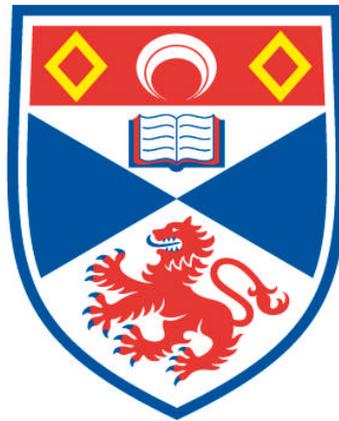


**ACOUSTIC BEHAVIOUR OF RISSO'S DOLPHINS,  
GRAMPUS GRISEUS, IN THE CANARY ISLANDS, SPAIN**

**Silvana Neves**

**A Thesis Submitted for the Degree of PhD  
at the  
University of St Andrews**



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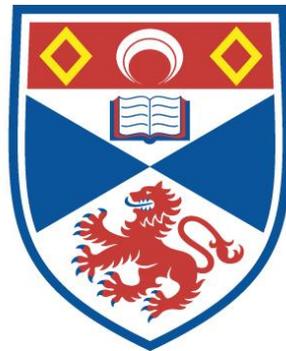
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# Acoustic Behaviour of Risso's dolphins, *Grampus griseus*, in the Canary Islands, Spain

Silvana Neves



University of  
St Andrews

This thesis is submitted in partial fulfilment for the degree of PhD

at the

University of St Andrews

Submitted October 2012

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I, Silvana Neves, hereby certify that this thesis, which is approximately 44,586 words in length, has been written by me, that it is the 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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# Abstract

The Risso's dolphin (*Grampus griseus*) is a poorly studied species, particularly with respect to its acoustic behaviour. The little we know about Risso's dolphin acoustics shows that they are an interesting case study given they combine acoustic features that places them in between very different delphinids.

I investigated the acoustic repertoire of the species showing that Risso's dolphins produce mainly whistles, burst-pulses and click trains. I discussed the possible functions of each type of vocalization by contextualizing them into group behavioural patterns, size and habitat features. Although capable of whistling, Risso's dolphins seem to favour burst-pulses to communicate and maintain group cohesion following deep dives.

Click trains were compared based on their inter-click interval patterns. Those were placed in their behavioural context and used to determine the number of animals echolocating at any given time. Risso's dolphins use a variety of inter-click intervals in each context. My data suggest that they may avoid predators by eavesdropping on the echoes of conspecific clicks while slow travelling and resting. Using 3D acoustic localization, I studied the biosonar performance and on-axis click characteristics of Risso's dolphin clicks. On one hand, Risso's dolphins do not seem to display range locking behaviour which makes them similar to beaked whales; on the other hand, they seem to apply automatic control to the transmitting side of their biosonar, which is similar to other delphinids such as the bottlenose dolphins. I also compared the whistle repertoire from Gran Canaria to that of another four locations. A discriminant function analysis using fundamental frequency parameters showed geographical distinction, most likely due to divergence caused by geographic isolation.

To conclude, the Risso's dolphin is an interesting species that combines acoustic features from different cetacean species. This could suggest that *Grampus griseus* may be misplaced within the *Delphininae* sub-family.

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# Chapter 1: General Introduction

## Introduction

### Vocal repertoires of animals in the wild and context studies

The first step when studying a species acoustically is to describe its vocal repertoire. This is crucial for understanding its communication system. Communication is a complex concept and one hard to define. Animal communication can be defined as “the transmission of a signal from one animal to another such that the sender benefits, on average, from the response of the recipient” (Slater 1983). Overall, in most cases, one animal influences the current or future behaviour of another animal or other animals (Dawkins & Krebs 1978). Some species are more easily accessible than others and that can reflect the information available for a certain taxa. In the case of vocal repertoires these can be very common for taxa ranging from primates (Becker et al. 2003; Range & Fischer 2004) to birds (Gammon & Baker 2004; Bradley & Mennill 2009) as examples of terrestrial species. As for the marine environment descriptions are also available from fish (Amorim et al. 2008), turtles (Giles et al. 2009) to pinnipeds (Rautio et al. 2009) and more rarely in cetaceans (Diazgranados & Trujillo 2002; Saulitis et al. 2005).

Researchers adapt the methodology employed to the target species of their study. Therefore, for different species and even within the same species (McShane et al. 1995) a different range of research methods is used. Inter and intra-species comparisons of vocal repertoires can be very difficult due to such variety of methods that use different nomenclature and acoustic analysis.

One of main research questions when studying the vocal repertoire of a species is to define the signals' function. For that our categorization of sounds must reflect the animal's own categorization. This is a difficult task because the animals might distinguish call types and subtypes that might not be apparent to humans (Janik 2009). Additionally, the same signal can have different functions depending on the receiver; an example of this is the acoustic advertisement signals produced by males that could either be used by females in mate choice or by other males in male-male interactions (Gerhardt & Huber 2002)

Checking if the categories defined by the researcher are context specific is the first step to investigate the biological validity of the sound categories. Studying a species' vocal behaviour and repertoire of sounds in defined contexts allows researchers to formulate hypothesis about the potential functions of different signals.

This also aids in the interpretation of what information may be beneficial for signallers to transmit, how receivers might respond, and what specific benefits signallers ultimately gain by producing those signals. The comparison of vocal repertoires of different species is important to understand the evolution of complexity in animal communication.

### **Acoustic signals of cetaceans**

The function of an acoustic signal can be defined as the adaptive consequences of communication (Smith 1968). Animal signals are used to find and capture prey, avoid predators, to call conspecifics, to find and select a mate, taking care of the offspring, and for orientation in geographical space. These are among the basic issues faced by both terrestrial and marine mammals. Despite sharing the same problems, these two groups of mammals developed their acoustic communication networks distinctively, according to the type of environment they are immersed in. To fully understand the function of animal communication, one has to take into account the environmental and social context in which communication occurs.

The marine environment favours the acoustic channel for rapid transmission of information ranging from a few meters to kilometres of distance (Tyack 1998; Tyack & Miller 2002). In cetaceans, sound became the most essential way of communication surpassing the visual, chemical and possibly chemosensory channels (Herman & Tavolga 1980).

The functional aspect of delphinid vocalizations generally places dolphins' vocalizations in two categories: social and echolocation (Cranford 2000). Again, for different species, a given sound could either have a social or communicative function or an echolocation one.

### **Social/communicative signals of dolphins**

Sounds used in dolphin's communication are mostly whistles, low frequency narrow-band sounds, calls and burst-pulses. Dolphins produce various types of whistle whose function is mostly related to communication. The most studied whistles are the highly stereotyped frequency modulated whistles known as signature whistles. Signature whistles are mainly attributed to the bottlenose dolphin, *Tursiops truncatus*, but have also been ascribed to

common dolphins, *Delphinus delphis* (Caldwell & Caldwell 1968), spotted dolphins, *Stenella plagiodon*, (Caldwell et al. 1973) and to Pacific white-sided dolphins, *Lagernorhynchus obliquidens* (Caldwell & Caldwell 1971). They have also been credited to both the Pacific humpback dolphin, *Sousa chinensis* (Van Parijs & Corkeron 2001a), and the Risso's dolphin (Caldwell et al. 1969; Favaro et al. 2011).

In bottlenose dolphins, individual signature whistles are developed in the first few months of life (Caldwell & Caldwell 1979). Infants use information from other whistles in their environment to build their own distinctive signature whistle, apparently through vocal learning (Fripp et al. 2005). Signature whistles can remain stable for at least 12 years in wild bottlenose dolphins (Sayigh et al. 1990) and are used in social interactions (Cook et al. 2004). These whistles are also used to maintain group cohesion (Janik & Slater 1998), including that of mothers and calves (Smolker et al. 1993). Signature whistles contain the identity information of the caller which is encoded in its frequency modulation pattern (Janik & Slater 1998; Janik et al. 2006). They are also used when dolphins encounter other groups at sea where they are an important component of the initial social interaction between groups when joining (Quick & Janik 2012). Other whistles can also be used to maintain distances between individuals (May-Collado & Wartzok 2007) and to facilitate recruitment during feeding activities (Acevedo-Gutierrez & Stienessen 2004).

Whistles are well suited for comparisons of vocalizations amongst different populations of a species due to their frequency modulation and their use in several aspects of a dolphin's life cycle.

Low frequency narrow-band sounds are commonly used during socializing (Schultz et al. 1995; Van Parijs & Corkeron 2001a). Low frequency calls have also been described for marine tucuxi, *Sotalia fluviatilis guianensis*, having been related to feeding events for 95% of observations (Monteiro & Monteiro-Filho 2001).

Burst-pulsed sounds are composed of individual clicks (similar to echolocation clicks) with a very high but variable repetition rate. In general, they are associated with social behaviour in dolphins. For example, bray calls are low frequency, burst-pulsed calls produced by the bottlenose dolphin. Janik (2000a) found that these calls were related to feeding events in the Moray Firth population in 93 % of events. The use of these calls by a foraging dolphin leads to the approach of conspecifics and might promote chases amongst individuals. High frequency, broadband (60-150 kHz) burst-pulsed sounds, have been associated with

aggressive encounters in captive bottlenose dolphins (Overstrom 1983; Blomqvist & Amundin 2004). The agonistic behaviour in intra- and inter-species interactions has also been associated with burst-pulsed vocalizations (Dawson 1991; Herzing 1996) in Hector's, *Cephalorhynchus hectori*, spotted, *Stenella frontalis*, and bottlenose dolphins.

Spinner dolphins, *Stenella longirostris*, seem to use burst-pulses for short range communication (Lammers et al. 2006).

Complex stereotyped sequences of burst-pulsed sounds have been reported for the northern right whale dolphins, *Lissodelphis borealis* (Rankin et al. 2007). Their function is speculated to be similar to that of whistles of bottlenose dolphins, i.e., one of a communicative nature.

The Western Australian bottlenose dolphins produce a pulsed "pop" sound which is correlated with courtship and/or dominance serving a social function. Additionally, it was suggested that dolphins use this typically loud sound to startle prey that uses sea grass beds as a refuge (Nowacek 2005).

Social signals of killer whales, *Orcinus orca*, comprise mostly calls that might serve as contact calls within pods thus playing an important role in maintaining cohesion of the pod and in the coordination of the spatial organization of its members (Ford 1989). The two-component calls of killer whales have a strong pattern of directionality. Such directionality could help to coordinate and synchronize the behaviour of individuals as well as to regulate the space between them. These, also called "two voice" calls, may carry information on the sex and orientation of the signaller (Miller et al. 2007).

### **Echolocation signals**

In echolocation, click trains are used, which are a series of brief ultrasonic broadband clicks emitted at varying repetition rates. These clicks are used as a biosonar for navigation and orientation, as well as for echolocation of prey and avoidance of predators. Echolocation was first suggested for dolphins in 1956 (Schevill & Lawrence 1956) and demonstrated in 1961 (Norris et al. 1961). In the latter study the authors trained a bottlenose dolphin to perform in a discrimination task where it correctly selected its food reward while blindfolded with latex suction cups. This animal was also capable of avoiding obstacles while blindfolded. The acoustic recordings during these experiments showed the production of echolocation clicks from the dolphin while performing the tasks.

Echolocating dolphins emit a click that is reflected by a target and the click echo returns to the dolphin. The dolphin then processes the information and then emits another click. The two way travelling time (TWTT) is the time that the click takes to get to the target and back to the dolphin and the time that the dolphin takes between hearing the first echo and emitting the second click is called the lag time (Au 1993).

Echolocation studies showed that dolphins when target approaching decrease the inter-click-interval (ICI) at distances closer to the target proportionally to the TWTT and keeping the lag time constant. This was called range-locking behaviour (Morozov et al. 1972) and it was shown in species like the bottlenose dolphins (reviewed in Au (1993)) and harbour porpoises, *Phocoena phocoena*, (Verfuss et al. 2005).

In both bats (Schnitzler et al. 2003) and small cetaceans (Verfuss et al. 2009) a typical target approach sequence starts with a search phase where dolphins range-lock on the target. An approach phase follows the search phase. Here the animal emits clicks at constant repetition rates initially but in the end part of the approach phase there is a sudden drop in the ICIs which leads to the final phase. The final buzz is formed by clicks with the highest repetition rate.

Besides the ICIs dolphins also adjust the gain of their biosonar according to the distance to a target. The changes can be done either on the receiver or the emitting level of the biosonar or both. False killer whales, *Pseudorca crassidens*, for example, adjust their hearing sensitivity (Nachtigall & Supin 2008), i.e. the receiving end of their sonar. Conversely, other dolphins such as Atlantic spotted dolphins and killer whales adjust the transmitting end of their sonar. This gain control is reflected by a  $20 \log(\text{range})$  relationship between the amplitude of the clicks emitted and the increasing target range (Au & Benoit-Bird 2003).

## Risso's dolphins

### *Systematics and distribution*

The Risso's dolphin taxonomic classification has always been controversial (Kruse 1989) due to this species' relationship with other delphinids. It is currently the only species of its genus and belongs to the *Delphinidae* family. The inclusion of the species in the Globicephalinae sub-family has been suggested based on a cytochrome b analysis (LeDuc et al. 1999). Nonetheless, the suggestion was never taken and it still remains in the *Delphininae* sub-family.

The Risso's dolphin has an extensive distribution in tropical and warm temperate waters of all oceans and seas, including the Mediterranean, Adriatic and Red Seas, but not the Black Sea (Reeves et al. 2002). They can also be found in the Indian Ocean (Alling 1987) and in the Indo-Australian Archipelago (Medway 1965).

In the Western Atlantic, Risso's dolphins have been reported as far north as Greenland (Vibe 1950) and as far south as Cape Horn (Kruse et al. 1999). In the Eastern Atlantic, sightings range from the Shetland Islands (Turner 1892) to about 34° S in South Africa (Kruse et al. 1999). In the Western Pacific, Risso's dolphins have been reported from as far north as the Kuril Islands, East China and Japan (Nishiwaki 1967), to as far south as New Zealand (Oliver 1922). In the Eastern Pacific, its distribution ranges from as far north as the Gulf of Alaska to as far south as 40° S in central Chile (Olavarria et al. 2001).

The Risso's dolphin is found mainly in waters with surface temperatures of 10-28 °C (Reeves et al. 2002). It has an apparent preference for steep shelf-edge habitats that are between 400 and 1000m deep (Baumgartner 1997; Baird 2002). In the Northern Gulf of Mexico such preference for the upper continental slope is probably related to the high concentration of prey in these areas due to the high primary productivity (Baumgartner 1997). Praca and Gannier (2008) also stated that Risso's dolphin habitat is mainly located on the upper part of the continental slope with a mean depth of 640m.

Risso's dolphins can be found year-round in the Canary Islands, particularly on the North-western coast of the island of Gran Canaria (Garcia et al. 2002). The submarine topography of the Northwest of the Island of Gran Canaria is characterized by a sharp increase in depth reaching 1000 m at short distance from shore (Clift & Acosta 2005) matching the species habitat preferences.

### *Diet*

Data on the feeding behaviour of Risso's dolphins have been obtained from stomach contents of stranded animals. Risso's dolphins are considered to have a teuthophageous diet, i.e. they concentrate on cephalopods. They feed on both neritic and oceanic species (Baird 2002) and seem to forage mainly at night (Soldevilla et al. 2010).

Risso's dolphins feed primarily on cuttlefish, *Sepia sp* (Turner 1892) (Scotland), Cape Hope squid, *Loligo vulgaris reynaudü*, (Cockcroft et al. 1993) (South Africa), octopus, *Argonauta argo* (Blanco et al. 2006) (Mediterranean Sea), and *Enoploteuthis sp.* (Clarke 1996) (Hawaii).

Fish constitute only an occasional component of their diet (Sekiguchi et al. 1992). Blanco et al. (2006) proposed that Thaliaceans should also be considered an occasional component of the Risso's dolphin diet.

### *Morphology*

Risso's dolphins are relatively large and robust animals. They have a torpedo shaped body, far more robust in the front than in the back, and a distinctive beakless head shape.

A particular feature of Risso's dolphin morphology is the V-shaped groove in the forehead which creates a distinctive cleft down the face. This extends from the top of the forehead down to the tip of the upper jaw (Leatherwood & Reeves 1983). This aspect makes the species unique among other odontocetes that have a very round and smooth melon. Given that the melon is thought to work as an acoustic lens, related to the directional propagation of an outgoing sonar pulse (Litchfield et al. 1979), "an indentation in the Risso's dolphins forehead could be functionally important for the sonar of the species" (Philips et al. 2003). Apparently this cleft "becomes more prominent with age and the skin within it pulses during vocalization" (Kruse et al. 1999). Nachtigall et al. (2005) speculated that the bifurcate melon of Risso's dolphins might create two sources of sound that interact to propagate highly directional echolocation signals. Nevertheless, the function of this unique characteristic in the Risso's dolphin has not yet been discovered.

At birth, Risso's dolphins measure between 1-1.5 m. Although there is not a marked sexual dimorphism, the males are slightly bigger than females, measuring an estimated average of 3.83 and 3.66m, respectively (Reeves et al. 2002). Their weight varies between 350-500 Kg (Gill 1996).

The dorsal fin is tall, erect and moderately falcate and the flippers are long and sickle-shaped. There are two to seven pairs of conical teeth in the front portion of the lower jaw and, occasionally, small vestigial teeth in the upper jaw.

They are easily recognized at sea by the abundance of white marks on their body which also make them individually identifiable. At birth, they are uniformly grey, changing to dark brown with age. They can turn to light grey and sometimes white as scars accumulate over the years (Würsig & Jefferson 1990); these are long lasting and are more numerous in older animals (Lien & Katona 1990).

The scarring is believed to be caused by intraspecific interactions but also by interactions with cephalopod prey. The presence of unpigmented scars as those found in Risso's dolphins are thought to be an indicator of male "quality" in aggressive social interactions (Macleod 1998).

### *Social structure*

Risso's dolphins have a unique social structure. Individuals form stable and long-term bonds that are organized as pairs or clusters of 3-12 animals, formed by both female and male adults. However, this strong stability is not found in young adults and females without calves. Risso's have a "hybrid" social organization, having been classified as a stratified community based on highly associated social units grouped by age and sex classes (Hartman et al. 2008).

Risso's have a social structure that somehow combines a fission-fusion nature observed in bottlenose dolphins (Würsig & Würsig 1977) and a more stable matrilineal structure as in killer whales (Bigg et al. 1990).

### *Acoustics*

Early recordings of Risso's dolphins vocalizations started in the 1960s (Kruse et al. 1999). Data from a captive sub-adult male lead to the hypothetical existence of a "signature" in the whistle of individuals (Caldwell et al. 1969). More recently, data from a captive juvenile of Risso's dolphins housed with several bottlenose dolphins also showed that Risso's dolphins produce signature whistles; in this case perhaps, through vocal learning from the other species (Favaro et al. 2011). The acoustic repertoire of Risso's dolphin was first described in Australia (Corkeron & Van Parijs 2001). Corkeron and Van Parijs (2001) found that Risso's dolphins in Australia produce a wide range of vocalizations between 30 Hz and 22 kHz. These include broadband clicks, burst-pulse vocalizations (barks and buzzes which are stereotyped vocalizations), low frequency narrow band sounds (grunts and chirps), and the simultaneous production of whistles and burst-pulsed sounds.

Hearing measurements were taken from a captive adult Risso's dolphin (Nachtigall et al. 1995) and a stranded infant (Nachtigall et al. 2005). The hearing threshold of the juvenile was lower than the adult's for high frequencies; for example, for a frequency of 110 kHz the threshold for the juvenile was 76dB re 1 $\mu$ Pa, and for the 30-year old animal it was 122.9 dB re 1 $\mu$ Pa. However, these measurements were taken under different conditions and using

different methods; for the infant, Auditory Evoked Potentials (AEP) were measured, while for the older dolphin a behavioural threshold was used. This might explain such a marked discrepancy between the two animals. The juvenile could hear higher frequencies up to 150 kHz, while the adult could hear only up to 110 kHz.

The temporal resolution of the Risso's dolphin's auditory system is very high, beyond that of most terrestrial animals, but still similar to that of other echolocating odontocetes (Mooney et al. 2006). The infant Risso's dolphin in the study showed a capability to follow stimuli (clicks) with a modulation (presentation) rate up to 1-1.2 kHz. This was measured estimating the modulation rate transfer function (MRTF), using auditory evoked potentials (AEPs) of the animal.

Like any other delphinid, Risso's dolphins can echolocate and have the ability to use sonar signals for underwater detections (Philips et al. 2003). A particular feature of these dolphins' echolocation system is that a subject was able to echolocate downward into the water from a position at the surface when the upper portion of the indented melon was above the water surface. Consequently, Philips et al (2003) proposed a uniquely angled sonar beam for this species.

Additionally, Madsen et al (2004) compared the echolocation clicks of free ranging animals with those of a trained Risso's dolphin used in the studies of Philips et al (2003). The click characteristics of these two studies were closely matched, except for a lower source level (SL) and longer click durations for the captive dolphin (Madsen et al. 2004). According to the authors, the Risso's dolphin was able to detect its primary prey, squid, at ranges of around 100 m.

In conclusion, Risso's dolphins combine a variety of unusual features in their acoustic faculty. Firstly, they produce highly stereotyped burst-pulsed sounds (buzz sounds) and combine their burst-pulsed sounds with whistles in a highly synchronized way (Corkeron & Van Parijs 2001). This aspect places them closer to killer whales (Miller & Bain 2000; Miller 2002) than to any other dolphin species. The suggestion of the presence of signature whistles in Risso's dolphins (Caldwell et al. 1969; Favaro et al. 2011) places them close to bottlenose dolphins. Thus, the Risso's dolphin seems to combine features of very different delphinid species. Similarly, their social system appears to lie somewhere between the highly stable matrilineal society of killer whales (Bigg et al. 1990) and the more labile fission-

fusion society of bottlenose dolphins (Würsig & Würsig 1977). Furthermore, the Risso's dolphin also has a unique feature in the anatomy of its vocal apparatus, namely the vertical indentation in the melon that is likely to impact sound production (Philips et al. 2003).

