showing dolphins produce significantly higher whistle rates during direction changing. Similarly, significantly higher rates were observed during socialising ($p<0.01$) than during surface travel. A higher whistle rate was seen during jumping / body slaps than during surface travel, but this was not significant ($p = 0.388$). Group size did not have a significant effect on whistle rate ($p=0.778$). However whistle rate was shown to positively increase with group size, (estimate 0.1180) but not in a linear relationship (+2 standard deviations still do not give an estimate of 1). This is demonstrated in Figure 8, where whistle rate per individual is variable with average group size across each of the behaviour types. The whistle rate per individual is highest when group size is between 9 and 20 animals, when group sizes are bigger than this, the whistle rate per individual declines.

Table 4: Estimates and p values for comparisons of whistle rates between surface travel and all other behaviours (SOC = socialising, JUM = jumping / body slaps, DC = direction changing). Significant differences are shown in bold.

	Estimate	Std. Error	T value	Pr(>|t|)
Intercept	-1.8680	1.2014	-1.555	0.12827
Behaviour SOC	2.2293	0.6976	3.196	**0.00281**
Behaviour JUM	1.5416	1.7646	0.874	0.38781
Behaviour DC	2.6652	0.5650	4.717	**0.00003**
I(log(Av.grp.size))	0.1180	0.4155	0.284	0.77797

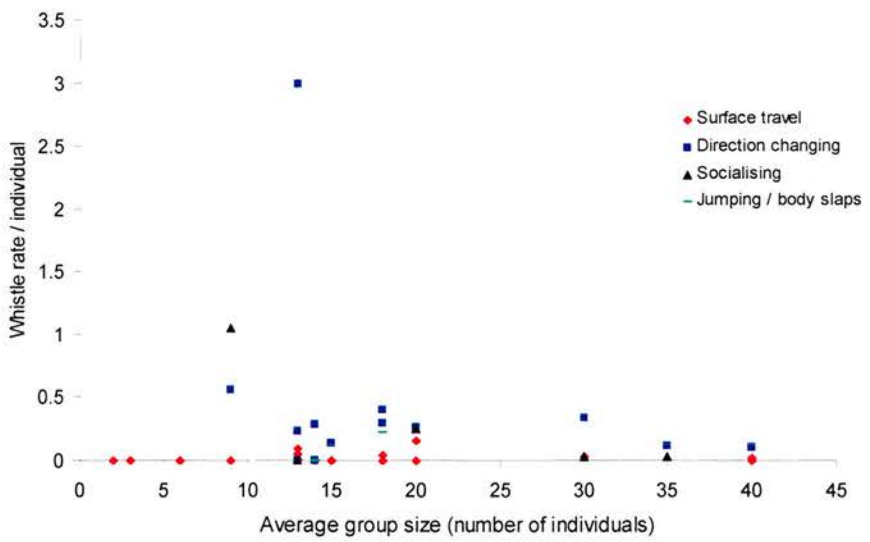


Figure 8: Whistle rate per individual for each behaviour type compared to group size.

DISCUSSION

This study showed that whistle rates of wild bottlenose dolphins are dependent on the behaviour type exhibited by the individuals within a group. Surface travel consistently showed the lowest whistle rate of all the behaviour types both between follows (Table 3, Figure 5) and averaged across follows (Table 3, Figure 6). Whistle rates during direction changing and socialising were significantly higher than the rates during surface travel (Table 4). However no significant difference was seen in the whistle rates during jumping / body slaps and surface travel. This is due to the very small sample size (n=2) for jumping / body slaps (Table 3) leading to a mean whistle rate of 2 whistles per 2 minute period with a variance of 2.83. This small sample size and high variance to mean value does not give enough data to support a significant difference with the GLM so more data would be needed to reliably discuss whistle rate differences during times of jumping / body slaps. An increase in group size did not produce a significant linear effect on whistle rate across behaviours. So if ten dolphins were present they would not produce twice as many whistles compared to when five dolphins were present. Some individuals are therefore whistling at a higher rate during direction changing and socialising compared to when they are engaged in surface travel (Figures 7 and 8). This study supports similar findings to other studies of wild bottlenose dolphins that have also shown increased whistling rates during times of social behaviour (Cook *et al.* 2004, Jones and Sayigh 2002) and milling (synonymous with direction changing here) (Cook *et al.* 2004) when compared with surface travel. During surface travel animals were all heading in the same direction and often surfaced synchronously and in close proximity. This would aid contact in either the visual realm where animals may be able to see other individuals to maintain contact or in the physical realm, where water movements may assist individuals in determining positions of others. These factors may contribute to a reduction in the number of whistles needed to maintain contact or communicate information. However whistles still obviously play a part during surface travel and it would be interesting to look at fine scale aspects of whistle use during travelling to see if they precede a change in behaviour or occur more or less depending on social structure or membership of the group.