All these features combined make the Risso's dolphin a highly interesting species that might help to explain the differences in acoustic behaviour within the Delphinidae family and the evolution of acoustic signals in dolphins with regards to their social structure.

## **Thesis overview**

This study aims to contribute to the knowledge of Risso's dolphin acoustic behaviour by describing its vocal repertoire, contextualizing and categorizing their different types of sounds and describing the species' echolocation behaviour.

In chapter two I describe the vocalizations of Risso's dolphins in Gran Canaria. I modelled the different types of vocalizations against the group behaviour patterns, group size and habitat features. I also suggest possible functions for such vocalizations.

In the following chapters, I studied the different types of sounds produced by Risso's dolphins in more detail. Click trains were analysed in chapter three where I categorized the different types of click trains based on their inter-click interval patterns. I also discuss the possible functions of such click train patterns and contextualize them with group behaviour patterns.

In chapter four, using acoustic localization, I explored the echolocation behaviour of the species in the wild. I showed that Risso's dolphins combine biosonar characteristics of smaller delphinids and bigger oceanic species like the beaked whales.

Comparisons of different vocal repertoires within and amongst species may provide information on environmental, ecological, biological and even cultural aspects of a species. In chapter five, I studied the geographic variation of the whistle repertoire of Risso's dolphins between five different locations. I suggest different causes for the variation identified.

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# Chapter 2 : Risso's dolphin vocalizations in relation to context in the Canary Islands

## Introduction

Describing the vocal repertoire of a species is a fundamental step in the investigation of its behaviour. Social behaviour relies largely on communication and having the knowledge of a species' vocal communicating system will benefit the understanding of its social organization (Bousquet et al. 2011), of phylogenetic differences between species (Range & Fischer 2004), behavioural functions (Barros et al. 2011), and ontogenetic aspects (Stoeger-Horwath et al. 2007). Also, it provides information about distinctive characteristics of individuals and groups (Janik & Slater 1998). The comparison of the vocal repertoires of different species is important to understand the evolution of complexity in animal communication.

Vocal repertoire descriptions are quite common in some taxa such as primates (Becker et al. 2003; Range & Fischer 2004; Hsu et al. 2005; Gros-Louis et al. 2008) and birds (Gammon & Baker 2004; Bradley & Mennill 2009; Seneviratne et al. 2009). But there are also descriptions for carnivores (Le Roux et al. 2009), elephants (Soltis 2010), ungulates (Kidjo et al. 2008), bats (Knornschild et al. 2010), sea otters (McShane et al. 1995), pinnipeds (Rautio et al. 2009), fish (Amorim et al. 2008), and even turtles (Giles et al. 2009). However, comparing vocal repertoires can be difficult. This is due to the existence of different criteria and methods to divide or aggregate calls differently between studies. Such differences in methodological approach result in repertoire descriptions with different levels of complexity even within species (McShane et al. 1995). The lack of a standard nomenclature and acoustic analysis across different studies hardens comparisons.

The main question with repertoire descriptions, and perhaps the reason for a great diversity of methods in the literature, is how well they reflect the animal's categorization of signals (Searcy et al. 1999). The animals themselves distinguish between different call types and subtypes in ways that are not necessarily apparent to humans (Janik 1999). One way to test any given sound classification is to look for context specificity. While this can be difficult for

some species such as taxa that spend most of their time out of sight of the researcher, it is a good way to confirm sound categorization.

Here, I describe the vocal repertoire of the Risso's dolphin, a species with a wide geographic distribution yet little presence in the cetacean literature. This is surprising since the repertoire of some cetacean species has been covered extensively.

The vocal repertoires of Killer whales (Deecke et al. 2005; Samarra et al. 2010), and bottlenose dolphins (Janik 2000a; Boisseau 2005; Sayigh et al. 2007) are examples. Killer whales live in stable matrilineal societies and form group-specific dialects while bottlenose dolphins live in fission-fusion societies and develop individually distinctive signature whistles that function as cohesion calls between associates (Janik & Slater 1998; Janik et al. 2006).

Individual Risso's dolphins form long term bonds of pairs or clusters of 3-12 adults of both sexes. Young adults and females without calves do not seem to form these strong stable bonds. Although it resembles the fission-fusion societies of bottlenose dolphins, Risso's dolphins differ in the fact that mature adults are organized in pods, very distinguishable units of the population.. As such they also resemble the matrilineal social structure characteristic of killer whales (Hartman et al. 2008). It seems therefore, that Risso's dolphins somehow have a hybrid social structure between the fission-fusion found in bottlenoses and the matrilineal found one found in killer whales.

Early recordings of Risso's dolphins vocalizations started in the 1960s (Kruse et al. 1999). The acoustic repertoire of Risso's dolphins has been studied so far in Australia (Corkeron & Van Parijs 2001). Australian Risso's dolphins produce a wide range of vocalizations between 30 Hz and 22 kHz. These include broadband clicks, burst-pulse vocalizations (barks and buzzes which are stereotyped vocalizations), low frequency narrow band sounds (grunts and chirps), and the simultaneous production of whistles and burst-pulsed sounds.

Like any other delphinid, Risso's dolphins can echolocate and have the ability to use sonar signals for detection underwater (Philips et al. 2003). They can detect prey (squid) at ranges of 100 m (Madsen et al. 2004). Risso's dolphins can be found year-round in the Canary Islands, Spain, particularly on the Northwest coast of the island of Gran Canaria. The submarine topography of this area, particularly around La Isleta, is characterized by a sharp increase in depth reaching 1000 m at short distance from shore (Clift & Acosta 2005) making it a preferred habitat for this species (Baumgartner 1997; Baird 2002).

The goal of this investigation was to describe Risso's dolphin vocalizations from Gran Canaria and place them into behavioural and habitat contexts.

## Methods

### Data collection

Recordings were obtained during daylight hours on Risso's dolphin surveys in the Northwest of Gran Canaria, using a 6 m rib with an outboard engine. When a group was encountered photo-ID data were taken and a focal group was selected for further observation. This focal group was observed using 2-min scan sampling (Altmann 1974; Martin & Bateson 2007). Data were collected on group composition, travel direction and size of the focal group. Simultaneously, another observer reported position, distance, group size and behaviour of other groups in a radius of 500 m. the presence of other species was monitored every two minutes together with the behavioural sampling.

A 15 m "chain" rule was applied to define groups as two or more animals in which each individual was within 15m of at least one other member of the group (Hartman et al. 2008) Risso's dolphins' vocal production was related to behaviour, group size, and water depth. Observed behaviour patterns were classed into four mutually exclusive categories: foraging, socializing, resting and travelling. The group's behaviour was defined as being one of these when at least 75% of the animals in the group displayed behaviour patterns that fell into the same category. Recordings in which the behaviour was uncertain or undefined were discarded.

Group size was divided in two categories: groups of less than 8 animals (smaller) and groups of 8 and more animals (bigger). This division was based in the median of group sizes of all encounters.

Water depth was also divided into two categories: shallow water (less than 100m) and deep water (more than 100 m).

Acoustic recordings were conducted continuously on a dispersed 4-hydrophone array, recording to a laptop with an Edirol FA-101 sound card. The acoustic array had 3 hydrophones tensioned to chains with waterproof tape at 2 m of depth (2 HTI-96 MIN and a HTI 94 SSQ, frequency response 2Hz to 30 kHz,  $\pm 1$ dB), and a fourth hydrophone at 10m of depth (SRD hydrophone HS/150, frequency response 1kHz to 100kHz  $\pm 1$ db). The acoustical

samples were taken for as long as possible during a follow when sea state was less than 3 (Beaufort scale) in dry weather. Initially, recordings were made using a sampling rate of 96 kHz (representing 33% of all recordings used) and later changed to 192 kHz (67% of all recordings) to cover the highest possible range of frequencies with our equipment. Sounds were not analysed in terms of their acoustical properties so, the fact that some sounds might be cut off due to low sampling rates, does not affect the results. Sounds presence/absence was still taken into account.

### **Data analysis**

Acoustic data were analysed visually with Adobe Audition 2.0 using spectrogram displays (Hanning window, 512 FFT) and recordings where other odontocetes were present were then discarded.

Risso's dolphin sounds were divided qualitatively into three categories according to their signal-to-noise ratio (SNR). Only sounds of the two best quality categories were used in the analysis.

The Risso's dolphin repertoire description presented focuses on the following types of vocalizations: whistles, click trains and burst-pulses. Whistles were defined as tonal sounds, often with harmonics; click trains were broadband clicks with a wide range of ICIs (inter click intervals). Burst-pulses were isolated click trains where all ICIs were less than 4 milliseconds. Using R 2.11.1 (R project for statistical computing; GNU project) I modelled the counts of each type of vocalization against group behaviour patterns, water depth and group size using a Generalized Linear Model (GLM) with a Poisson family and a log link function coupled with Generalized Estimating Equations (GEE). GEE were used to avoid the temporal and spatial autocorrelation within the encounters of Risso's dolphin (Panigada et al. 2008). I ran a separate model for each type of vocalization. Due to the structure of the data frame of the burst-pulses data R could not compute the GEE model with a correlation parameter for those data. Therefore, the modelling of the burst-pulses data was done without considering the possible correlation between vocalizations within the same encounter. The counts of each type of vocalization were considered as the Poisson distributed response variables. Behaviour patterns, depth and group size categories were modelled as categorical predictor variables. The logarithm of both recording time and the number of animals per encounter

was included as an offset in the model to allow for differences in number of vocalizations due to these parameters.

To evaluate the use of each different type of sound produced I used a measure of how often dolphins produced each type of sound. I counted the number of type of sounds recorded by animal and by minute, the sound type rate. I then compared the sound type rates across different behavioural contexts, water depth and groups size.

## Results

A total of 30 encounters with Risso's dolphins were considered. From the analysis of 45 hours of recordings, 115 whistles, 674 isolated burst-pulses and 3019 click trains were extracted (Figure 2.1).

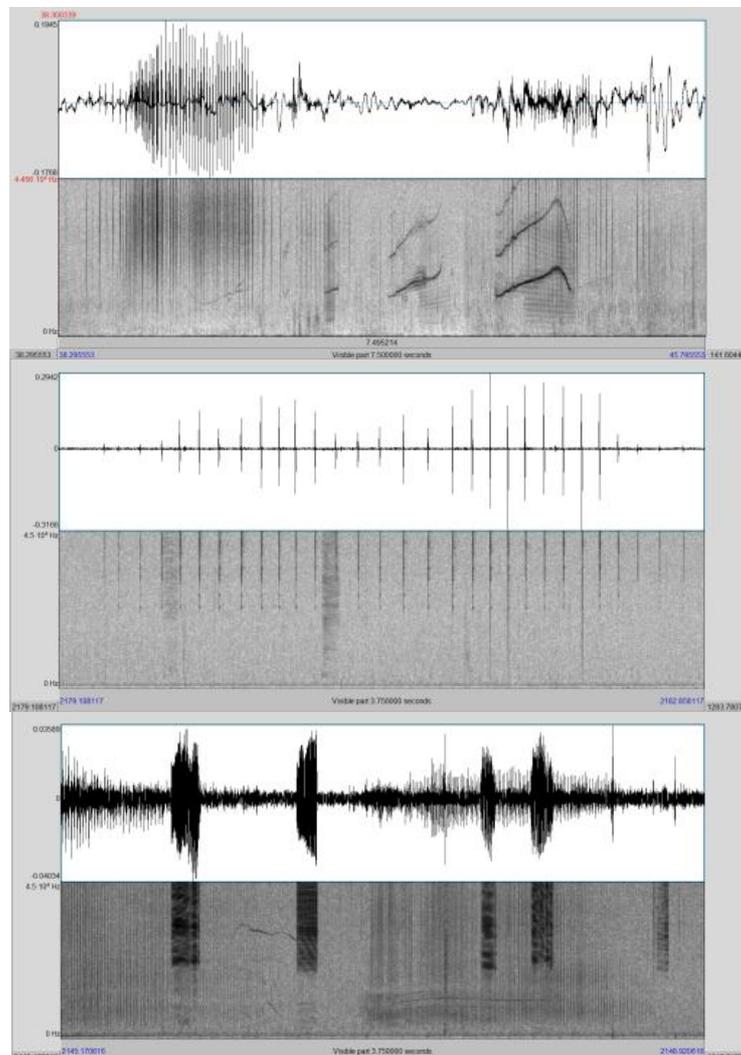


Figure 2.1- Examples of the main vocalizations analyzed (from top to bottom respectively):whistles (with click trains in the background), click trains (with 2 burst-pulses in the background) and isolated burst-pulses.

Both whistles and isolated burst-pulses were produced mainly in social contexts (Figure 2.2). Click trains were most commonly produced during foraging but the animals also produced click trains in other behavioural contexts. Overall there was a very low production rate of whistles when compared to the other two types of vocalizations.

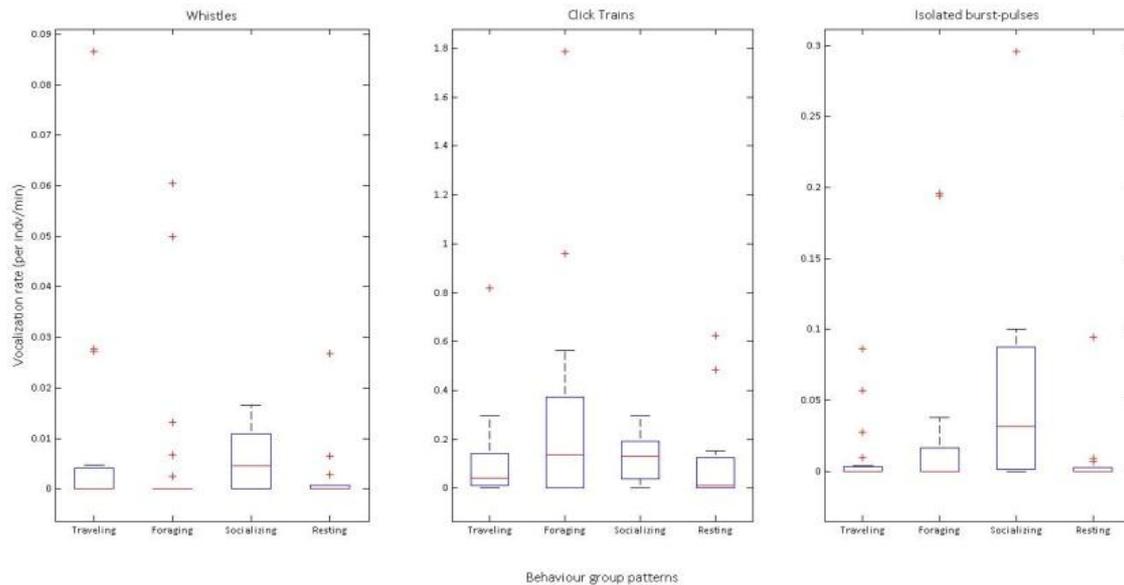


Figure 2.2– Boxplot of the rates (number of vocalization/individual/minute) of the 3 types of vocalizations in each behaviour group pattern

In general Risso’s dolphins were much more vocal in deeper waters (Figure 2.3). Overall, the animals spent most time socializing and travelling (Figure 2.4). When found in deeper waters they spent their time in a similar way (Figure 2.5). However, in shallower waters they spent most their time resting and travelling, although the differences were not statistically significant (Figure 2.6). Eighty per cent of the socializing events occurred with the bigger groups of Risso’s dolphins.

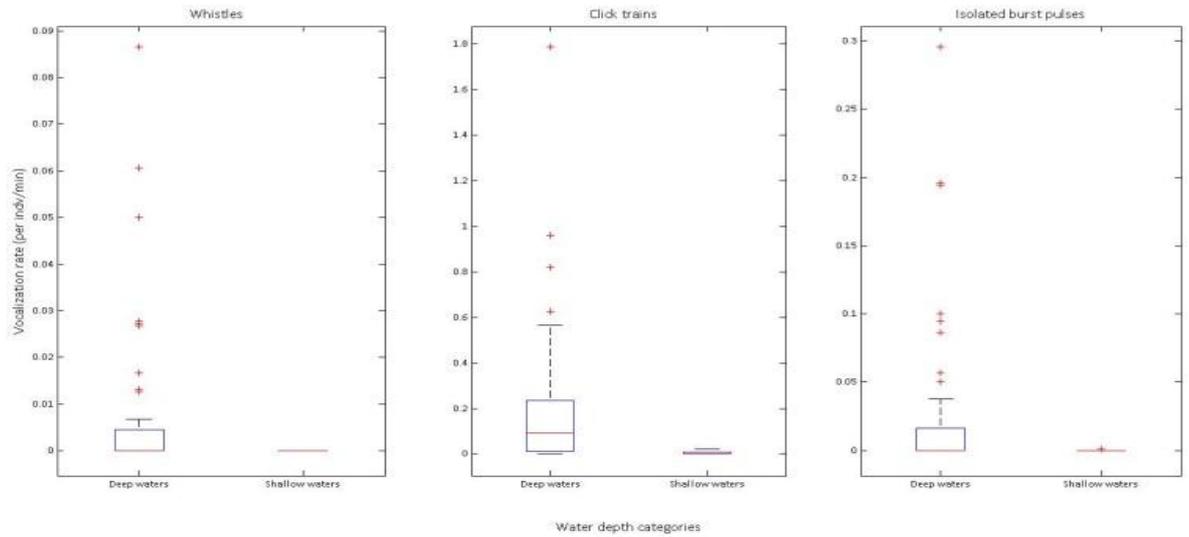


Figure 2.3– Boxplot of the rates (number of vocalization/individual/minute) of the 3 types of vocalizations in each depth category: shallow waters- less than 100m and deep waters  $\geq$  100m

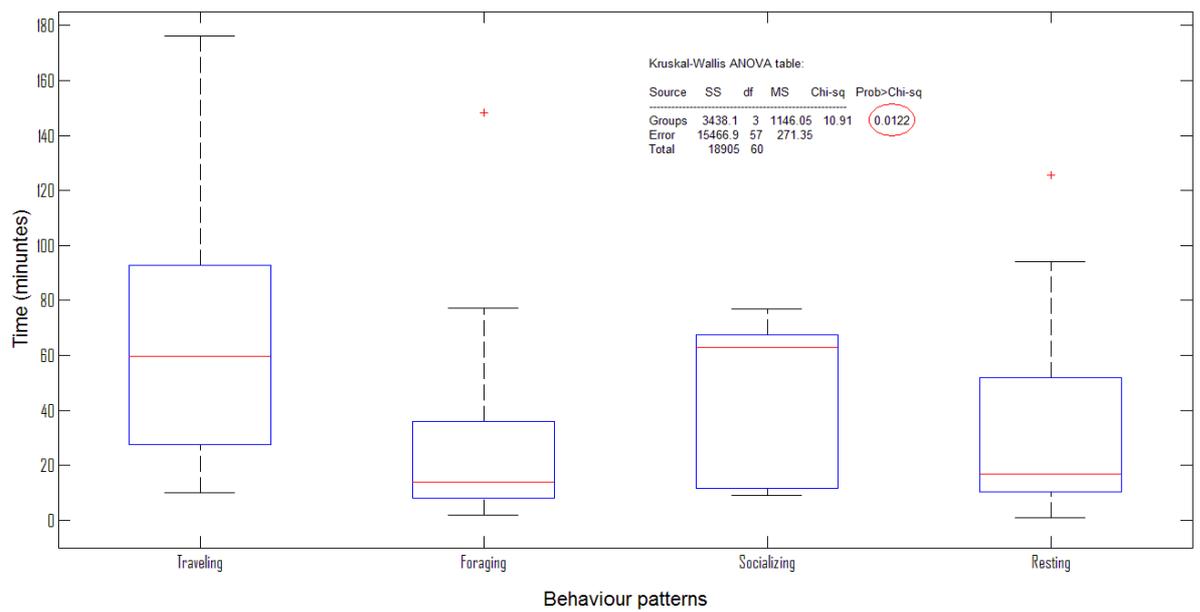


Figure 2.4- Time spent by Risso's dolphins in each type of group behaviour pattern and the Kruskal-Wallis table.

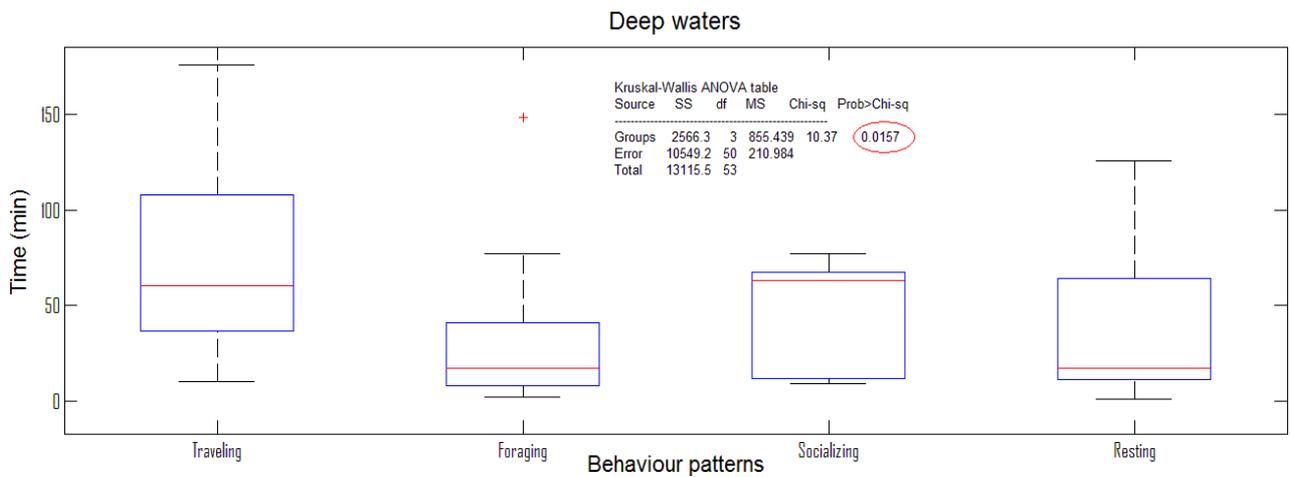


Figure 2.5- Time spent by Risso's dolphins in each type of behaviour in deep waters; and Kruskal-Wallis Anova table.

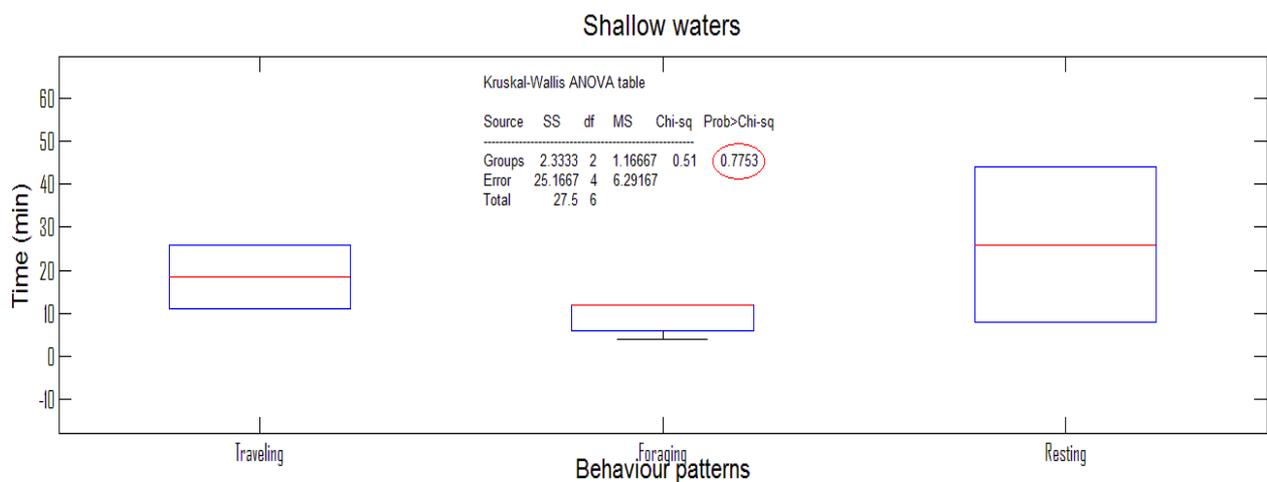


Figure 2.6- Time spent by Risso's dolphins in each type of group behaviour pattern in shallow waters; and Kruskal-Wallis Anova table.

On the contrary, in the majority of the foraging events I found groups of less than 8 animals. While traveling and resting the proportion of larger and smaller groups is approximately the same within each group behaviour category (Table 2.1).

Risso's dolphins produced most whistles while socializing and foraging. When found in shallower waters they decreased their whistle production. Individuals in groups of less than 8 animals produced more whistles than in larger groups (Table 2.2).

Table 2.1- Number of encounters where I found groups of less than 8 animals against number of encounters of 8 and more Risso’s dolphins across the distinct group behavior patterns.

	Socializing	Resting	Foraging	Traveling
Groups of less than 8 animals	2	9	18	15
Groups of 8 and more animals	8	8	4	11
<b>Total of encounters</b>	<b>10</b>	<b>17</b>	<b>22</b>	<b>26</b>

Table 2.2- Estimates and p values from the GLM-GEE for comparisons of Risso’s dolphin whistle production between behavioural patterns (eg. socializing VS traveling), deep and shallow waters, and groups of 8 and more individuals and groups of less than 8 individuals. ‘\*\*\*’ - p <0.0001; ‘\*\*’ - p <0.001; ‘\*’ - p <0.01; ‘.’ -p <0.05

	Estimate	Std.err	Wald	Pr(> W )
Intercept	-6.0590	0.7126	72.296	< 2e-16 ***
<b>Shallow waters</b>	<b>-2.6647</b>	<b>0.9836</b>	<b>7.339</b>	<b>0.00675 **</b>
<b>Groups of less than 8 animals</b>	<b>1.5396</b>	<b>0.7124</b>	<b>4.670</b>	<b>0.03070 *</b>
Resting vs Foraging	-0.4960	0.6412	0.598	0.43917
Socializing vs Foraging	0.9392	0.6958	1.822	0.17708
Traveling vs Foraging	-0.2988	0.8003	0.139	0.70888
Resting vs Traveling	-0.197	0.542	0.13	0.71579
<b>Socializing vs Traveling</b>	<b>1.238</b>	<b>0.329</b>	<b>14.17</b>	<b>0.00017 ***</b>
<b>Socializing vs Resting</b>	<b>1.435</b>	<b>0.415</b>	<b>11.98</b>	<b>0.00054 ***</b>

Click train production was highest when the dolphins were found in deep waters (Table 2.3). ANOVA was used to select variables and revealed that group size and group behaviour patterns were not statistically significant for the model and I, therefore, excluded them from the click trains model.

Table 2.3- Estimates and p values from the GLM-GEE for comparisons of Risso’s dolphin click train production between behavioural patterns (e.g. socializing VS traveling), deep and shallow waters, and groups of 8 and more individuals and groups of less than 8 individuals. ‘\*\*\*’ - p <0.0001; ‘\*\*’ - p <0.001; ‘\*’ - p <0.01.

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Risso's dolphins produced most burst-pulses while socializing and foraging, followed by travelling and resting behaviour (Figure 2.2 and Table 2.4 ). In areas where water depth was less than 100m there were significantly fewer burst-pulses. Similarly, Risso's dolphins produced less burst-pulses when found in groups of less than 8 animals (Table 2.4)

Table 2.4- Estimates and p values from the GLM-GEE for comparisons of Risso's dolphin isolated burst-pulsed production between behavioural patterns (e.g. socializing VS traveling), deep and shallow waters, and groups of 8 and more individuals and groups of less than 8 individuals. '\*\*\*' - p < 0.0001; '\*\*' - p < 0.001; '\*' - p < 0.01;

	Estimate	Std.err	Wald	Pr(> W )	
Intercept	-4.0365	0.6238	41.870	9.75e-11	***
<b>Shallow waters (&lt;100)</b>	<b>-2.8348</b>	<b>1.1732</b>	<b>5.839</b>	<b>0.0157</b>	<b>*</b>
<b>Foraging VS Traveling</b>	<b>1.3681</b>	<b>0.6180</b>	<b>4.901</b>	<b>0.0268</b>	<b>*</b>
<b>Socializing VS Traveling</b>	<b>1.2019</b>	<b>0.5471</b>	<b>4.826</b>	<b>0.0280</b>	<b>*</b>
Resting VS Traveling	-1.1404	0.8111	1.977	0.1597	
Foraging VS Socializing	0.1623	0.4260	0.145	0.70332	
<b>Resting VS Socializing</b>	<b>-2.4406</b>	<b>1.0661</b>	<b>5.241</b>	<b>0.02206</b>	<b>*</b>
<b>Groups of less than 8 animals</b>	<b>-1.4428</b>	<b>0.6202</b>	<b>5.412</b>	<b>0.0200</b>	<b>*</b>

## Discussion

Behaviour patterns, group size and water depth affected sound type production in Risso's dolphins recorded in Gran Canaria, Spain.

Whistling was relatively rare in this species. In many cetaceans, like the bottlenose dolphins, whistles are seen as the primary communication signal. Bottlenose dolphins produce several types of whistles, some of which are used to maintain group cohesion and signal individual identity (Janik & Slater 1998; Janik et al. 2006). In the Risso's dolphins investigated, 45 hours of recordings yielded only 115 good quality whistles. Groups of 10 to 25 socializing Risso's dolphins produced on average, less whistles (0.01 whistles per individual and minute) than socializing bottlenose dolphins in similar group sizes (0.42 whistles per individual and minute (Quick & Janik 2008). Such low production of whistles suggests that Risso's dolphins might have been using another type of social sound to communicate.

Nevertheless, Risso's dolphins produced more whistles while socializing than in any other behaviour context indicating that their role in communication is not lost in this species. In groups of 8 or more animals a significant decrease in whistle production was observed. In bigger groups, Risso's may try to avoid masking by conspecifics and save energy by reducing the number of whistles as has been found for bottlenose dolphins (Quick & Janik 2008). Perhaps in these cases, a short-range communication sound might be used instead such as the burst-pulse (Lammers et al. 2006).

In shallow waters, dolphins did not socialize at all, which explains the decrease in whistle production in the shallows when compared to deeper waters (>100m). However, in our study the animals spent only 2 hours of their time in shallow water. Risso's dolphins have a preference for deep water prey, such as the squid (Wurtz et al. 1992) which is concentrated in the upper continental slope, between 400-1000m of depth (Baumgartner 1997; see Bearzi et al. 2011 for a review). Since these dolphins forage mainly in deeper waters, this would explain a low click train production in the shallow waters of Gran Canaria.

In shallow waters, Risso's dolphins tended to spend more time travelling and resting than socializing or foraging (Figure 2.6). Therefore, the observed decrease in click train production in waters up to 100m deep was expected. Conversely, the fact that no difference in the click train rates of Risso's dolphins across different group behaviour patterns was found reveals that Risso's dolphins use click train in different contexts. For example, click trains were still very common during travelling similar to what was found in other dolphins (Verfuss et al. 2005) and bats (Schnitzler et al. 2003) since echolocation is used in spatial orientation.

Risso's dolphins produced most burst-pulses during socializing and foraging. No correlation was taken into account when modelling the counts of burst-pulses. Therefore, their significance could be misleading. I found that when running the click train model without the correlation I got more significant results than the ones obtained with the current model (correlation included). However, when I modelled the whistles counts with and without the correlation I got the same results. As such the group behavioural patterns comparisons based on the burst-pulses count modelling should be interpreted with caution. Nevertheless, the results from the model are supported by the higher burst-pulses rates during socializing and foraging as seen in Figure 2.2 and by the similarity with other species. When looking at the effect of depth, Risso's dolphins decreased burst-pulse production in shallower waters. Since animals spend less time socializing and foraging in the shallow waters, a decrease of this type of vocalizations was to be expected.

Risso's dolphins primarily produced isolated burst-pulses while socializing which suggests a communicative function for this type of vocalization. This is supported further by the fact that isolated burst-pulse production decreased in smaller groups. Assuming a social

function, smaller groups might not have the need to use burst-pulses as often as larger groups.

Burst-pulses have been reported to be communicative in other species (see Janik 2009 for a review). For example, northern right whale dolphins produce stereotyped sequences of burst-pulsed sounds which seem to have a communicative function similar to that of whistles in other dolphins (Rankin et al. 2007). Burst-pulses in spinner dolphins have also been reported to be communicative (Lammers et al. 2004), and are thought to be a more intimate and directional form of communication when animals are close together as opposed to whistles that play an important role in dispersed groups maintaining group cohesion (Lammers et al. 2006). Similarly in Risso's dolphins when groups are larger and densities can be higher, burst-pulses could assume the same highly directional and more intimate form of communication, avoiding masking.

The isolated burst-pulses in Risso's dolphins are broadband and structurally similar to echolocation click trains, but the trains are much shorter and with a higher repetition rate. These sounds were isolated, they did not constitute the terminal part of a foraging click train sequence, which makes it unlikely that they were used in target approaches (Madsen et al. 2005). However, Risso's dolphins use burst-pulses in foraging contexts quite frequently. This is also the case in pilot whales, *Globicephala macrorhynchus*, when in the ascent phase of a deep dive use "rasps" which are short click series to maintain short range coordination (Jensen et al. 2011a). Comparably Risso's dolphins could use burst-pulses in a similar manner when foraging since both species are deep and solitary foragers.

Echolocation clicks in bats serve a dual role, they are used to orientation and foraging but also to communicate species and group affiliation (Voigt-Heucke et al. 2010). Further studies are needed to understand the role of these isolated burst-pulses of Risso's dolphins. They could be used only in communication or, as in bats, serve more than one function.

In conclusion, while the general vocalization categories of Risso's dolphins were similar to those of other delphinids, there were significant differences in how they used them. Further studies on Risso's dolphins are needed to investigate the functional aspects of these vocalizations in more detail.

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# Chapter 3 : Click Train Use and Echolocation

## Behaviour of Risso's Dolphins off the Coast of Gran Canaria

### Introduction

Acoustic energy propagates further than visual energy in water (Au & Hastings 2008). Therefore, sound constitutes an important means of communication, navigation and prey detection in the life of odontocetes. Odontocetes evolved a range of acoustic signals which fall in two broad categories: tonal sounds (whistles) and pulsed sounds. Pulsed sounds can be categorically divided into click trains and isolated burst-pulses. This division is often based on the aural analysis and/or the visual inspection of spectrograms and sometimes can be too simplistic. Dolphins might not categorize or perceive sounds in the same categorical way defined by humans (Janik 2009). Moreover there is often a continuous transition between these two types of sounds. For example, false killer whales present a structure of its vocalizations that lies around a continuum with trains of discrete exponentially damped sinusoidal pulses at one end and continuous sinusoid signals at the other end (Murray et al. 1998). This means that there is not a clear cut between click trains and burst-pulsed sounds, but instead there is a continuum between the two types of sounds based on their inter click intervals (ICIs). This also has implications on the signals functions. If there is a graded structure of the vocalizations with no clear acoustic division, perhaps the function of the signals might also not be discrete. Conversely, if the signals are in fact discrete that might mean that their functions could also be uniquely discrete (Murray et al. 1998). This makes more difficult the study of some dolphins' communication system since the function of the pulsed sounds could be hard to define.

Clicks trains are a series of brief ultrasonic broadband clicks emitted at varying repetition rates which are used for echolocation. Generally these clicks have a duration of 30-50  $\mu$ s and cover a frequency range from 10 to 150kHz with most energy concentrated at either 40 or 120 kHz (Au 2000). Isolated burst-pulses are click series with a high repetition rate and

are thought to be used in transfer of information contexts (Caldwell & Caldwell 1966). Similarly, tonal sounds are primarily used for communication (Janik 2009).

In echolocation dolphins emit a sound pulse which travels through the water and gets reflected by any object with density different from water. The echo of the pulse travels back and it is received by the dolphin's ears. This information is processed in the brain before a second pulse is emitted. This is called the pulse mode of echolocation (Au 2000). The time it takes for the sound pulse to travel through the water and back is called the two-way travel/transit time (TWTT). The time that the dolphin takes to process the sound, i.e., the time delay between hearing the echo and emitting the following click is called the lag time or processing time (Au 1993). Some dolphins, like the Hector dolphin, don't whistle and only produce clicks. They produce 9 different types of clicks and some of which are likely to be used in communication contexts (Dawson & Thorpe 1990). The main issue in a species like this is to understand when a click is used in communication and when in echolocation. In spinner dolphins click trains with an average ICI of less than 10ms function as short range communicative signals. Conversely, click trains with an average ICI of more than 10ms are considered typical echolocation click trains (Lammers et al. 2004; Lammers et al. 2006).

Early echolocation studies were done with captive bottlenose dolphins. The animals were stationary and had to detect targets at different distances (see Au 1993 for a review). In one of these experiments, when instructed, the animal swam to the entrance of a pen, stopped and echolocated at a target positioned at different distances in different trials (Au et al. 1974). The dolphin decreased the inter click interval at distances closer to a target proportional to the TWTT with the lag time remaining constant. Non stationary bottlenose dolphins also decreased the ICI with the decrease in distance at which the target was presented, which was called range locking (Morozov et al. 1972). Free swimming animals also show range locking behaviour. Even when not asked to detect any target, harbour porpoises, for example, show a distance dependent decrease in the inter click interval proportional to the decrease in the TWTT to the presumed target with the lag time remaining constant (Verfuss et al. 2005). Finless porpoises, also exhibit a similar behaviour to range locking during foraging (Akamatsu et al. 2005). However, not all odontocetes use range locking behaviour. Blainville's beaked whale, *Mesoplodon densirostris*, on the other hand, seem to show stable inter click intervals in the approach phase to a target (Madsen et al. 2005). This could be due the lack of landmarks to lock on while navigating in the deep

water environment that beaked whales inhabit. Also, the targets are so far away in these situations that the animals might include echoes from far distances keeping, this way, a window open for possible detections in between. Animals inhabiting open waters might therefore, adjust their click interval to a specific search range most likely their maximum perceptual range (Verfuss et al. 2009).

Echolocation behaviour evolved similarly in dolphins and bats (see Schnitzler et al. 2003 for a review in bats echolocation). Small cetaceans (Verfuss et al. 2009) when capturing a prey item assume a very similar behaviour to insectivorous bats (Griffin et al. 1960).

Echolocation behaviour while foraging can be divided in three different parts: the search phase, the approach phase and the terminal part by this order. In the search phase the dolphins show a range locking behaviour on a target/landmark with a linear decrease of the inter click intervals with the approaching distance (Verfuss et al. 2005). When a prey is detected the search phase leads to the approach phase characterized by constant ICIs. This is followed by the terminal phase where we can find a sudden drop in the ICIs leading to a final buzz. The final buzz is made of high repetition series of clicks that might end up with a prey capture.

Again, beaked whales show a different pattern of foraging behaviour (Madsen et al. 2005). There are also the same three phases on the process of echolocation during prey capture as in bats and small delphinids. However, beaked whales show constant ICIs during both the search and approach phases with an abrupt change to the buzz phase.

In summary, in a target approach and/or foraging behaviour dolphins can either make a gradual transition from the click train to a terminal buzz phase or present a sudden drop in the ICIs directly to the buzz phase. Either way, the buzz phase is always preceded by a click train in that kind of behavioural contexts. Contrarily, if a burst-pulse is used in a communicative context it usually occurs isolated, i.e. not preceded by a regular click train. This feature could help to tell feeding clicks from communicative ones. But these criteria might not be mutually exclusive and behavioural context studies are needed to verify that.

It seems, therefore, that click trains' ICI patterns are a relevant indicator for the function of sound emitted by species in both taxa that excel in the use of this type of sounds: bats and dolphins. In this study I looked at the use of pulsed sounds (echolocation and burst-pulses) in different behaviour contexts in an oceanic species of odontocetes.

Risso's dolphins can be found in Gran Canaria in the Northwest of the island where the underwater topography allows this oceanic species to be found closer to land and where the main vessel traffic passes. Although click train production by Risso's dolphins has been described in the wild (Corkeron & Van Parijs 2001; Philips et al. 2003; Madsen et al. 2004) there is a lack of knowledge on the relationship between ICI patterns and behavioural context. This chapter describes and categorizes wild Risso's dolphins click train production for the first time both at population and species level and puts it into a behavioural context.

## Methods

### Data collection

Recordings were obtained during daylight hours on Risso's dolphin surveys in the Northwest of Gran Canaria, Spain. When a group of dolphins was encountered a focal group was selected for further observation. This focal group was observed using 2-min scan sampling (Altmann 1974; Martin & Bateson 2007). Data were collected on the following mutually exclusive group behaviour patterns: traveling, socializing, foraging and slow travel. Traveling Risso's dolphins were all moving in the same direction with a speed greater than 2 knots. When the groups had high cohesion (less than one body length between two animals, traveling at less than 2 knots, sometimes almost stationary at the surface or just below the water surface, I considered that the animals were slow traveling. When foraging, animals acquired non directional movement and spread out, sometimes speeding up and diving. Socializing animals were in close proximity, rubbing together, exposing bellies and fins and sometimes exhibiting the "head standing" (Bearzi et al. 2011) behaviour.

I also recorded group composition, travel direction and size of the focal group. Simultaneously, another observer was reporting position, distance, group size and behaviour of other groups in a radius of 500m. A 15m "chain" rule was applied to define groups as two or more animals in which each individual was within 15m of at least one other member of the group (Hartman et al. 2008).

Acoustic recordings were conducted continuously on a dispersed 4-hydrophone array, recording to a laptop with an Edirol FA-101 sound card. The acoustic array was formed by 3 hydrophones tensioned to chains with waterproof tape at 2m of depth (2 HTI-96 MIN and a HTI 94 SSQ with a frequency response of 2Hz to 30 kHz,  $\pm 1$ dB), and a fourth hydrophone at

10m of depth (SDR hydrophone HS/150, frequency response 1kHz to 100kHz  $\pm$  1db). The acoustic recordings were collected for as long as possible during a follow but only when sea state was less than 3 (Beaufort scale) in dry weather. Recordings were made initially using a sampling rate of 96 kHz (33% of all recordings analysed). Risso's click trains go beyond that range so I switched to 192 kHz (67% of all recordings analysed), the highest our equipment permitted at the time, to try capturing the full range of Risso's dolphins signals. Sounds were not analysed in terms of their acoustical properties so, the fact that some sounds might be cut off due to low sampling rates, does not affect the results. Sounds presence/absence was still taken into account. I searched for other species every two minutes together with the behavioural sampling.

### Data analysis

I discarded recordings where other odontocetes were present and recordings where animal behaviour was uncertain or undefined.

Click trains were identified visually with the software Adobe Audition 2.0, using spectrogram displays (Hanning window, 512 FFT). A click train was considered to be composed of clicks where the inter click interval (ICI) between two consecutive clicks was less than the double of the previous ICI. Risso's dolphin click trains were divided qualitatively into 3 categories according to their signal-to-noise ratio (SNR). Only sounds of the two best quality categories were used in the analysis. For the classification and quantification of click train ICIs, only non-overlapping click trains were analysed. For each non-overlapping click train the following were measured:

- ICI, which is the time difference between two consecutive clicks. I measured all the ICIs within each click train. This was measured automatically using the *Pulse train analysis* tool of the Avisoft SasLab software. This software uses a waveform-based analysis of temporal patterns.
- Number of clicks in a click train. This was also automatically measured with the *Pulse train analysis* tool of Avisoft SasLab software.
- Maximum and minimum ICI calculated using an custom written Matlab program (Mathworks, v.7 R2010b)

To calculate production rates of click trains overlapping click trains were included in the analysis.