Increased whistle rates during direction changing may be due to animals remaining in contact at a time when individuals are more random in their movements and are easily lost within the group. Or it may be a transitional state preceding a behavioural change when animals communicate to group members their intention to change behaviour. Direction changing is commonly referred to as milling in a number of studies (Cook *et al.* 2004, Jones and Sayigh 2002) and can be very subjective. It is often a term used to refer to times when animals are not definitely engaged in a defined behaviour such as socialising or travel and as such its function is not completely clear. It is also likely that the behaviour termed as direction changing here may also be classed as foraging in some studies. This is due to the classification of erratic movements or rushing behaviour at the surface as foraging (Jones and Sayigh 2002, Van Parijs and Corkeron 2001) by some researchers. In this study, direction changing was the second most observed behaviour after surface travel, but whether it is merely a less obvious form of what is often considered socialising is unclear. The main reason for only testing differences between surface travel and all other behaviour types in this study is to discount subjective observer bias when splitting direction changing and socialising, as it is unclear if these categorisations are irrelevant to the dolphins and merely easier for the observer.

Increased rates during socialising may be due to animals communicating information to social associates or using calls to maintain contact. For this study when animals were socialising they were within very close proximity, often rubbing body parts and touching (see definition in Table 1). Rates may be dependent on social bonds between the individuals present or may be a consequence of increased arousal due to contact with individuals and not be dependent on social relationships. Cook *et al.* (2004) showed higher signature whistle production during socialising and suggest that this may function to maintain contact as other group members get more dispersed whilst individuals are engaged in socialising. However they did not use localisation during their study so it is unclear if the actual socialising individuals were emitting the signature whistles. Due to the localisation techniques used in this study, the animals engaged in social activity could have whistles localised to their position, suggesting the whistles are a direct result of the socialising activities.

The studies by Cook *et al.* (2004) and Watwood *et al.* (2005) that looked at whistle rates with behaviour types focused on the use of signature whistles and hence the idea of maintaining contact with group associates was enforced when signature whistles were identified. However, without knowledge of social affiliations in this population it is problematic to predict if exhibited whistles are primarily signature whistles that animals may be using to stay in contact or whether they are non-signature whistles that contain characteristics associated with given behaviours. Animals may increase whistle rates to stay in touch with selected conspecifics in times when group sizes are larger and individuals more active, rather than producing more whistles directly as a result of exhibiting a particular behaviour. However, the localisation procedure did give reliable indications of the number of whistles that could be attributed to a specific focal animal and its associates whilst engaged in one of four behaviour types, supporting the idea that whistle rates are variable between behaviour types. Further studies on bottlenose dolphins have shown differences in whistle rates with different context. In a captive experiment, Janik *et al.* (1994) showed an increase in whistle rates when no reward was given for an incorrect choice during a discrimination task. Buckstaff (2004) showed increased whistle rates in bottlenose dolphins at the onset of a vessel approach. This could be due to an increased motivation for the animals to come together or a compensation for increased background noise. Studies on other delphinid species have also shown differences in whistle rates with behaviour. A study of Pacific humpback dolphins showed increased whistle rates during socialising and foraging and when more mum-calf pairs were present, (Van Parijs and Corkeron 2001). Hawaiian spinner dolphins (*Stenella longirostris*) show increased whistle rates during times when individuals are more active or spread out (Brownlee and Norris 1994). Both these studies support the hypothesis that increases in whistle rates occur during increases in activity when maintaining contact is more difficult.