I used a custom written Matlab program to plot the ICI values against the click train (CT) duration for each CT. A linear regression line was then fitted for each plot and the residuals (the difference between the real value of the ICI and the correspondent one of the regression line-the fitted value) were calculated for each ICI.

Eight mutually exclusive CT categories were defined based on the combination of the following parameters:

- the slope of the regression line of the plots created,
- the residuals of each click train,
- the number of clicks in each click train,
- and the mean ICI of click trains.

I was interested in checking if range locking behaviour was present in the click train sequences I analysed. One indication for the presence of range locking could be if the continuous decrease in the inter click interval reflects the approach speed of an animal to a target and is therefore related to typical swimming speeds. If we fit a regression line, the slope reflects a decrease in ICI within a certain time period, which is correlated with a swimming speed of an animal, i.e, the approach speed of animal to a target. I used the lowest and highest swimming speed commonly observed in Risso's dolphins in my field site. I translated those speeds into two slopes,  $a$  and  $b$ , that would mark the range in which range locking behaviour may occur. I considered 6 knots (3.087m/s) and 2 knots (1.029 m/s) as the maximum and minimum swimming speed observed in the Canary Risso's dolphins while traveling (personal observation).

In the regression line of a graph where the X-axis represents time (s) and the Y-axis represents the ICI (s), the slope equals the change in the ICI (s) for each unit change in the time (1 second). In other words, the slope of the regression line fitted to a potential range locking sequence is the decrease on the Y-axis (ICI) in seconds divided by 1 second. A dolphin swimming at the maximum observed speed of 6 knots will travel 3.087 m in one second. Assuming a sound speed of 1500m in one second, it would take 0.002058 (3.087/1500) seconds to cover 3.087 m. Considering that the dolphin processes the echo of its own emitted pulse, the sound has to travel to the target and back to the dolphin. Hence we need to divide the sound speed by a factor of two. Therefore, in a potential case of range locking, the slope value that corresponds to the highest speed observed in Risso's is 0.004116 (3.087/(1500/2)) which constitutes hereafter the constant  $b$ . Applying the same

calculation for the slowest swimming speed, the slope value was calculated as 0.001372 (1.029/(1500/2)), the constant  $a$ .

Therefore, a potential range locking sequence would be one whose slope fell between  $-b$  and  $-a$ , speeds where a constant decrease of ICIs with distance is possible considering the sound speed and the two way travel time.

If the slope of the regression line was lower than  $-b$ , the click train would be considered as a decreasing ICI because the decrease would be much faster than that correlated with the observed swimming speeds Risso's of our study. An increasing ICI click train was defined when the slope value was higher than  $a$ . If the slope fell in between  $-a$  and  $a$ , the click train would be considered to have a constant ICI.

In order to allow some variation in the ICIs of a click train I established 10% of variation of a certain ICI from its fitted value in the regression. Therefore, if the absolute values of each residual were within the 10% range of the correspondent fitted values I considered the click train to have constant ICI.

To summarize, the following CT categories were defined:

1- CT with **constant** ICI:

- The absolute value of each residual is less than 10% of the corresponding fitted value;
- The absolute value of the regression line slope is equal or lower than  $a$ ;
- The total number of clicks is higher than 2;
- The average ICI is higher than 4ms.

2- CT with **increasing** ICI:

- The absolute value of each residual is less than 10% of the corresponding fitted value;
- The slope of the regression line is higher than  $a$ ;
- Total number of clicks is higher than 2;
- The average ICI is higher than 4ms.

3- CT with **decreasing** ICI:

- The absolute value of each residual is less than 10% of the corresponding fitted value;
- The slope of the regression line is higher than  $-b$ ;
- The total number of clicks is higher than 2;

- The average ICI higher than 4ms.

4- CT with **variable ICI**:

- The absolute value of each residual is equal or higher than 10% of the corresponding fitted value;
- The total number of clicks is higher than 2;
- The average ICI is higher than 4ms.

5-Click trains composed of **2 clicks**:

- The total number of clicks is equal to 2.

6- Isolated **burst-pulses**:

- Selected manually by visual inspection of the plots “ICI vs duration of the click train”. These are defined as isolated short click trains (67 clicks on average) with very low ICIs (less than 4ms).

7- Click trains ending in a **buzz**:

- Selected manually by visual inspection of the plots ‘ICIs vs duration of the click train’. Click trains that initially had constant or variable ICI, followed by a decrease in the ICI, ending with a sudden drop in the ICI, the buzz phase.

8- Click trains that might be a result of **range locking behaviour**:

- The absolute value of each residual is less than 10% of the corresponding fitted value;
- The value of the slope of the regression line is lower than  $-b$  and higher than  $-a$ ;
- The total number of clicks is higher than 2;
- The average ICI is higher than 4ms.
- 

ICIs can reflect the distance at which dolphins are echolocating, so I calculated the average distances at which dolphins were “looking at” in each group behavioural category. Therefore, I used the maximum value of the ICIs of the click trains produced during each group behavioural category (Table 3.1). Similarly to Simard et al. (2010) I used the following formula:

$$d = (ICI - t)/2 * c,$$

where  $ICI$  is the mean ICI (s) of the click train produced while the dolphins were engaged in a specific group behavioural pattern,  $d$  is the estimate maximum distance (m),  $t$  is the lag time

(s) and assumed the mean value of 0.032 s which is the average between 0.019 and 0.045 s found for bottlenose dolphins (Au et al. 1974); and  $c$  is the sound speed which was considered to be 1500 m/s.

To evaluate how different types of click trains changed with Risso's dolphins' behaviour, four mutually exclusive categories of group behaviour patterns were used: foraging, socializing, slow travel and travelling. The group behaviour was defined when at least 75% of the animals in the group of the focal animal had the same behaviour pattern.

To evaluate the use of echolocation I used a measure of how often dolphins echolocated. I counted the number of click trains recorded by animal and by minute, the click train rate.

To model the counts of click trains and burst-pulses against behaviour patterns I used a Generalized Linear Model (GML) with a Poisson family and a log link function coupled with Generalized Estimating Equations (GEE) (Panigada et al. 2008) using R 2.14 (R project for statistical computing; GNU project). The counts of each type of vocalization were considered as the Poisson distributed response variables. Group behaviour pattern was modelled as a categorical predictor variable. The logarithm of both recording time and the number of animals per encounter was included as an offset in the model to allow for differences in number of vocalizations due to these parameters. To assess the differences of the mean ICIs against click train classes I used Kruskal Wallis tests. To test the differences of the proportions of click train classes against the group behaviour patterns, I used crosstabs with z-tests and a Bonferoni correction.

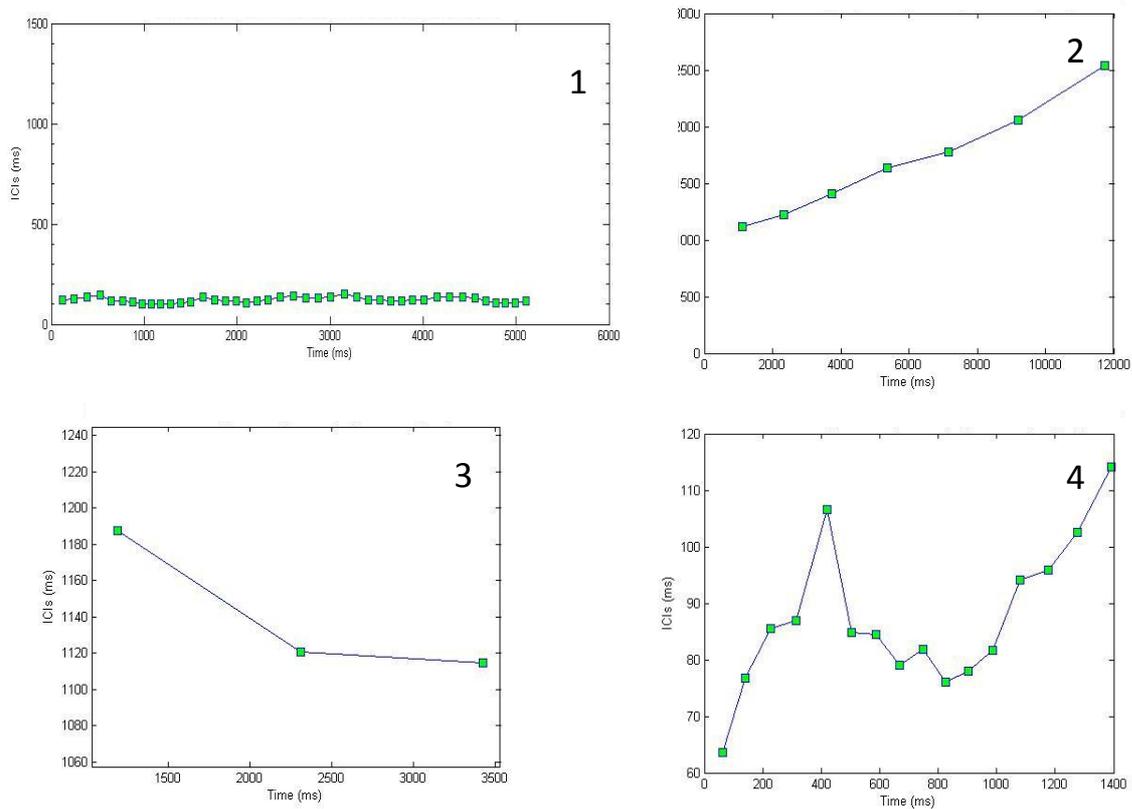
To test the frequencies of occurrence of recording sessions across different group behaviour patterns in shallow and deep waters I used the Freeman-Halton extension of the Fisher exact probability test for a 2 x 4 contingency table.

These analyses were performed using IBM SPSS STATISTICS 19.0. Since the isolated burst-pulses are such a stereotyped type of click train and they are thought to have a different function from the other click trains in other species (Dawson 1991; Lammers et al. 2004), click trains hereafter described include all classes defined before except class 6 (burst-pulses).

## Results

I extracted a total of 1757 click trains from 45 hours of recordings. These were used for the classification analysis. For the click train rate analysis a total of 2126 click trains were analysed.

Risso's dolphins showed a variety of click train classes (Figure 3.1). The histogram in Figure 3.2 shows the variability of ICIs in the click trains produced by Risso's dolphins. The average ICIs (Table 3.1) did not differ across different group behaviour patterns (Kruskal-Wallis test,  $p=0.072$ ) with a large range of ICIs being present within each behavioural category. This variability of ICIs within the same behavioural category was tested and revealed a heterogeneity of variance of ICIs across the four behaviour categories ( $p=3.82 \times 10^{-59}$  Levene Test, Figure 3.3).



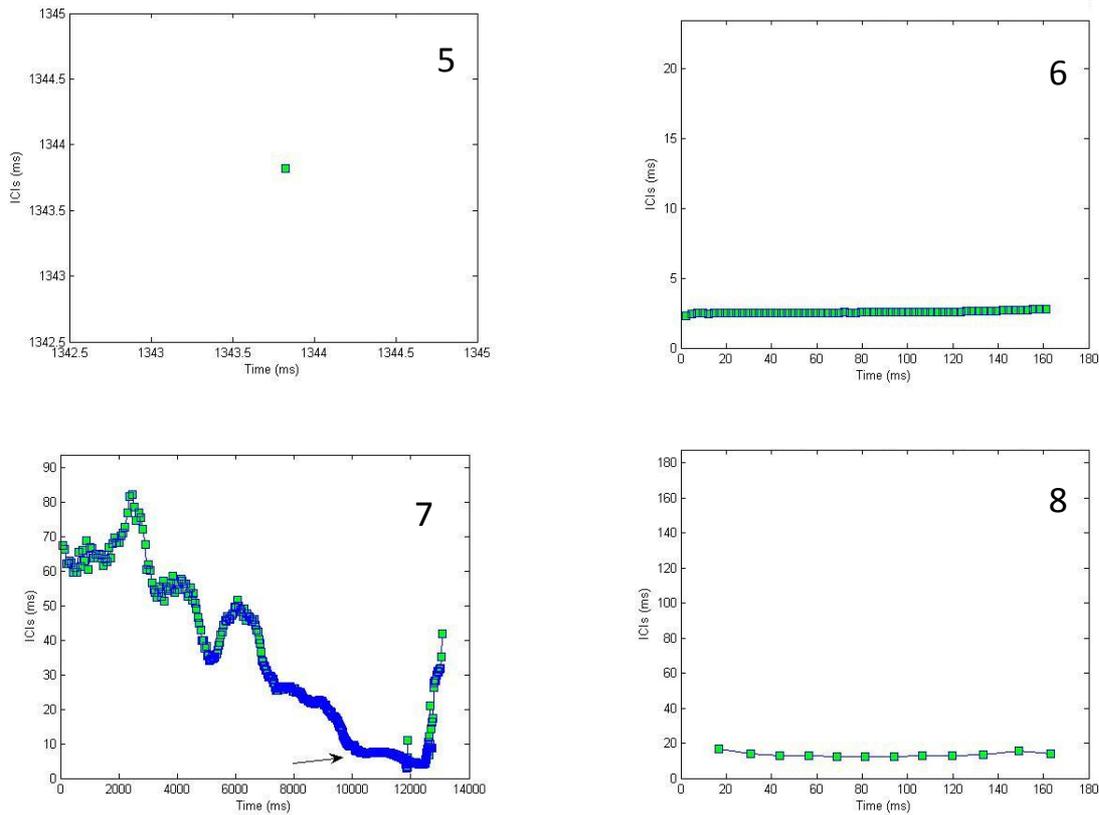
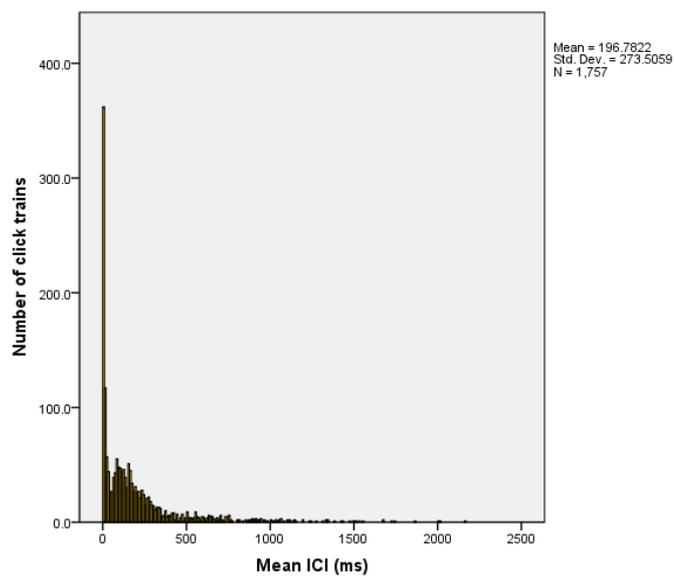


Figure 3.1- Examples of each class of click train: plots of ICIs (s) vs duration (s) of a click train. Class 1- click train with constant ICI, class 2 – click train with increasing ICI, class 3- click train with decreasing ICI, class 4- click train with variable ICI, class 5- click train of 2 clicks, class 6-isolated burst-pulses, class 7- click train ending with a buzz, 8- potential range locking click train.



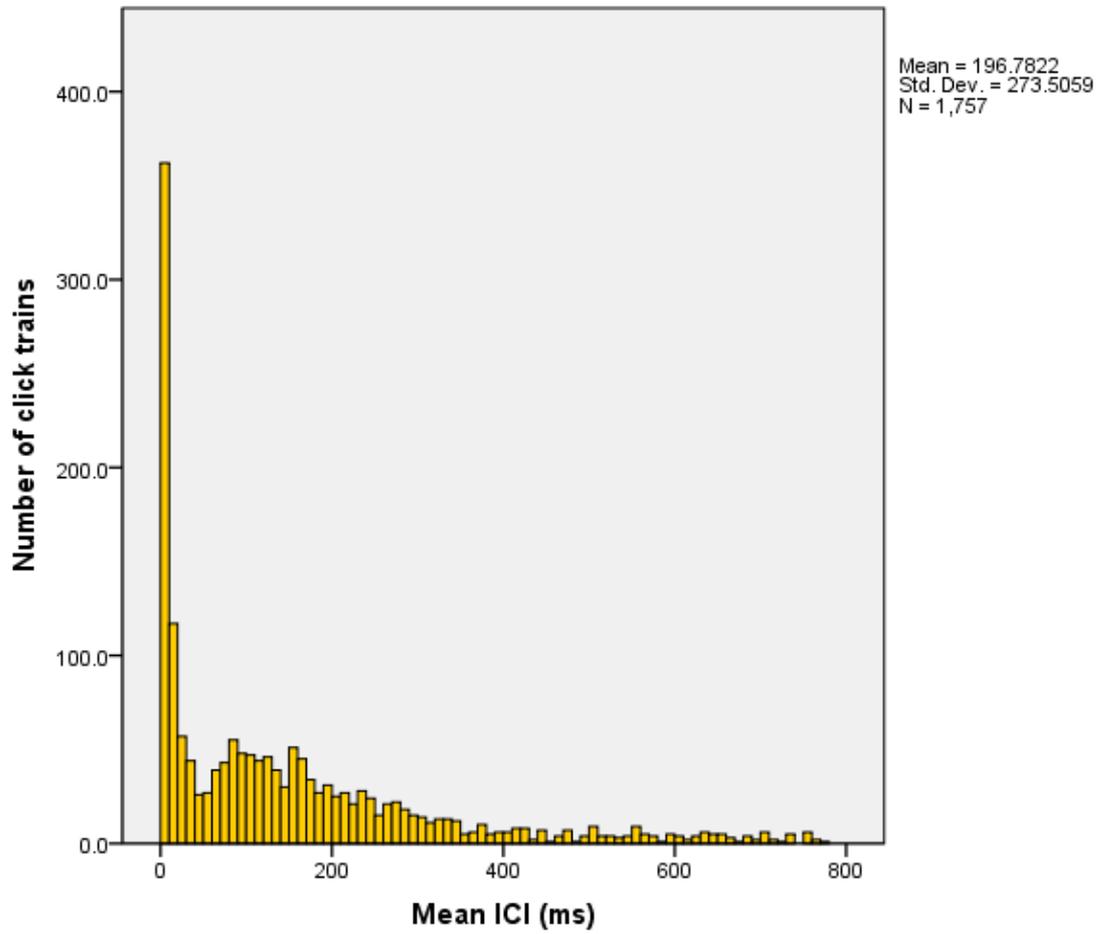


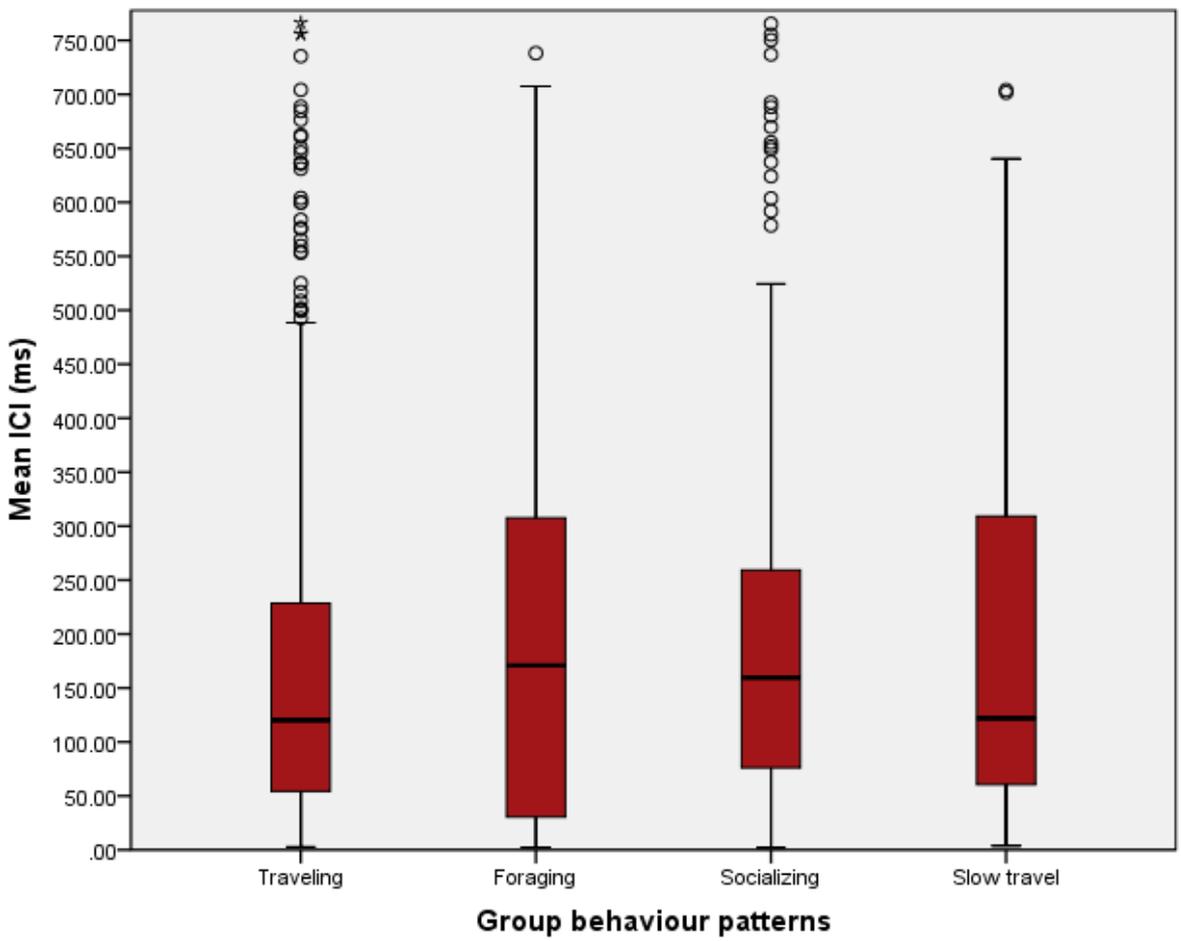
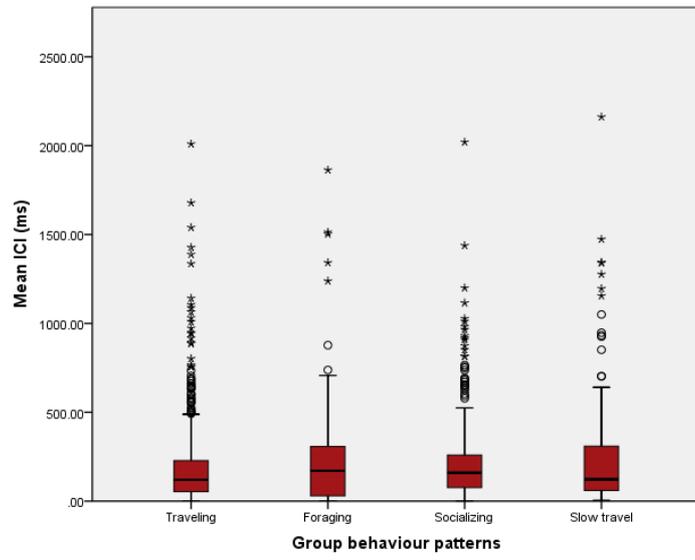
Figure 3.2- Histogram of the number of click trains (burst-pulses included) by the mean ICI. Total number of clicks, mean and standard deviations are included in the graph. Bin size is 10ms. The second graph is a zoom in of the first one.

Table 3.1 – Median, Mean and Standard deviation of the number of clicks, ICIs (ms), minimum ICI (ms), maximum ICI (s) per group behaviour pattern

Group behaviour patterns		Number of clicks	Mean ICI (ms)	Max. ICI (ms)	Min ICI (ms)	Click train duration (ms)
Foraging	Mean	19.79	202.05	276.59	160.31	1346.89
	N	301.00	301.00	301.00	301.00	301.00
	Std. Deviation	25.91	247.36	316.11	222.42	1669.15
	Median	10.00	141.96	201.80	78.92	834.66
Slow travel	Mean	29.80	270.04	406.62	188.69	2352.28
	N	107.00	107.00	107.00	107.00	107.00
	Std. Deviation	36.87	392.70	512.08	325.88	2581.06
	Median	15.00	112.39	196.01	66.25	1343.82
Socializing	Mean	26.47	183.67	275.13	134.68	1827.08
	N	416.00	416.00	416.00	416.00	416.00
	Std. Deviation	46.88	237.55	333.40	208.82	2599.07
	Median	14.50	128.67	178.57	85.68	1001.04
Traveling	Mean	29.84	190.97	289.79	139.22	2062.55
	N	435.00	435.00	435.00	435.00	435.00
	Std. Deviation	50.98	274.75	365.06	239.20	3032.27
	Median	15.00	100.72	161.90	56.01	1096.40
Total	Mean	26.32	197.93	291.72	146.97	1838.27
	N	1259.00	1259.00	1259.00	1259.00	1259.00
	Std. Deviation	43.72	269.77	360.33	234.80	2593.06
	Median	13.00	118.26	177.20	70.32	1038.80

Table 3.2– Mean ICIs and estimated distances of potential targets across group behaviour patterns

Group behaviour pattern	Mean ICI (ms)	Estimated distance (m)
Traveling	0.19	119.23
Slow traveling	0.27	178.53
Socializing	0.18	113.75
Foraging	0.20	127.54



Group behaviour pattern		N	Mean Rank
Click Train Mean ICI	Traveling	387	519.57
	Foraging	273	574.66
	Socializing	348	573.57
	Slow travel	99	562.81
	Total	1107	

	Click train mean ICI
Chi-Square	7.009
df	3
Asymp. Sig.	.072

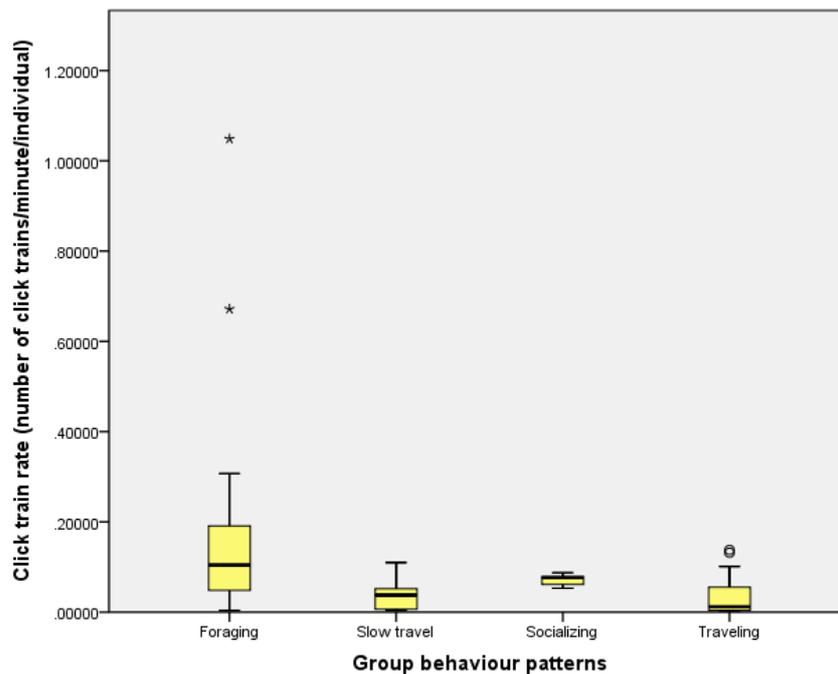
**Test of Homogeneity of Variances**

ICI mean

Levene Statistic	df1	df2	Sig.
45.256	7	1749	3.82x <sup>10-59</sup>

Figure 3.3 –Boxplot of the mean ICI (ms) of the click trains (isolated burst-pulses not included) across the group behaviour patterns and Kruskal Wallis test of the mean ICI across the group behaviour patterns. \* - outliers; o – extreme values. The second graph is a zoom in of the first one. On the bottom a Levene test the homogeneity of variances across group behaviour patterns.

When calculating the click train rate (number of click trains produced by individual per minute) the highest rates were found during foraging and socializing (Figure 3.4). Risso’s dolphins also echolocated regularly while traveling, even at slow speeds (less than 2 knots).



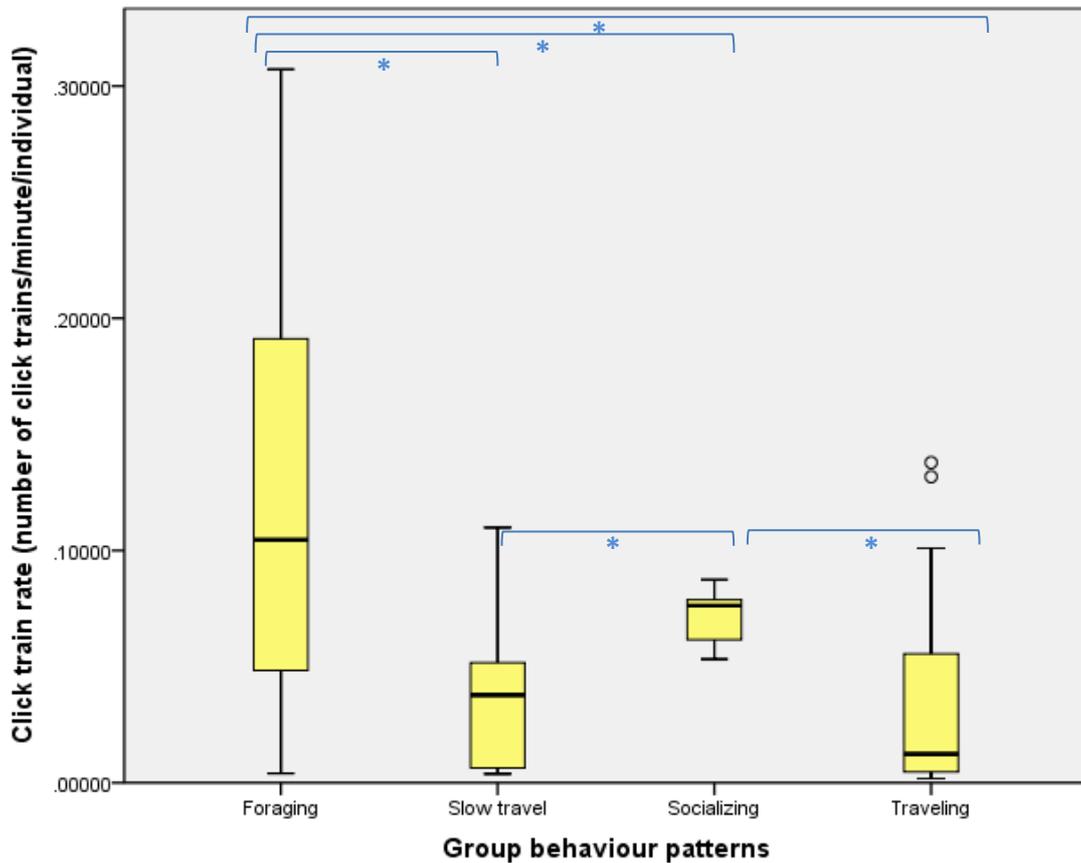


Figure 3.4 - Boxplot of the click train rates (isolated burst-pulses not included) across group behaviour patterns. The blue lines and asterisks show the significant differences of click train rates across Risso's dolphin's group behaviour patterns. These lines and asterisks are the result of the interpretation of the Table 3.2. The second graph is a zoom in of the first one. \* - outliers; o – extreme values.

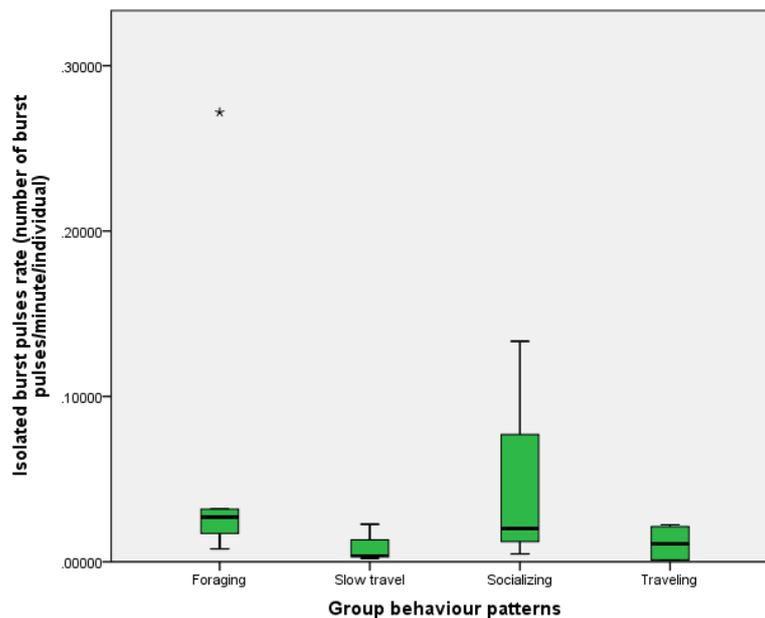
Results of the GEE model (Table 3.3) performed on the rates of click trains supported this, as illustrated in Figure 3.4 by the blue lines and asterisks shown. Risso's dolphins produced significantly more click trains per individual per minute when engaged in foraging behaviour, followed by socializing behaviour when compared with any other group behaviour pattern. No differences could be found in the click train production between traveling and slow travel.

Table 3.3 - Estimates and p values from the GLM-GEE for comparisons of Risso's dolphin click train production between group behavioural patterns (eg socializing VS traveling).

	Estimate	Std.error	Wald	Pr(> W )
Intercept	-4.180	0.573	53.22	<b>3e-13</b> ***
<b>Foraging VS Slow travel</b>	2.035	0.683	8.87	<b>0.0029</b> **
<b>Socializing VS Slow travel</b>	1.281	0.549	5.44	<b>0.0197</b> *
Traveling VS Slow travel	0.296	0.582	0.26	0.6110
<b>Foraging VS Traveling</b>	1.739	0.511	11.59	<b>0.00066</b> ***
<b>Socializing VS Traveling</b>	0.985	0.374	6.93	<b>0.00847</b> **
<b>Socializing VS Foraging</b>	-0.7544	0.2990	6.364	<b>0.011648</b> *

Significance codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

A higher production of burst-pulses occurred when Risso's dolphins were socializing and foraging, while a lower production of burst-pulses was found when traveling (Figure 3.5). The model showed a trend (p=0.078) of increase of burst-pulses production rate when the animals were engaged in socializing behaviour compared to slow travel (Table 3.4). The higher whisker on the boxplot (Figure 3.5) towards higher rates of burst-pulses while socializing suggests that burst-pulse production may be clustered and perhaps associated to bouts of higher activity.



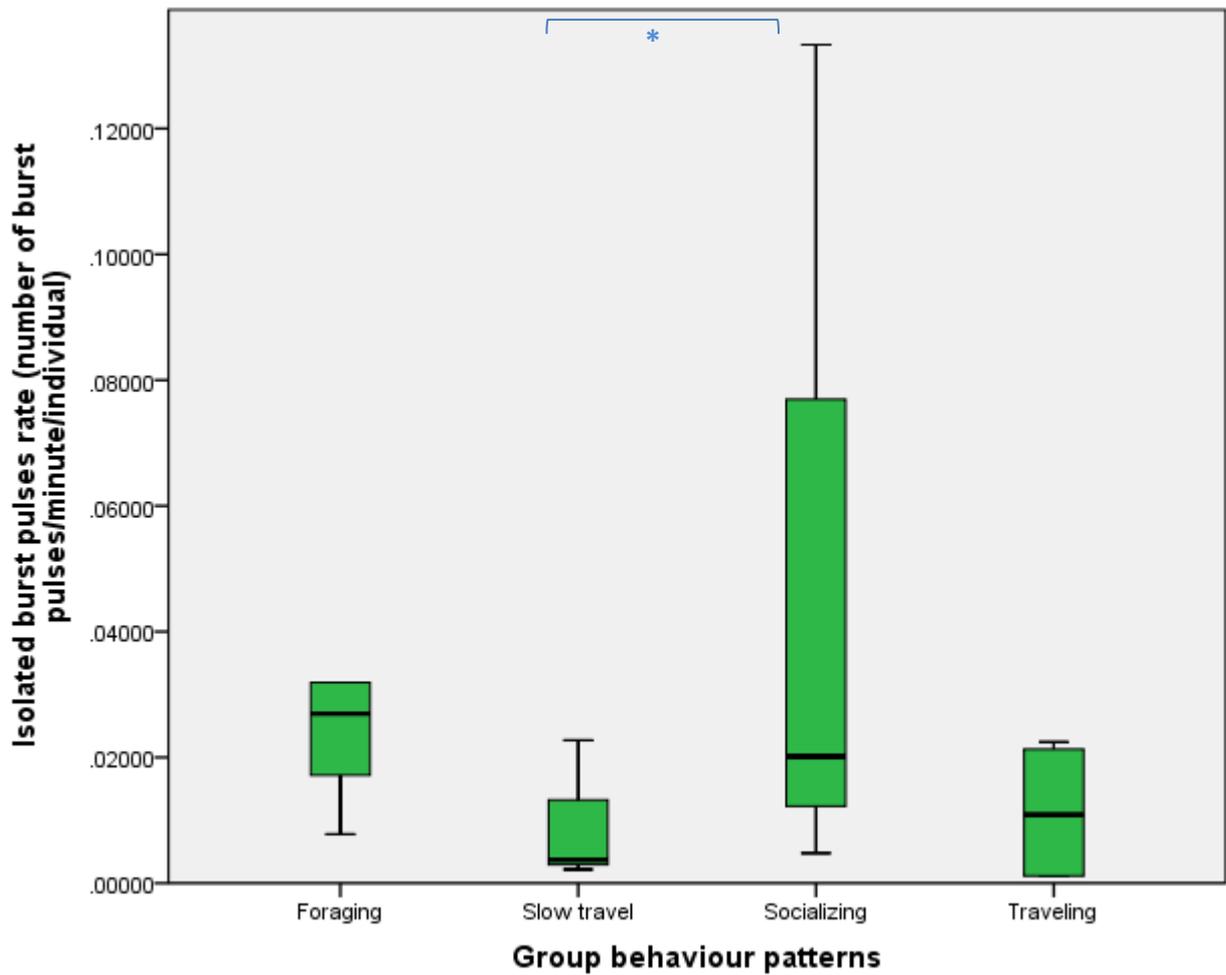


Figure 3.5 – Boxplot of the isolated burst-pulses rates across group behaviour patterns. The blue line and asterisk show the significant differences of burst-pulses rates across Risso’s dolphin’s group behaviour patterns. These line and asterisk are the result of the interpretation of the Table 3.3. The second graph is a zoom in of the first one. \* - outliers.

Table 3.4 - Estimates and p values from the GLM-GEE for comparisons of Risso’s dolphin burst-pulses production between group behavioural patterns (eg socializing VS traveling).

	Estimate	Std.err	Wald	Pr(> W )
Intercept	-4.2702	0.4424	93.148	<2e-16 ***
Slow travel VS Foraging	-0.3841	0.6042	0.404	0.525
Socializing VS Foraging	0.3417	0.5830	0.344	0.558
Traveling VS Foraging	-0.4840	0.6205	0.608	0.435
<b>Socializing VS Slow travel</b>	<b>0.7258</b>	<b>0.4113</b>	<b>3.11</b>	<b>0.078 .</b>
Traveling VS Slow travel	-0.0999	0.2536	0.16	0.694
Socializing VS Traveling	0.8256	0.5234	2.49	0.11

Significance codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

For both click trains and burst-pulses I compared the number of each sound type produced by a single animal at a given time with the number of the same sound type produce by more than one animal at a given time. This comparison was done for each group behaviour pattern. Risso’s dolphins changed their echolocation behaviour (more than one animal vs single animal echolocation) with the group behaviour patterns (Figure 3.6 and Figure 3.7).

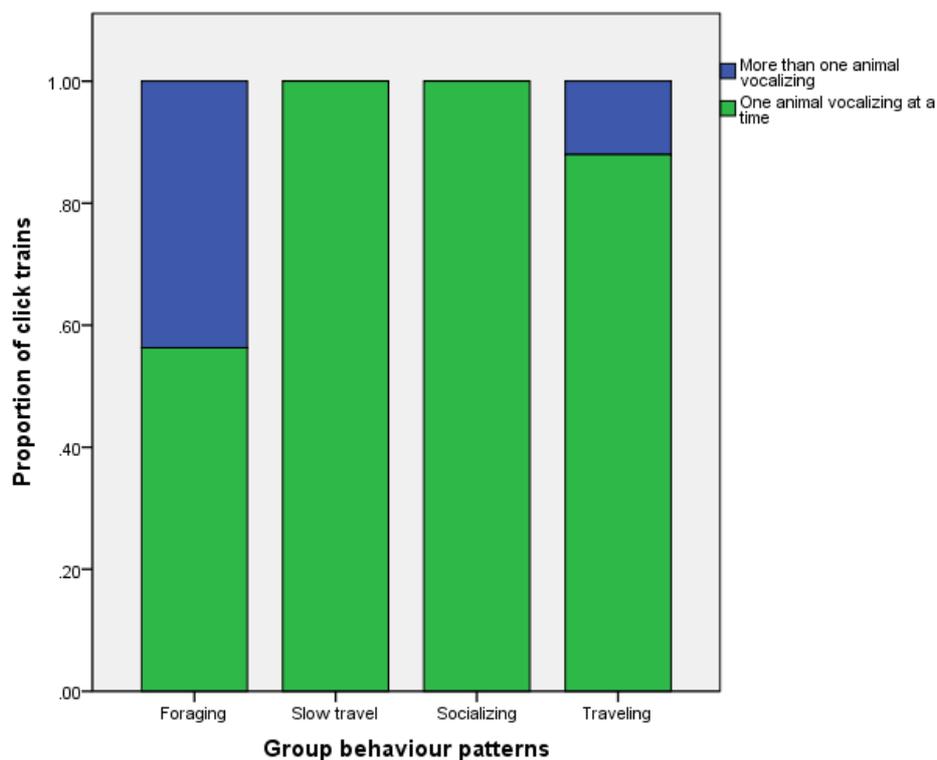


Figure 3.6 – Graph showing the proportion of click trains (isolated burst-pulses not included) produced by one animal singularly (green) and more than one animal at a given time (blue) across group behaviour patterns.