Differences in call rates in other species that exhibit fission-fusion living has also been shown. Spider monkeys emit a whinny call, thought to be used for maintaining contact, at an increased rate when another sub-group is within hearing range (Ramos-Fernández, 2005). In chimpanzees (*Pan troglodytes*) the rate of production of the pant hoot vocalisation has been shown to be dependent on male rank and context. High ranking males exhibited a higher pant hoot call rate than low ranking males and pant hoot rate was highest before and after travelling behaviour (Mitani and Nishida 1993), suggesting the calls may help to maintain contact between conspecifics. Additionally males hooted significantly more often when their allies and associates were nearby than when they were accompanying them (Mitani and Nishida 1993). This system of maintaining contact is similar to that outlined in bottlenose dolphin signature whistles. However, little is known about dominance rank in wild dolphins or if dominant males are more likely to produce more calls than other individuals. Male-male alliances have been shown to use signature whistles to maintain contact in wild bottlenose dolphins (Watwood *et al.* 2005), but it is difficult to quantitatively assess if these rates are markedly greater than non alliance groups. Further studies on the sex composition of wild dolphin groups and if this relates to whistle rates would be an interesting area of future study.

This study has shown that assigning the loudest whistles to the closest groups may be misleading if localisation is not used. In this study a number of cases of whistles being localised to groups other than the focal and its associates occurred. This was particularly evident during times of surface travel (Figure 4a) and direction changing (Figure 4b) where whistles were localised to the direction of another subgroup or a submerged animal that were not the closest to the boat. Similarly this and other studies have not looked at the role other vocalisations such as clicks, calls and brays may play within different behaviour types. By assessing the occurrence of these other vocalisations, a clearer picture of call use in wild dolphins may emerge. Very little is known about the functionality of dolphin calls and this study shows an insight into differences in whistle rates associated with different behaviour types. However more fine scale analysis into the variation of whistle contour shapes and how these relate to different individuals and different behaviours is needed to further address the variation in rates seen in this study.

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CHAPTER SEVEN

GENERAL DISCUSSION

Details on how cetaceans use acoustic signals during communicative events in the wild are limited. Whistles, especially signature whistles, have been the focus of many studies (Caldwell *et al.* 1990, Cook *et al.* 2004, Janik *et al.* 1994, 2006, Janik and Slater 1998, Sayigh *et al.* 1990, 1995, 1998, Smolker *et al.* 1993, Watwood *et al.* 2005), but much still remains unknown about the specific contexts of signal use in wild unrestrained bottlenose dolphins. Additionally, despite a number of studies on the movements, abundance and distribution of the bottlenose dolphin population found off north-east Scotland (Bailey and Thompson 2006, Hastie *et al.* 2004, Wilson 1995, Wilson *et al.* 1997, 1999, 2004) limited information exists on the numbers using areas outside the Moray Firth. The main aims of this study were to investigate the vocal behaviour and abundance of bottlenose dolphins in St Andrews bay. In this study I have used localisation, computer based whistle categorisation, photo-identification and behavioural observations to piece together communicative events and abundance for the bottlenose dolphin population under study.

In Chapter 1 the current literature available on the vocalisation abilities of bottlenose dolphins is reviewed. Since Caldwell and Caldwell (1965) first hypothesised the presence of signature whistles in five captive bottlenose dolphins, many studies have continued in this vein, producing supporting evidence for Caldwell and Caldwell's claim (Cook *et al.* 2004, Janik *et al.* 1994, 2006, Janik and Slater 1998, Sayigh *et al.* 1990, 1995, 1998, Smolker *et al.* 1993, Watwood *et al.* 2005). However some studies dispute the signature whistle claim (McCowan and Reiss 1995, 2001) concluding that dolphins have a predominant shared whistle type with individually distinct features. However, the wealth of evidence in captive (Janik and Slater 1998, Tyack 1986) and wild (Cook *et al.* 2004, Smolker *et al.* 1993, Watwood *et al.* 2005) studies shows convincing evidence for signature whistle existence. Additionally, in this thesis, instances of stereotyped whistles are identified, which exhibit stereotypy equal to that of signature whistles (Chapter 4 and Chapter 5) providing further support for the signature whistle hypothesis.

The difficulty of determining caller identification, when animals show no visible signs of sound production and are out of sight of the observer, has been a consistent problem in cetacean research. As such, determining caller position through analysis of whistles from bottlenose dolphins provides a logistic challenge from the outset. Chapter 2 details how this problem was tackled with the use of a 4 element distributed array. The array allowed synchronised recordings on four hydrophone receivers maintaining a time of arrival difference to allow localisation. The array gave accurate details on direction and depth of the caller allowing whistles to be correlated with visual observations of dolphin positions and activity. The ability to confidently assign calls to positions is vital in the study of communication and proved an invaluable tool during the course of this thesis. The analysis of calls without the use of localisation is common in the study of cetaceans (Cook *et al.* 2004, McCowan and Reiss 1995, Smolker *et al.* 1993). However, in situations where animals are in large groups and frequently changing position, the ability to localise calls greatly increases our ability to correlate observational data with acoustic data. The increased certainty given by localisation is an invaluable tool when studying animals that spend the majority of their time out of sight of the observer and the system described in chapter 2 has been used successfully in behavioural studies (Chapter 5 and Chapter 6).