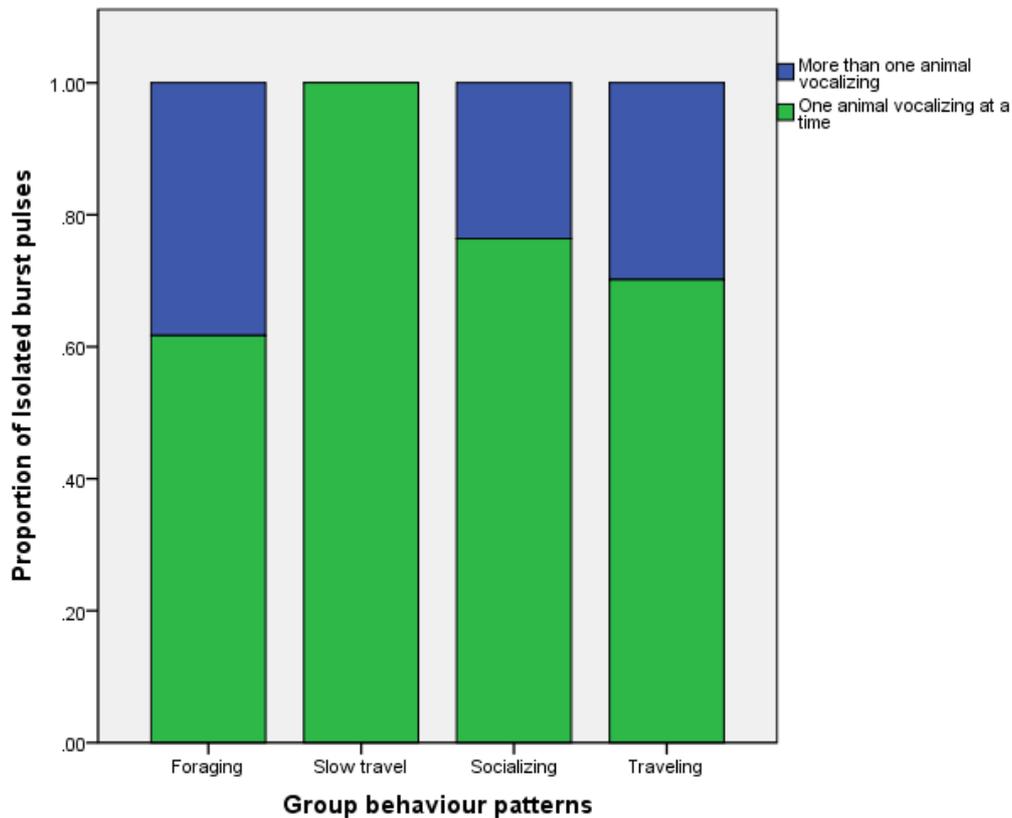


Figure 3.7 – Graph showing the proportion of isolated burst-pulses produced by one animal singularly (green) and more than one animal at a given time (blue) across group behaviour patterns.

While foraging approximately 55% of the overall click trains were overlapped and were been produced by more than one animal. However, when engaged in traveling behaviour only 10% of the overall click trains were overlapped. On the other hand, when socializing and when engaged in slow travel only one animal produced click trains at a given time (Figure 3.6) i.e. there was no overlap of click trains.

Twenty five per cent of the overall burst-pulses were produced by more than one animal at a given time, i.e., overlapping when Risso’s dolphins were socializing. While foraging approximately 35% of the overall burst-pulses were overlapped. When traveling, 30% of the overall burst-pulses were also overlapped. On the other hand when slow traveling, burst-pulses are only produced by a single animal at a given time (Figure 3.7), i.e., there was no overlap between click trains.

I looked at the percentage of the different classes of click trains and burst-pulses in each group behaviour category (Figure 3.8). Across all group behaviour categories the click trains used most often by Risso’s dolphins were the variable ICI click trains. Click trains with an

increasing ICI represented the second highest proportion of use across all group behaviour patterns. Burst-pulses were more commonly used when Risso’s dolphins were found socializing (Figure 3.9). The very low proportion of potential range locking click trains suggested very little use of range locking by Risso’s dolphins.

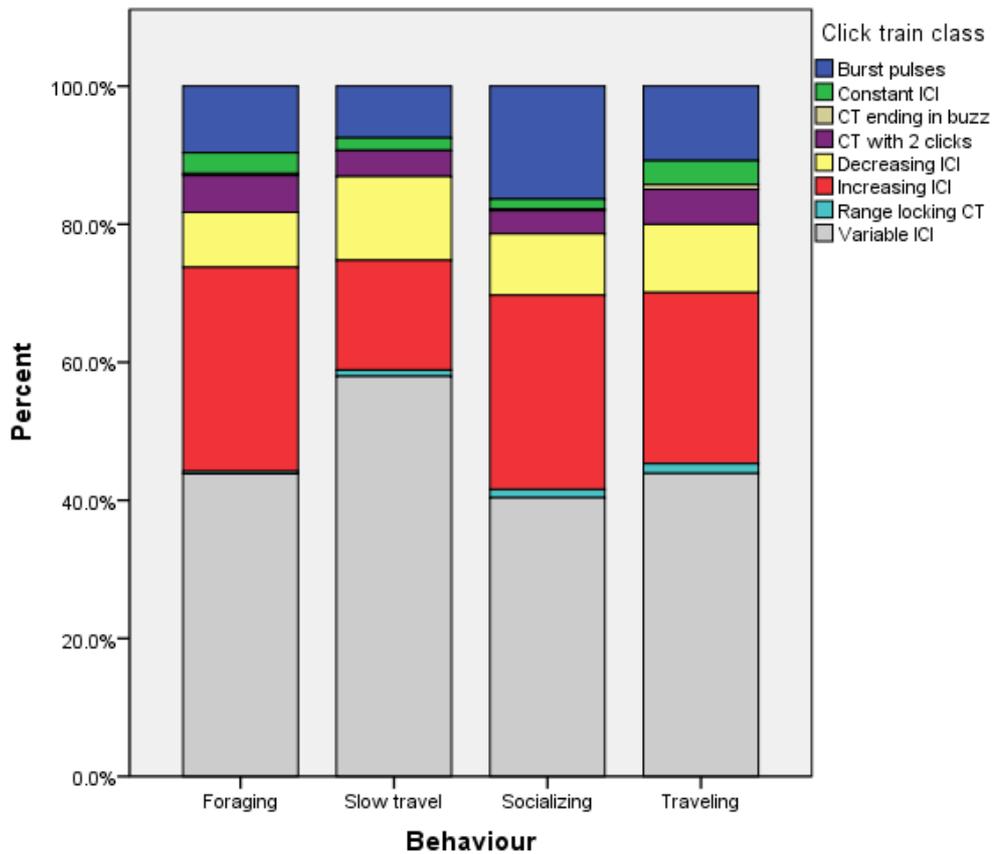


Figure 3.8 – Graph showing the proportion (as a percentage) of click trains classes within each group behaviour pattern.

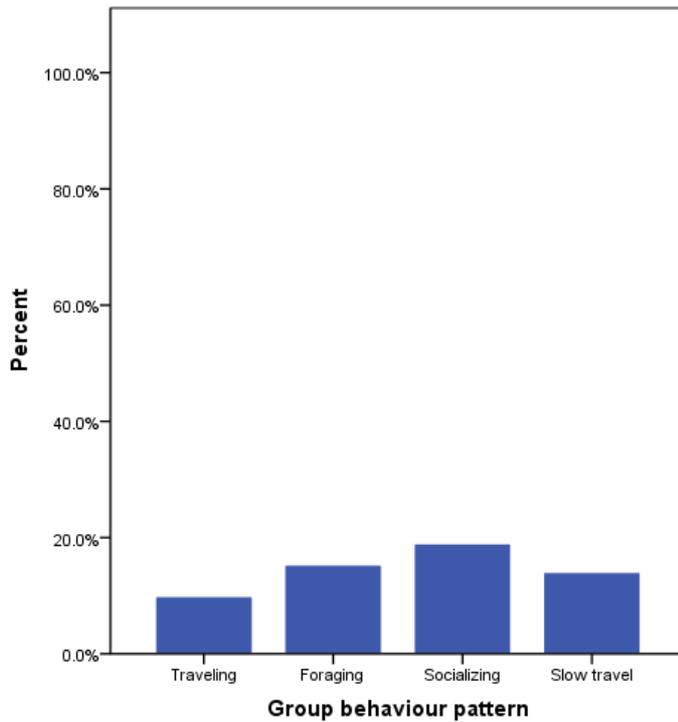


Figure 3.9 – Graph showing the proportion (as a percentage) of burst-pulses in the totality of sounds, across each group behaviour pattern.

The crosstab comparison of the proportions of each click train class within group behaviour categories (Table 3.5A) showed that there was a higher proportion of foraging behaviour associated to increasing ICI click trains than slow travel behaviour associated to the same class of click trains (Table 3.5B). Also, a higher proportion of slow travel behaviour than socializing behaviour was associated with the production of click trains with variable ICIs.

Table 3.5 - A- Proportion (percentage) of each class of click train across all group behaviour patterns. B- Comparison of the proportions of each click train class across all group behaviour categories. A pairwise comparison (at the significance level of 0.05) was done using a z-test and the p-values were adjusted with the Bonferroni correction. A key letter was assigned to each behavioural category. For each significant pair, the key of the smaller category is placed under the category with the larger proportion.

A		Group behaviour pattern			
		Traveling	Foraging	Socializing	Slow travel
		Column N %	Column N %	Column N %	Column N %
Click train class	Constant ICI	3.4	3.0	1.4	1.9
	Increasing ICI	24.8	29.6	28.1	15.9
	Decreasing ICI	9.9	8.0	8.9	12.1
	Variable ICI	43.9	43.9	40.4	57.9
	Click train with 2 clicks	5.1	5.3	3.4	3.7
	Burst-pulses	10.8	9.6	16.3	7.5
	Ct ending in a buzz	.7	.3	.2	.0
	Possible range locking CT	1.4	.3	1.2	.9

B		Group behaviour pattern			
		Traveling	Foraging	Socializing	Slow travel
		(A)	(B)	(C)	(D)
ICI class	Constant ICI				
	Increasing ICI		D		
	Decreasing ICI				
	Variable ICI				C
	Click train with 2 clicks				
	Burst-pulses				
	Ct ending in a buzz				. <sup>a</sup>
	Possible range locking CT				

a. This category is not used in comparisons because its column proportion is equal to zero or one.

In order to see if some behavioural categories were more associated with shallow or deeper waters, I also looked at the proportion of recording sessions obtained during each group behaviour pattern in relation to water depth (Figure 3.10). Overall Risso's were recorded more frequently in waters of more than 100 m of depth. While foraging, the species was recorded 80 of the times in deeper waters. Conversely, traveling and slow travel behaviour patterns presented the lowest proportion of recordings in deeper waters ( $p=0.76$  Freeman-Halton extension of the Fisher exact test).

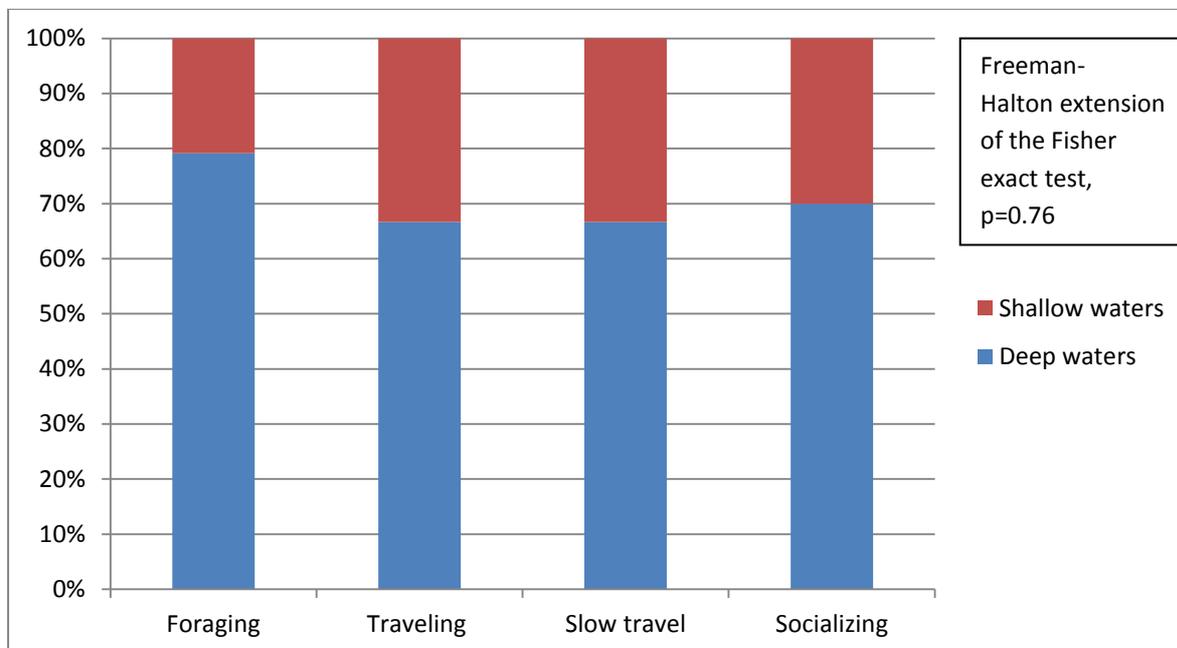


Figure 3.10 - Proportion of recording sessions during each behaviour category spent in shallow waters (less than 100 m) and in deep waters (more than 100 m) and the result of the Freeman-Halton extension of the Fisher exact test.

## Discussion

Click rates are a measure of how often echolocation behaviour is used. In Risso's dolphins echolocation behaviour is used frequently in all different behaviour categories, not just in foraging behaviour (Figure 3.3). I obtained higher click train rates when the animals were foraging (Figure 3.4). This was expected since echolocation is used for prey search, approach and capture (Verfuss et al. 2009). Also, while foraging animals need a finer scale resolution of the targets, which explains the higher number of click trains being produced per animal and minute. Bottlenose dolphins besides echolocation use passive listening to detect prey. Once the prey is detected they use echolocation to investigate the sound source (fish vocalization) (Gannon et al. 2005). Gannon et al suggested that the Florida bottlenose dolphin population some occasions can balance the benefits and costs of echolocating by using passive listening instead of echolocation. Nevertheless, the bottlenose dolphins' response in that study could have been elicited by the playbacks performed. Data in my study shows that Risso's dolphins do not seem to use the same strategy since they echolocate in several contexts and even more while foraging. This could be due to ecological differences like the different type of prey targeted by Risso's dolphins.

The second highest click train rates were found while animals were engaged in socializing behaviour. While socializing animals are more agitated, interacting with conspecifics in a more spatially complex environment and may even echolocate at each other within the same group. In fact during socializing I found the lowest estimated distances for potential targets which could reflect the higher spatial complexity of movements of the animals that could be in closer proximity. Although click rates were lower during travelling, Risso's dolphins like other delphinids also echolocate while traveling, even at slow speed when the animals are most likely resting (Au 2000; Sekiguchi & Kohshima 2003). Echolocation while traveling may be important for obstacle detection and avoidance, landmark based navigation, especially closer to shore when these animals were mostly found slow traveling, and even in occasional prey detection (presumably leading to a change in behaviour). Moreover, when animals were found slow traveling the research boat had an easier task following them than when animals were traveling with higher speed. This means that the chances of recording highly directional sounds such as click trains (Ding et al. 1995a; Wang et al. 2012) are higher when the boat is positioned parallel or slightly ahead of a group of dolphins (when slow traveling) than when the boat is behind the group of dolphins (when traveling at higher speeds). This methodological problem could have biased the travelling click rates obtained.

Click trains were found to be produced by one animal or more than one animal at a given time depending on the different behavioural contexts (Figure 3.6 and Figure 3.7).

I found that while foraging more than one animal echolocated at any given time. Risso's dolphins, like pilot whales, (Jensen et al. 2011b) seem to forage solitarily. This is consistent with visual observations in the field where, when engaged in foraging behaviour, Risso's dolphins spread out over large areas. So, each animal will actively forage and echolocate for themselves, hence the overlapped production of click trains by more than one animal at a time observed. When socializing, echolocation clicks were only produced by a single animal at any given time. Within each encounter, the number of Risso's dolphins remained the same despite the behavioural context. So, group size is discarded as a factor of influence in this case. Although not excluding an exchange of click trains while socializing, the singular production of click trains at a time might be used to perceive conspecifics in a more spatially complex environment where communicating is most likely present and assumed by the exchange of burst-pulses and whistles as it seems to be in spinner dolphins (Lammers et al.

2006). While traveling, more than one animal echolocated in a overlapped way occasionally at a given time. On the other hand, while slow traveling, only one animal at any given time echolocated, that is, there was no overlapped click train production. This could be an indication of less animals per group echolocating. A combination of highly synchronous swimming with echolocation by only one animal when traveling suggests eavesdropping behaviour in rough tooth dolphins, *Steno bredanensis* (Götz et al. 2006). Eavesdropping might help other members of a synchronized group to get information on potential targets ahead by listening to the echoes from the sonar of conspecifics (Dawson 1991). Similarly, Risso's dolphins when traveling and slow traveling with higher group cohesion (less than one body length) and with high synchrony could be eavesdropping on conspecifics sonar echoes.

When echolocating dolphins produce a click that travels to a given target, is reflected back to the animal that processes it during a certain period of time (lag time) before producing the next click. Lag time and the inter click intervals of a click train reflect the distance animals echolocate at (Au 1993). That distance could be a reflection of the behavioural state of the animals. Risso's dolphins do not show any differences in the mean ICI across group behaviour patterns (Figure 3.3). These animals used a wide range of ICIs across and within all behaviours.

Simard et al (2010) found that bottlenose dolphins significantly increase the mean click train ICIs with mean water depth. Risso's dolphins were found in deep water 80% of the recording sessions while foraging. When engaged in this behaviour pattern click trains seemed to present higher ICIs (Figure 3.10). This is consistent with Simard's study since these animals forage in very deep waters (Baumgartner 1997). Since dolphins use echolocation for navigation and foraging, this variety of ICIs is most likely the result of animals having to perform various echolocation tasks within a certain behavioural category. For instance, foraging behaviour can have several phases such as a search phase, approach phase, terminal phase, prey capture, re-unions, after capture dives, surface resting after a dive or traveling. In all of these activities within foraging behaviour dolphins assess different situations and distances, hence the wider range of mean ICIs observed. A mean distance of 128m was estimated for potential targets when dolphins were foraging. This seems to agree with the distances found by Madsen et al. (2004). Using localization of on-axis clicks they estimated a range of 100m, or possibly more, for detection of prey by wild Risso's dolphins.

Although Risso's dolphins inhabit deep waters, while traveling our research vessel could be in the dolphin's way, making the ICIs shorter and varied. Navigating dolphins can echolocate in the open water column for obstacle avoidance such as an occasional boat approach or even the research platform, hence the variety of ICIs found within this group behaviour category. Furthermore, anthropogenic objects at our field site such as the ferries and cargo boats are likely to be in the animal's path, and can affect the species' energetic balance. A higher density of objects in the water could lead to more object avoidance by the dolphins and therefore, more click train production with shorter ICIs. In turn this could lead to extra energy expenditure with possible long term effects relevant for the species conservation.

Some dolphins like harbour porpoises (Verfuss et al. 2005) show a range locking behaviour. This means that these animals linearly reduce their inter-click intervals with distance. Looking at click train patterns based on inter click intervals of Risso's dolphins, we could see that range locking is rare or almost non-existent in Risso's dolphins (Figure 3.8). This could be due to the fact that, like beaked whales (Madsen et al. 2005), these dolphins navigate through an environment of very deep waters, with little landmarks to lock on to.

Risso's dolphins in my study only produced seven sequences containing a search, approach and terminal phase and not all of them were recorded while dolphins were engaged in foraging behaviour (Figure 3.8 and Table 3.5A). I found typical foraging sequences with all phases while animals were traveling and socializing. Similar sequences have previously been described during explorative approaches in harbour porpoises (Verfuss et al. 2009). Due to the small amount of sequences found no conclusions should be drawn. Risso's dolphins, when foraging, occupy a very large area and good signal-to-noise ratio foraging sequences are difficult to record. While traveling and socializing some dolphins, particularly calves, could, out of curiosity, be echolocating and "targeting" the hydrophones of the research boat.

Click train patterns from Hector dolphins do not show any close association with a particular type of group behaviour pattern. Constant, decreasing and increasing ICIs click trains do not seem to be socially important (Dawson 1991) to this species. Similarly, in Risso's dolphins I could not find a striking association between click train ICI patterns and group behavioural context (Table 3.5B). The only exception is a significantly higher proportion of foraging behaviour associated with increasing ICI click trains than slow travel behaviour associated to the same click train patterns. Given that while slow travel Risso's dolphins had one of the

lowest click train rates observed and that the proportions of increasing ICI click trains while foraging, socializing and traveling are quite similar, the association obtained could be a result of the statistical methodology and not necessarily biologically relevant. A significantly higher proportion of slow travel behaviour than socializing behaviour was associated with variable ICI click trains. During slow traveling animals need to detect objects at varying distances therefore, click trains with variable ICIs could be advantageous in these situations. Echolocating at varying distances could also be advantageous for the echolocating animal and its group to be able to detect potential predators.

High repetition rate series of clicks, the burst-pulses, are thought to be associated with communicative behaviour in several species of odontocetes. Lammers et al. (2003) suggested that burst-pulses in spinner dolphins might have a communicative function. Other dolphin species that do not produce whistles also rely on clicks to communicate. Among those, Hector's dolphins produce "cries" which are high repetition series of clicks that are highly associated with excitement such as aerial and aggressive behaviour (Dawson 1991). Harbour porpoises also use click trains to communicate employing stereotyped aggressive click patterns (Clausen et al. 2010). Sperm whales, *Physeter macrocephalus*, use codas, a temporal sequence of clicks in a click train with a stereotyped pattern of ICIs, which are used for communication conveying clan affiliation (Rendell & Whitehead 2005). Depending on the ICI and the physical properties of their click trains, sperm whales could use click trains for communication or echolocation (Madsen et al. 2002).

Even in bats, click trains serve a dual function. In some species clicks are used to orientation and foraging and also to communicate species and group affiliation (Voigt-Heucke et al. 2010).

Risso's dolphins in the Canary Islands are a social species that produce whistles but also produce burst-pulses, stereotyped high repetition rate series of clicks similarly to the Australian population (Corkeron & Van Parijs 2001). When in groups of more than eight animals Risso's dolphins produced more burst-pulses individually per minute but decreased their individual whistle production. It was also found that these sounds were highly associated with socializing and foraging behaviour. It was suggested that burst-pulses in Risso's dolphins function as an intimate and more directional form of communication when the density of animals increases (see chapter two). This seems to be consistent with the findings of the present study where the highest rates of burst-pulses occurred during

foraging and socializing, behaviour patterns where the animals are spread out over a larger area and may, therefore, need to facilitate and or mediate reunions. Also, an increase of burst-pulses rate could be seen when animals were socializing when compared to slow traveling.

Moreover, when dolphins were engaged in socializing behaviour 25% of overall burst-pulses were produced in a overlapped way by more than one animal at a given time and 55% while foraging which is consistent with a communicative function for this type of sounds (Figure 3.7). This overlapped production of burst-pulses by more than one animal at a given time could indicate an exchange of these signals among Risso's dolphins either in a social context to communicate or in a foraging context maintaining short distance communication after a long dive similarly to what happens with short finned pilot whales that have "rasps" which are short click series that function to maintain short distance coordination in the ascent phase of long dives (Jensen et al. 2011a). Similarly, spinner dolphins (Lammers et al. 2006) produce both whistles and burst-pulses. Whistles are thought to play an important role in dispersed groups maintaining the contact among animals, while burst-pulses are a more intimate form of communication when animals are close together.

In conclusion, Risso's dolphins being an oceanic species have a particular echolocation behaviour that seems to be adapted to an oceanic environment with few landmarks or structures. They may employ burst-pulses to facilitate reunions after long dives when foraging. Further studies on diving behaviour would improve our knowledge about the use and function of the diverse click train patterns and burst-pulses that this unique species uses.

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# Chapter 4 : Biosonar characteristics of wild Risso's dolphins off the coast of Gran Canaria

## Introduction

Echolocation is used extensively by bats (Schnitzler et al. 2003) and dolphins (Au 1993) to perceive the surrounding environment (navigation), to detect and capture prey while foraging and even to communicate (Dawson 1991; Voigt-Heucke et al. 2010).

When an echolocating dolphin emits a sound pulse (click) to the environment, this pulse is reflected by an object (such as a prey, a landmark, or a boat) in the water column and the echo of the object is received by the phonating dolphin. That information is processed by the dolphin and then a second pulse is emitted. The time lag between the two consecutive emitted clicks is called inter-click-interval. The time that the pulse emitted takes to travel to the object and back is called the two-way travel/transit time. The time delay between hearing the echo and emitting the following pulse is called the lag time or the processing time (Au 1993). This means that usually a dolphin waits to process the returning echo before emitting the following click. That is not always the case since when dolphins use clicks in a communication context very often they don't wait to process the echo before emitting the following click and therefore the pulsed train ICIs do not exceed the TWTT for a given target range. This happens because since the ICISs are so short the dolphin lacks auditory resolution to distinguish the outgoing clicks and their echoes without masking either (Mooney et al. 2006).

When approaching a target, both in the wild and in captivity, cetaceans, to our knowledge so far, can assume two different strategies.

On one hand, small cetaceans like the harbour porpoises and bottlenose dolphins decrease their ICI at distances closer to a target, proportionally to the TWTT with the lag time remaining constant. This is called range locking behaviour (Morozov et al. 1972; Verfuss et al. 2005).

On the other hand, beaked whales show a different pattern of foraging behaviour (Madsen et al. 2005). They keep constant ICIs when searching and approaching a target. As these animals are deep divers the absence of landmarks where to lock on might explain the absence of range locking while navigating. Also the targets are so far away in these

situations that the animals might include echoes from far distances keeping a window open for possible detections in between.

On most biological (Kick & Simmons 1984) and man-made sonars the gain of the receiver is adjusted to compensate for acoustic propagation loss. In this case, changes in the received echo level are handled on the receiver side by a time varying gain (TVG). This means that the gain of the receiver increases with time after the transmission of a signal to compensate for the decreasing echo levels from progressively more distant targets. More recently, it was suggested that some bats also adjust the source level on the transmission end of their sonar (Hiryu et al. 2007).

Cetaceans adopt varied strategies when it comes to sonar gain adjustments. False killer whales seem to have a similar mechanism, i.e. to adjust the receiving level of its hearing (Nachtigall & Supin 2008). Recently it has been shown that captive harbour porpoises present a higher degree of flexibility of its biosonar system according to the echolocating task. They show gain control in both the transmitting and receiving side of its biosonar (Linnenschmidt et al. 2012). On the other end of the spectra, Au and Benoit-Bird (2003) showed that Hawaiian spinner dolphins, pan-tropical spotted dolphins, *Stenella attenuata*, Atlantic spotted dolphins, white-beaked dolphins, and killer whales, have a gain control in the transmission phase of the biosonar. The amplitude of the clicks emitted is range dependant, increasing with increasing target range,  $R$ , in a  $20\text{Log}(R)$  fashion in order to compensate for propagation loss. They suggested that there is a coupling between ICI and source level. When approaching a target, a dolphin decreases the ICIs and thus reduces the source level resulting in an adjustment of source level to the target range. This form of TVG is considered a passive consequence of the ICI to the TWTT adjustment and it is termed automatic gain control (AGC). While this seems to be the case for most delphinids, beaked whales do not seem to have this kind of AGC (Madsen et al. 2005; Johnson et al. 2008). Additionally, another study of biosonar adjustments of wild bottlenose dolphins (Jensen et al. 2009) suggests that AGC of those dolphins might be an active form of TVG in the biosonar independent of the ICIs instead of a passive consequence of the TWTT adjustment.

This ample variability in the biosonar characteristics and the contrasts in the findings for the same species show that the biosonar of wild dolphins still has a lot of ground to cover and it is yet not fully understood.

Risso's dolphins are an oceanic species in Gran Canaria and its biosonar description is yet to be completed. Captive (Philips et al. 2003) and wild (Madsen et al. 2004) Risso's dolphins click parameters have been described, but the echolocation behaviour and biosonar characteristics such as range locking and automatic gain control have not been investigated to date. We still do not know where Risso's dolphins fit in the biosonar performance discussion described above.

In this chapter I am focusing on click parameters, and the navigation and foraging functions of the Risso's dolphin's echolocation system. I describe the click parameters of wild Risso's dolphins from Gran Canaria for the first time. My experimental design also allowed me to investigate the presence of range locking behaviour and automatic gain control in the biosonar of wild Risso's dolphins by promoting several approaching sequences of the dolphins towards a target (my hydrophone array).

## **Methods**

### **Data collection**

Recordings were obtained during daylight hours on Risso's dolphin surveys in the Northwest of Gran Canaria, from October 2010 to March 2011, using a 6 m rib with an outboard engine.

A 15 m "chain" rule was applied to define groups as two or more animals in which each individual was within 15 m of at least one other member of the group (Hartman et al. 2008). When a group was encountered a focal group was selected for further observation. When the focal group was engaged in travelling behaviour, i.e. all animals moving in the same direction with high directionality the research vessel surpassed the focal group and crossed its path. At that moment the boat engine was turned off and the hydrophone array was deployed in the water.

The animals orientation towards the array, the position and distance visual estimation in relation to the boat (the bow at 12 o'clock, the stern at 6 o'clock) were registered using continuous behavioural sampling (Martin & Bateson 2007). Once all animals from the focal group passed our boat the sound acquisition was stopped; the same procedure was repeated once the group of dolphins was again surpassed.

The acoustic array (Figure 4.1) was built of PVC pipes that housed four HS/150 SRD hydrophones (frequency response 1 kHz to 100 kHz  $\pm$  1 db, sensitivity -205 dB re 1 V/ $\mu$ Pa). The PVC structure had a T shape and the hydrophones were distributed to form a star array (see Figure 4.2 for details and measurements). Three hydrophones were connected each to an ETEC A1001 pre-amplifier with either 20 or 30 dB gain; the fourth (centre hydrophone) was connected to an ETEC B1501 pre-amplifier.



Figure 4.1 – Acoustic array and on the right hand side Risso's dolphins that are about to cross the stern of the research vessel.

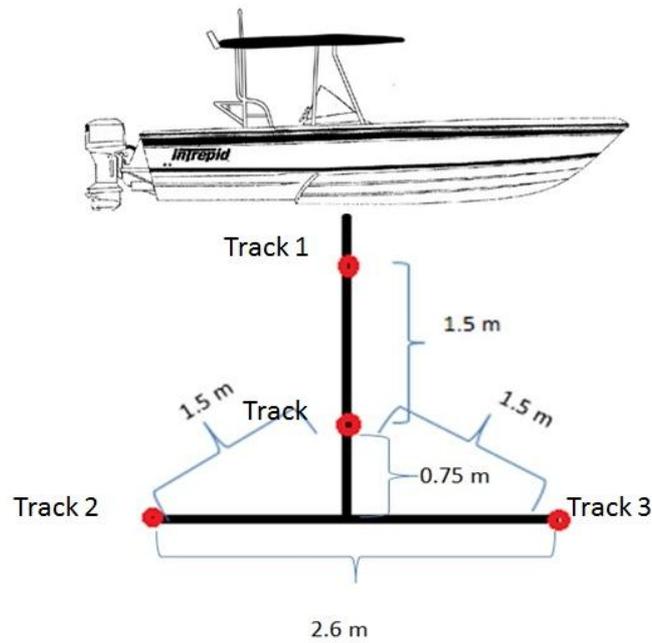


Figure 4.2 - The PVC structure had a T shape and the hydrophones were distributed to form a star array with details and measurements. The array was always deployed on port side of the research vessel.

Acoustic recordings were made at a 500 kHz sampling rate to capture the full spectra of Risso's dolphins clicks. I recorded to a laptop using two synchronized USB-3165 National Instrument sound cards and the software PAMGUARD (Gillespie et al. 2009).

## Data analysis

### *Click selection*

Similar to the methodology used previously in chapter three, click trains were identified visually with the software Adobe Audition 2.0, using spectrogram displays (Hanning window, 512 FFT). A click train was considered to be composed of clicks where inter click interval (ICI) between two consecutive clicks was less than the double of the previous ICI. Risso's dolphins click trains were divided qualitatively into three categories according to their signal-to-noise ratio (SNR). Only sounds of the best quality category were used in the analysis. Click trains where two or more animals were echolocating were also marked.

### *ICI calculation*

The methodology used to calculate the ICIs of each click train was the same used in chapter three using the software Saslab from Avisoft. ICIs were measured automatically using the Pulse train analysis tool of Saslab using a waveform-based analysis of temporal patterns.

### *Click processing*

Click structure was analysed using a Matlab custom-written program. The methodology to calculate the different click parameters was similar to the one used by Gotz et al. (2010) when analysing echolocation clicks of Chilean dolphins, *Cephalorhynchus eutropia*.

Given the importance of using the signals on or as close as possible to the acoustic axis (Madsen et al. 2004; Madsen & Wahlberg 2007), measurements were performed only to potential on-axis clicks.

The potential on-axis clicks were selected based on the following criteria:

- louder clicks of a click train; and
- if the clicks selected on the first criterion were also the loudest in the centre hydrophone (Au & Benoit-Bird 2003).

Madsen et al. (2004) used 98.5% of the signal energy to calculate the duration of wild Risso's dolphins clicks. We followed the same procedure to calculate the duration of the clicks, but we obtained very long durations for each click, resultant from the selection of large tails of echoes after the primary pulse. Discarding the energy criterion for click selection, clicks were selected from background noise using a 20 dB criterion. This means that only the parts of the signal between the -20 dB power points on the envelope were selected.

The following spectral parameters of Risso's dolphins clicks were calculated on the selected part of the clicks, using a Fast Fourier Transformation (4096 steps, Hanning window) and based on Au (1993):

- peak frequency: the frequency with the maximum amplitude in the power spectrum;
- 3 dB and 10 dB bandwidth: the frequency width between the half power points (3 dB and 10 dB down from the maximum peak) of the power spectrum;
- centroid frequency is the frequency that divides the power spectrum into two equal parts.

Peak to peak received levels, RL, and root mean square, RMS, received levels were calculated from measured signal voltage after compensating for the gain of the recording system and using the known transducer sensitivity.

### *Localization*

To determine the three dimensional (3D) position of the source (dolphin(s) that emitted a click train) and be able therefore to quantify its parameters, I used passive acoustic localization. This was based on the time of arrival differences (TOADs) of the same click on the four receivers. The TOADs were obtained using a cross correlation of the click recorded on the centre hydrophone with the same click recorded at the other three peripheral hydrophones (Schotten et al. 2004). Sound speed was calculated based on the average water temperature measured with a diving computer (PUK, Mares) attached to the bottom of the array. Based on the Mackenzie (1981) equation we estimated a sound speed of 1527 m/s (water temperature of 22 °C, salinity 35 p.p.m.).

I used a customized Matlab routine incorporating the equations as in Wahlberg et al. (2001). As such, I was able to obtain a 3D localization of the phonating dolphin. Nevertheless, since all hydrophones of the vertical star array used were in the same spatial plane, a front/ back ambiguity to that spatial plane occurred. This uncertainty in the localization was eliminated using the continuous behavioural sampling data. Only unambiguous click trains were used in the analysis.

I also used an underwater video camera positioned immediately above the centre hydrophone to check the orientation of the dolphins and where they might have been targeting. The localization precision of the array used was tested by transmitting artificial dolphin clicks and whistles using a Lubell UW30 loudspeaker at known ranges from the array. Received frequencies by the array ranged from 2Hz to 20 kHz. The root-mean-squared range deviations from the true range (Villadsgaard et al. 2007) were calculated (Figure 4.3).

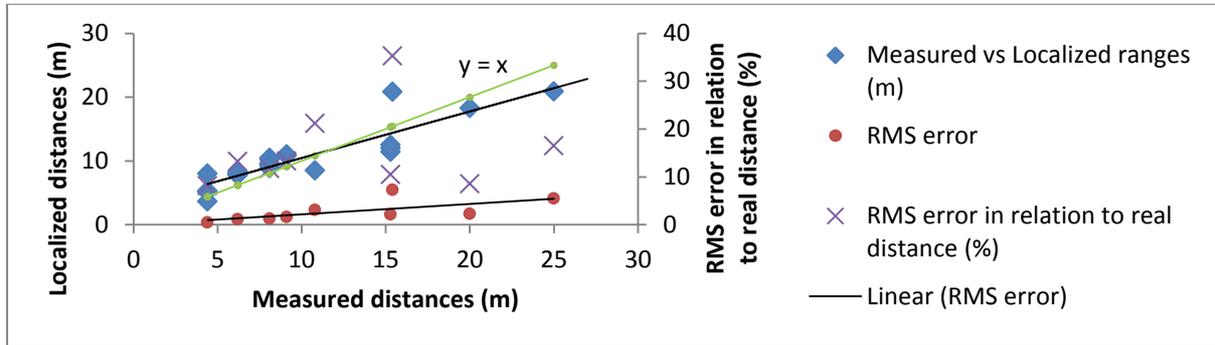


Figure 4.3 – Results of the calibration performed in Gran Canaria. RMS error in relation to real distance is shown in grey. It presents a high variability most likely due to the few trials performed for any given distance.

Once the range of the source (phonating dolphin) was determined, the apparent source levels (ASL) could be back-calculated. These were calculated based on the equation also used in Madsen et al. (2004):

$$ASL = RL + TL = RL + 20 \log(R) + \alpha R$$

The transmission loss, TL (dB) was estimated from spherical spreading and frequency dependent absorption ( $\alpha$ ) over the range, R (m). The coefficient of absorption, 0.023 was calculated for a centroid frequency of 81kHz, using Fisher and Simmons (1977) equations.

## Results

I obtained a total of 3553 clicks from 122 click trains recorded during 11 encounters with groups of Risso's dolphins.

Of those 122 click trains 13 were isolated burst-pulses. I did not record any typical approach sequences where the dolphins increase ICI rate when approaching a target leading gradually to a buzz sequence (Verfuss et al. 2009).

Results from the range localization of phonating dolphins can be seen in Figure 4.4 and Figure 4.5. I plotted the ranges given by localization per click train against the visual estimated distance (Figure 4.4). I also plotted the same distances localized averaging all clicks from all click trains per visually estimated distance (Figure 4.5).

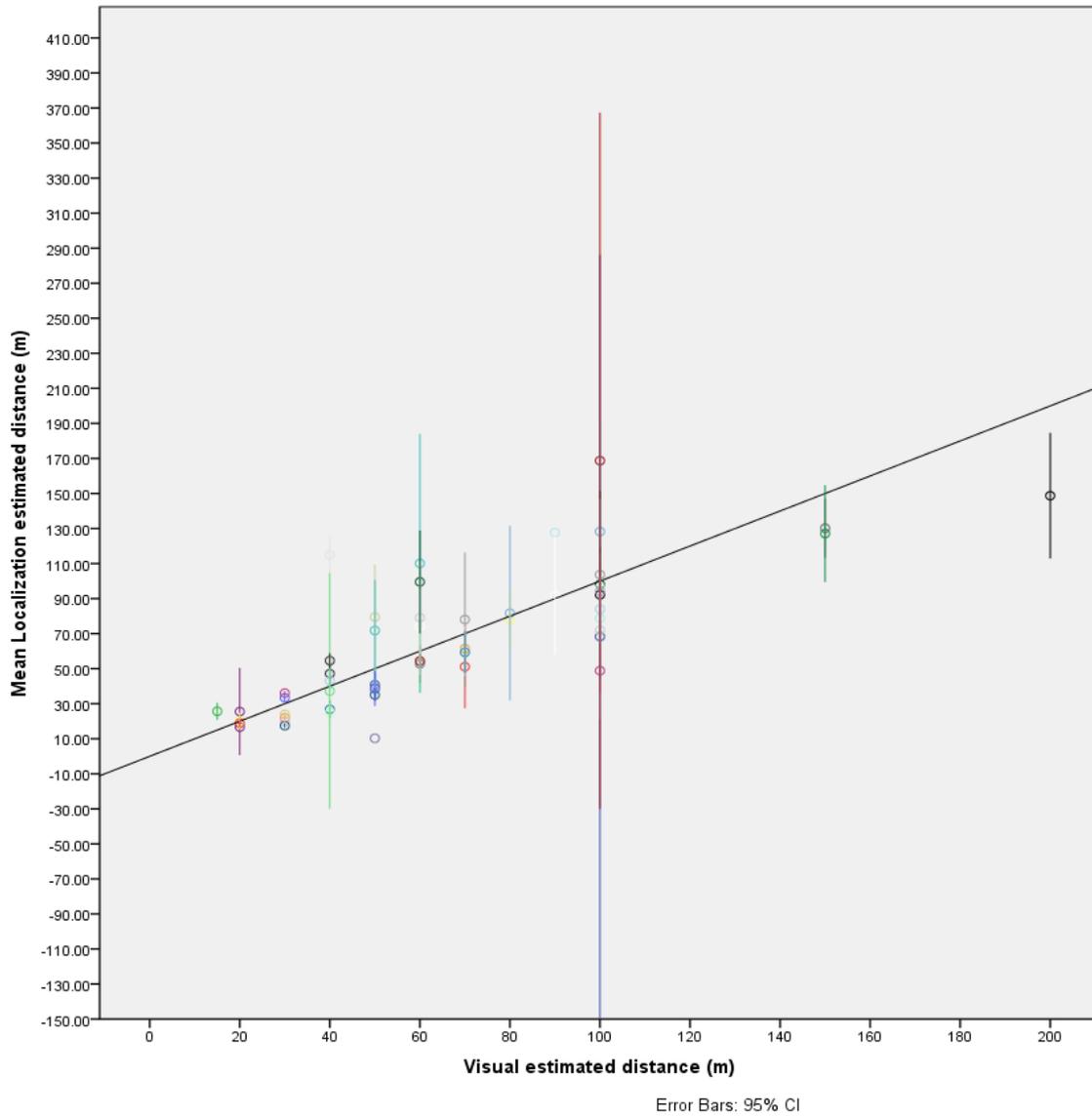


Figure 4.4 - Distances obtained for each click with localization against the visual estimation of dolphins seen at the same time in the same relative position to the boat as the one given by the localization algorithm. Error bars for the estimated distances of each click train are shown (95% confidence interval). Higher errors occur at distances of 100m.

For distances up to 100 meters all estimated distances by localization fit quite well the 1:1 regression line. This means that the calculated distances are similar to the ones visually estimated. At 100m there are higher errors in the calculation of the distances and it seems that distances calculated are underestimated in relation to the visual ones for distances higher than 100m.