Previous studies of bottlenose dolphins in the Moray Firth suggested a resident population of approximately 130 animals (Wilson *et al.* 1997, 1999). However the recent evidence (Wilson *et al.* 2004) suggests the animals may not be resident in the Moray Firth but may range over large distances. These changes in distribution and abundance in different areas are likely to be strongly influenced by the pressures exerted by the distribution of resources and the social structure of the population. Chapter 3 supports the finding by Wilson *et al.* (2004) of mobility of this resident population. The finding that a large number of the 130 individuals are found in the St Andrews bay area during the summer raises interesting questions. Firstly, the development of the special area of conservation (SAC), in the Moray Firth, to protect the habitat of this population, faces the possibility of inadequate coverage over the majority of the population range. Secondly, because the distances moved by individuals are large, interesting questions about ranging patterns, social structure and behaviour of the groups found in St Andrews bay abound. We have limited information on the genetic structure of this population (Parsons *et al.* 2002), and no information on the relatedness, or sex structure of the social groups found in St Andrews bay. The abundance estimates generated in this thesis suggest at least 80 individuals are present in the study area, so determining genetic structure and how this relates to the animals seen in St Andrews bay would be a fruitful area of future study and would allow us to determine how social groups use the St Andrews bay area. Additionally, detailed work on foraging behaviour in St Andrews bay may help to explore reasons for an apparent range shift in this population. It is likely that the dolphins are distributing themselves based on prey availability and animals were frequently seen with fish during the course of this study. Insights into prey distribution in the area and detailed observations on foraging activity of the dolphins would help to identify any important foraging areas and further contribute information to managers responsible for protecting this population.

An important area in the study of dolphin whistles is the categorisation of types. This importance is heightened in signature whistle studies where whistles are described as stereotyped. Differences in methodology have yielded differences of opinion as to whether stereotyped signature whistles exist (Janik 1999, McCowan, 1995, McCowan and Reiss 2001) and whether some methods using human judges are repeatable (Jones *et al.* 2001). Although subjective views on similarity will always exist, the use of a repeatable quantitative method should minimise disagreements. The results in chapter 4 detail such a method and investigate how categorisation varies with changes in vigilance levels and similarity of whistle types. This system provides a tool for objective categorisation and has already been successfully used in the study of bottlenose dolphin and killer whale calls (Deecke and Janik 2006). Effective categorisation of whistle types is vital for future study. The ability to consistently assign signature whistles in wild studies would allow further investigation into how whistles are related to behavioural events. Conversely, the ability to determine if whistles are not stereotyped and belong instead to the large repertoire of non signature whistles of bottlenose dolphins, may provide exciting insights into whistle usage. It is possible that certain whistle types are associated with specific events in a similar way to bray calls during feeding events (Janik 2000a) and pop vocalisations as a threat during mating attempts (Connor and Smolker 1996). Or it may be that certain individuals use specific whistle types more frequently than others depending on associations or behaviour. Another area where signature whistle classification may prove invaluable is the potential for using signature whistles in abundance estimation. If stereotyped whistle production can be determined reliably from hydrophone recordings, it may be possible to remotely monitor the presence of bottlenose dolphins in given areas. Of course restrictions to this will exist and this method is currently a long way from being viable. However, as our knowledge on how and when signature whistles are used and our understanding of social interactions increases it may be possible to use categorisation of signature whistles to obtain a crude estimate of individuals using certain areas.

Localisation and categorisation of calls are important in the study of communicative events between individuals. In Chapter 5, I show how stereotyped whistles are used in a communicative event as a precursor to subgroups joining. Firstly I showed how sequences of stereotyped calls were unlikely to occur by chance and how their stereotypy matched that seen in signature whistles. Secondly, by localisation of these calls to identify caller position, I was able to demonstrate a context specific use for these sequences, showing their increased chance of occurrence prior to subgroups joining. Given what is already known about the fission-fusion structure of bottlenose dolphin groups (Wells 1991, Connor *et al.* 2000), a mechanism to maintain contact with close associates is necessary. This mechanism has previously been identified as the signature whistle (Caldwell *et al.* 1990, Cook *et al.* 2004, Janik *et al.* 1994, 2006, Janik and Slater 1998, Sayigh *et al.* 1990, 1995, 1998, Smolker *et al.* 1993, Watwood *et al.* 2005), however the range of contexts in which individuals need to maintain contact is still under study. Many studies have focused on isolation of individuals either through capture

(Caldwell *et al.* 1990, Sayigh *et al.* 1990) or voluntary separation (Janik and Slater 1998, Smolker *et al.* 1993, Watwood *et al.* 2005). However the results presented here demonstrate that individuals also use stereotyped whistles to convey information to associates other than those in their immediate subgroups in times when they are not isolated or completely separate from a group. This opens up a number of questions about how whistles are used in bottlenose dolphin groups. With only one stereotyped call originating from each subgroup, it is unknown if that one individual elicits a join for the entire group or if the join is on an individual level, with the remaining group members joining spatially but not necessarily interacting socially. Or it may be that the entire group engages in a social interaction, with other members eavesdropping on the exchange sequences thus negating the need for all group members to call, if each group member recognises the identity of the one caller. In white-faced capuchin monkeys (*Cebus capucinus*) the initiation and trajectory of troop movement is governed by the production of a trill vocalisation by one individual (Boinski 1993). Furthermore, the position of the animal at the edge of the troop is highly predictive of the troop movement. It may be in dolphin groups that certain individuals initiate joins more than others depending on social experience or position within the group. These questions are difficult to answer for the study population, but information on genetic relatedness of subgroups and the frequency with which subgroups interact may help to establish a better picture of when exchanges occur. A further interesting point raised by these results is that researchers often define associations and social structure of dolphin groups based on animals seen within one photo-identification frame or in close proximity. Although associations and interactions between these proximal animals are likely to occur, this study demonstrates that individuals are communicating with animals in other subgroups. This finding along with the demonstrated active space of dolphin whistles (Janik 2000b) suggests that individuals may be acoustically interacting with associates for periods when they are not in spatial proximity and is an interesting consideration when defining dolphin groups.

Matching whistles to surface behaviours and activity types has been demonstrated in previous studies (Cook *et al.* 2004, Smolker *et al.* 1993, Watwood *et al.* 2005). However, none of these previous studies, localised whistles to individual groups, therefore making conclusions about whistle rates with activity uncertain. In Chapter 6, I demonstrate how whistle rates vary with activity type for whistles localised to individual groups. Increased whistle rates during direction changing and socialising suggest communicative functions for these behaviours and are in line with increased whistle rates during socialising found in other dolphin populations (Cook *et al.* 2004, Jones and Sayigh 2002). For other behaviour types, the subjective nature of behaviour classification makes comparison more problematic. Milling is a term frequently used by researchers to define times when animals are not definitely engaged in a defined behaviour such as socialising or travel and as such its function is not completely clear. Further studies may benefit from better definition of behaviours using things such as travel speeds or orientations of individuals and groups. Although patterns of whistle rates across activity types were documented, variation within activity type was evident and future studies that better define behavioural types may help to further define the contexts associated with whistle rates. Furthermore, the large repertoires of bottlenose dolphins suggest that vocalisations other than whistles may be important during different behaviours and in coordinating social interactions. This thesis concentrates solely on the whistle vocalisations but these other sounds are areas that would also benefit from further study of context specificity.

Overall, the results presented here provided a number of insights into the vocal behaviour and abundance of the bottlenose dolphins of St Andrews bay. Despite a number of previous studies on the vocal behaviour of bottlenose dolphins, the results of this thesis have contributed significantly to existing knowledge. The existence of vocal exchanges prior to subgroup fusion and the localisation of whistles to individual groups and behaviour types have provided new insights into the use of whistles in communicative events. Additionally, the contribution of an abundance estimate for the St Andrews bay area has provided the first detailed estimation for animals using St Andrews bay and will be invaluable to managers as they proceed to protect this population. As with most studies, the results presented here have raised a number of questions. How do social relationships and relatedness affect vocal production? Do certain individuals use the St Andrews bay area more than others? Is it possible to identify signature whistles in this population from focal follows and repeat recordings? Can these signature whistles be used as a tool in abundance estimation? How are vocal exchanges used between social affiliates? In fact the questions are almost endless and provide opportunities for interesting future studies. However, this thesis and many other studies have shown that with the correct techniques it is possible to answer some of these questions and provide fascinating insights into the behaviour of wild cetaceans.

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