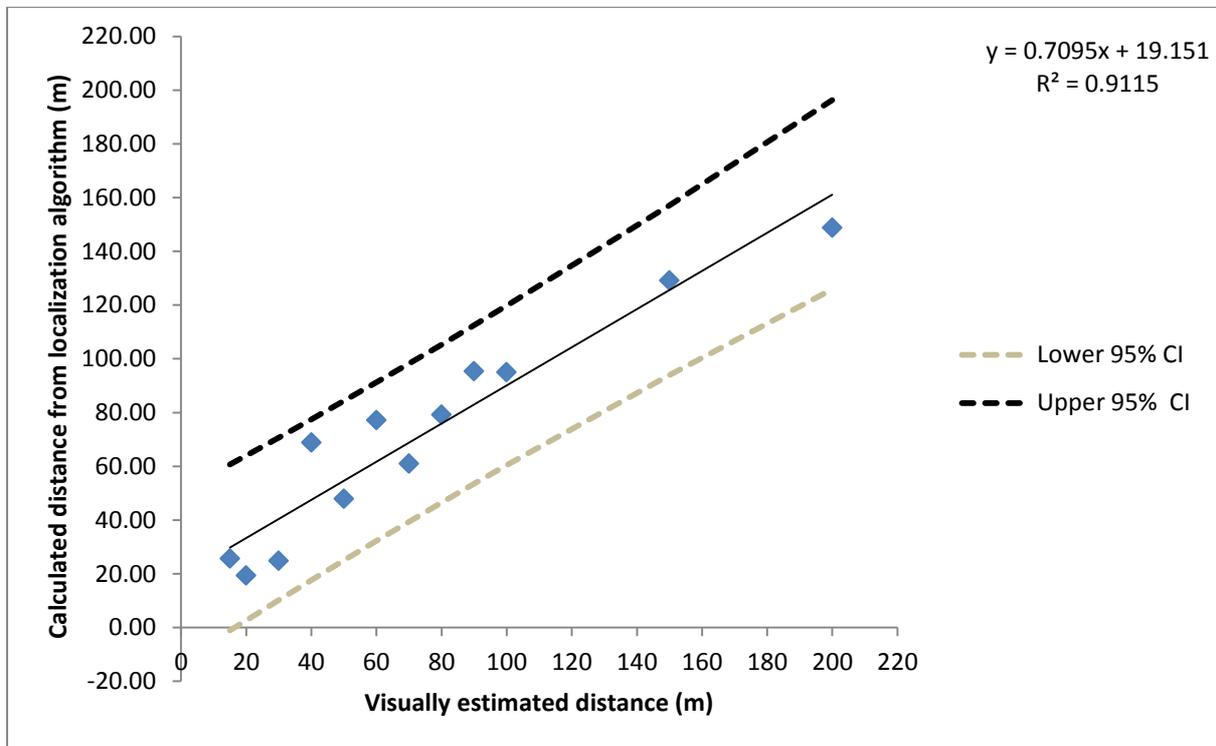


Figure 4.5 - Results from the range localization of phonating dolphins. The results are not shown per click train as in the previous figure but instead the estimated distances are estimated for each bin of visually estimated distances.

To match real distances with theoretical ones (visually estimated) I cross-checked the 3D position given by the localization algorithm against the position registered while doing the continuous behavioural sampling. An example is show in Figure 4.6.

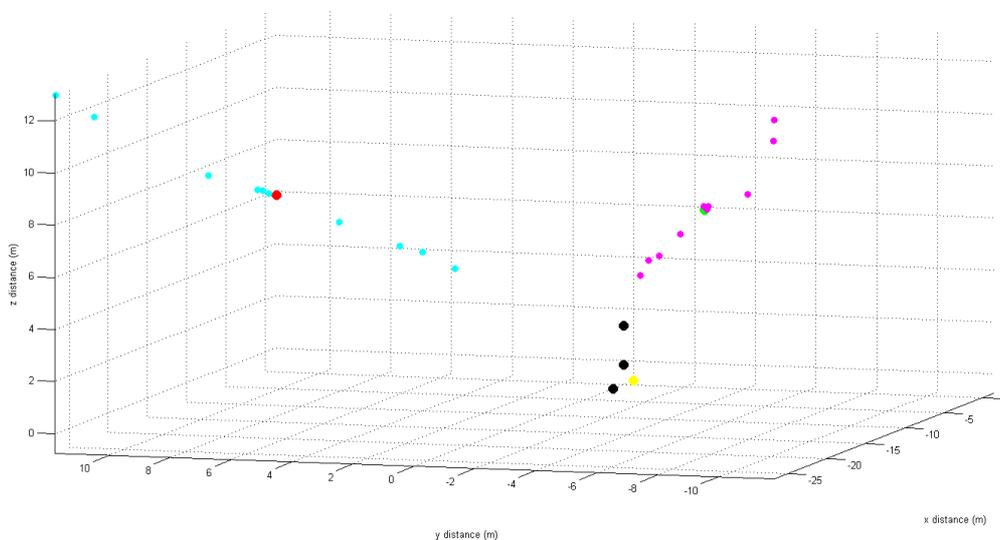
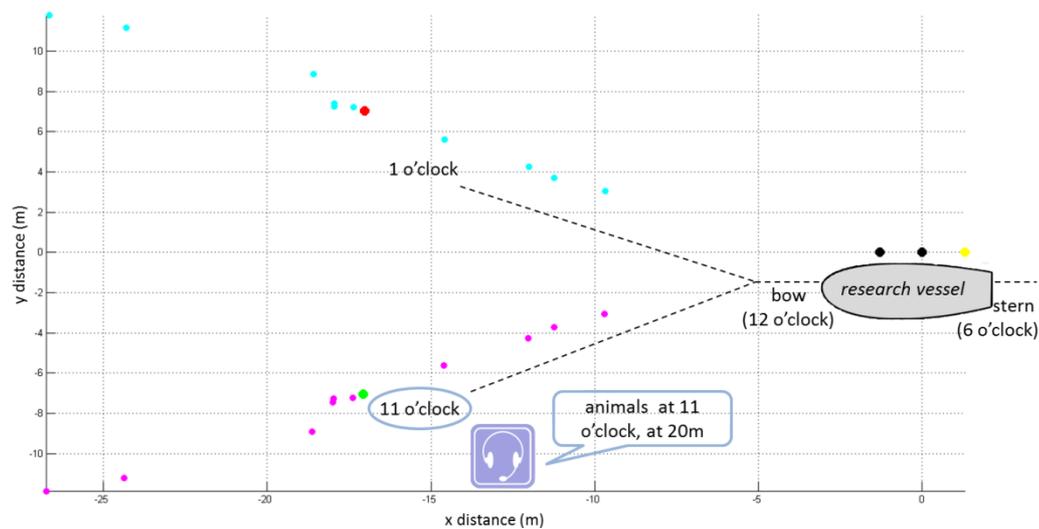


Figure 4.6- The front/back ambiguity given by the vertical plane of the array always gives us two possible 3D locations of the phonating dolphin. In the illustrated case the dolphin targeting the array could be either at one o'clock or on the other side of the plane, at eleven o'clock. The continuous behavioural sampling data described that there were dolphins only at eleven o'clock around the time that these clicks were recorded. Below is the 3D representation of the same situation. The Cartesian coordinates are given in meters. The green and red dots represent the average position obtained from all locations given by each click (blue or purple dots). The array is represented by the three black and the yellow dots. To help define the dolphin's position regarding the boat, the yellow dot represents the hydrophone closer to the stern.

From all the clicks selected for analysis only 183 (5%) were considered potential on-axis clicks, i.e. clicks that fulfilled the “on-axis” criteria.

Potential on-axis clicks had a mean ICI of 241ms. Variance was high with a standard deviation of 198ms. ICIs ranged from 2 to 769ms. This high variability was also found in the click train description in chapter three.

We did not find any correlation ( $p=0.335$ , Pearson correlation) between ICIs and range. All ICIs exceeded the TWTT except the ones belonging to the isolated burst-pulses which were always below the TWTT (Figure 4.7) by a mean lag time of  $186 \pm 20$  ms.

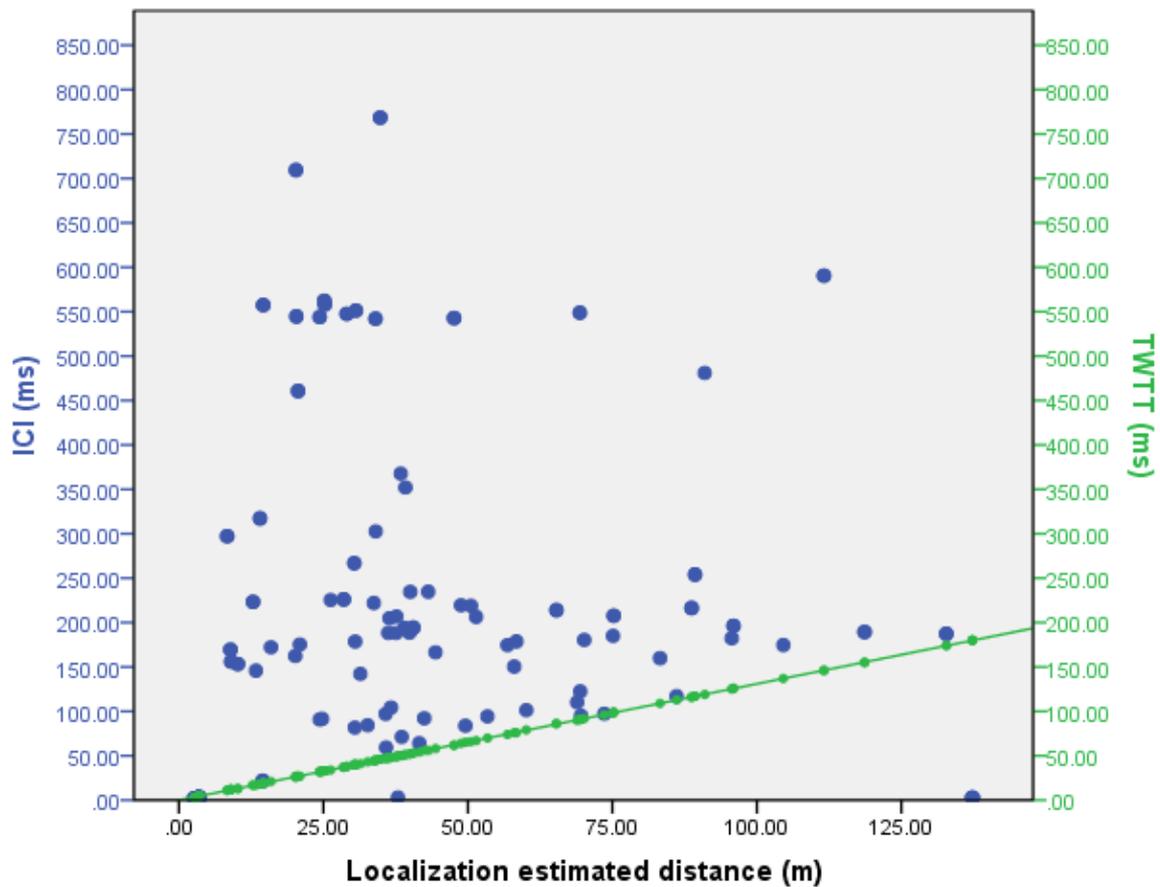


Figure 4.7 – All potential on-axis clicks exceeded the TWTT, except for the ones belonging to the isolated burst-pulses but no correlation was found between ICIs and distance. For each distance estimated by localization, I calculated the TWTT for that distance (green dots and line).

Signal parameters calculated for the potential on-axis clicks are summarized in Table 4.1. Back-calculated source levels for the potential on axis clicks were significantly lower at closer distances to the array (Figure 4.8) (linear regression:  $ASL_{pp} = 20.8 \times \log(R) \text{ dB} + 163.7 \text{ dB}$ ,  $p < 0.0001$ ,  $r^2 = 0.72$ ).

Table 4.1 - Signal parameters calculated for potential on-axis clicks of wild Risso's dolphins from Gran Canaria, wild Risso's dolphins from Sri Lanka (Madsen et al. 2004) and a captive animal in Hawaii (Philips et al. 2003).

Parameters	Wild dolphins Gran Canaria	Risso's from Lanka	Wild dolphins Sri Lanka	Risso's from Sri Lanka	Captive dolphins in Hawaii	Risso's
ASL <sub>pp</sub> (dB re. 1μPa,pp)	197 (175-214)		220 (202-222)		200 (170-216)	
ASL <sub>rms</sub> (dB re. 1μPa,rms)	173 (163-190)		207 (190-210)		NA	
20dB duration (μs)	49 (26-118)		40 (30-75)		50 (40-70)	
Rms duration (μs)	9 (4-27)		NA		NA	
Rms bandwidth (kHz)	24 (13-64)		25 (19-31)		25	
3dB bandwidth (kHz)	33 (8-54)		27 (15-84)		40 (30-84)	
10db bandwidth (kHz)	68 (28-89)		60 (20-124)		100	
Centroid frequency (kHz)	81 (55-131)		75 (58-91)		57 (53-83)	
Peak frequency (kHz)	77 (50-100)		49 (42-110)		48 (27-104)	

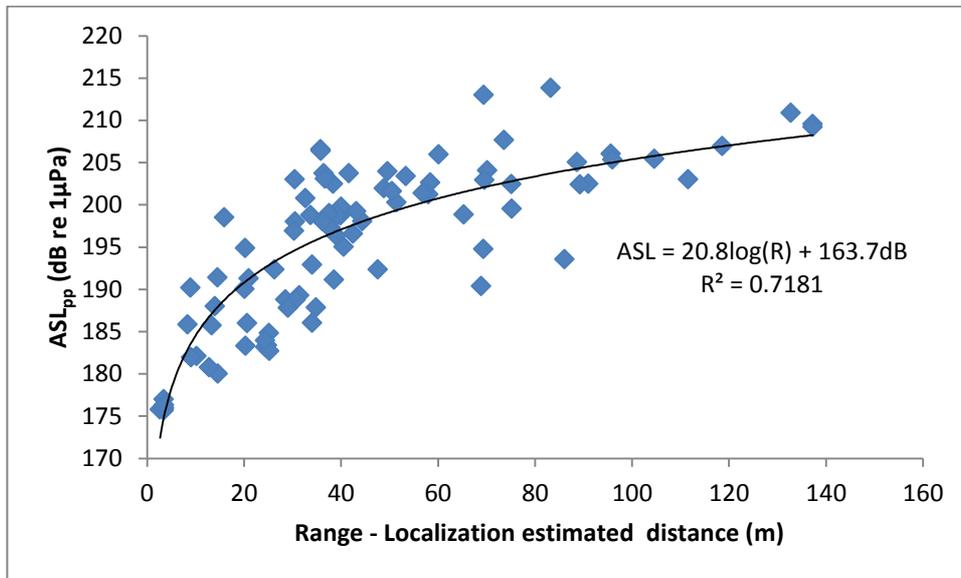


Figure 4.8 - Back-calculated source levels for the potential on axis clicks as a function of Range. The best fitting logarithmic relationship is given by  $ASL = 20.8\log(R) + 163.7\text{dB}$ .

## Discussion

### *Click parameters*

The parameters (Table 4.1) of Risso's dolphins clicks from Gran Canaria did not differ much from the parameters reported for this species in Sri Lanka (Madsen et al. 2004). Overall they presented similar peak to peak and RMS ASL to both wild (within the same range) and captive dolphins (Philips et al. 2003), as well as higher centroid and peak frequencies than the ones reported before.

The 81 kHz centroid frequency is right at the frequency cut off for the audiogram of a mature Risso's dolphin (Nachtigall et al. 1995). However it fits quite well within the audiogram of a younger Risso's dolphin (Nachtigall et al. 2005) which was more sensitive to higher frequencies (Figure 4.9)

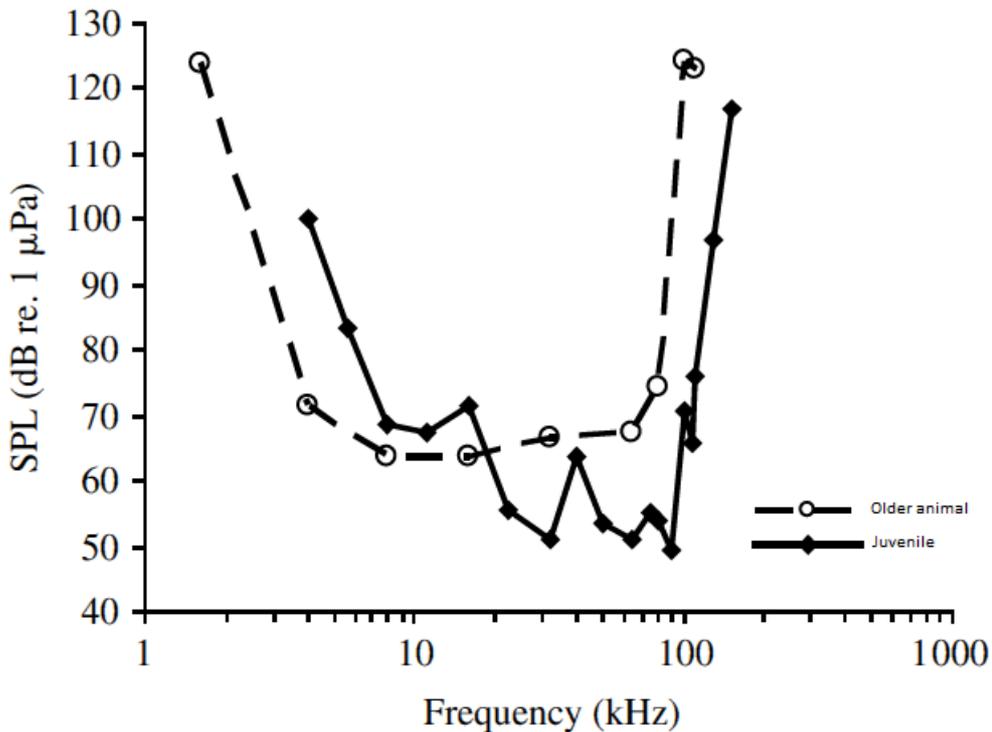


Figure 4.9 – Figure adapted from (Nachtigall et al. 2005). Audiograms from a juvenile and an older Risso’s dolphin. The 81 kHz centroid frequency is right at the frequency cut off for the audiogram of a mature Risso’s dolphin (Nachtigall et al. 1995). However it fits quite well within the audiogram of a younger Risso’s dolphin (Nachtigall et al. 2005) which is more sensitive to higher frequencies.

#### *ICI and target range*

One of the big constraints of the target approach in the wild is that we are never sure whether the dolphins are targeting our array and we assume that the range of the dolphin to the target is actually the range to the array.

I placed a video camera right above the centre hydrophone as an attempt to check the orientation of the dolphins towards the array. However, despite my best efforts to confine the approaches directly towards the array, most approaches did not come right from the front of the array. This was particularly so in bigger groups as dolphins could approach the array from the side or the back, not being caught on camera. When approaching a target, a dolphin decreases the TWTT with the decreasing range to the potential target. Usually ICIs in target detection can be calculated given the TWTT plus a constant lag time of 19 to 45 ms (Au 1993).

All potential on-axis clicks were found to have ICIs higher than the TWTT, which gives some confidence that the dolphins were in fact targeting my array or a target further away. The only exceptions were the clicks that formed the isolated burst-pulses. Most likely these clicks have not been used in target detection but in communication (as discussed in chapters two and three).

The relationship between the target distance and ICIs seems to be uncertain even within a given species. Wild finless porpoises, *Neophocaena phocaenoides*, seem to decrease their ICIs over time during prey approaches (Akamatsu et al. 2005). Verfuss et al. (2005) showed that captive harbour porpoises show a distance dependent decrease in the ICI, proportional to the decrease in the TWTT to the potential target with the lag time remaining constant. Both captive (Au 1993) and wild (Linnenschmidt et al. 2012) bottlenose dolphins show a reduction in ICI with decreasing target range. Additionally, both Blainville's beaked whales and sperm whales seem to have constant ICIs during search phases for prey (Madsen et al. 2005). Occasionally, even for beaked whales, during the buzz phase of a target approach/capture, the ICIs measure at the start of a buzz are correlated with the TWTT (Johnson et al. 2008).

In Risso's dolphins, even though all regular click ICIs exceed the TWTT, ICIs did not correlate with the distance to the target ( $p=0.0335$ ). The lag time of  $186 \pm 20$  ms had a great variance and a standard error (20ms) which is in the same order of the lag time of the cetaceans that have range locking behaviour (Au 1993; Verfuss et al. 2005).

In chapter three I could not find evidence that Risso's dolphins had range locking behaviour. The fact that the lag time is not constant and that there is no correlation between ICIs and the target range, leads me to corroborate the hypothesis proposed in chapter 3. Therefore, Risso's dolphins, similarly to beaked whales, might not range-lock on targets and instead might include echoes from far distances keeping a "window" open for possible detections in between. Animals inhabiting open waters might as such, adjust their click interval to a specific search range most likely their maximum perceptual range (Verfuss et al. 2009).

#### *Source levels and range*

Risso's dolphins from Gran Canaria decreased the source level of their clicks significantly as a function of  $20.8 \log(R)$  (Figure 4.8). This source level compensation on the emitting side of the Risso's dolphin biosonar agrees with the automatic gain control found in other

delphinids (Au & Benoit-Bird 2003; Jensen et al. 2009) but not in beaked whales (Madsen et al. 2005; Johnson et al. 2008)

Nevertheless we must take into account, as Jensen et al. (2009) pertinently pointed out, that the type of methodology we use in click selection and parameter calculation favours a  $20 \log(R)$  relationship between source level and range, since clicks that are further away with lower source levels are excluded from the analysis. By selecting clicks with higher SNR on the spectrogram clicks with low source levels from further distances fall below the SNR threshold and are more likely not to be included in the analysis, whereas clicks closer to the array with the same source level might be included since transmission loss is smaller due to the short distance and, therefore, the received levels are higher. This might create a slightly sharper lower cut off of the source levels in a type of graph like the one shown in Figure 4.8. Nevertheless, in my data there isn't that sharp cut off that could be caused by the methodology (Figure 4.8) presenting a scatter at the lower source levels, indicating that this is not a major problem biasing the data.

#### *Advantages and caveats of the study*

Dolphin clicks are highly directional and it is important to select the clicks in the acoustic axis of the dolphins echolocation beam to avoid an underestimation of the apparent source level (Madsen & Wahlberg 2007).

I adopted a strict criterion to select on-axis clicks similar to the one used by Au and Benoit-Bird (2003). As in Jensen et al. (2009), of the overall clicks analysed only a small percentage (5%) of clicks were found to be potentially on-axis. However, contrary to the mentioned studies I did collect information on the individual behaviour and movements of the dolphins; coupled with the acoustic localization, this permitted me to detect where the clicks were coming from, as well as the number of animals involved in the approach sequences (Figure 4.6).

Nevertheless, my data still presented some scatter; rather frequently the dolphins could not be detected visually and individual differences in the parameters and behaviour of dolphins could not be detected, possibly causing such scatter.

Due to logistical constraints, my on-site calibration yielded few trials. More trials would be necessary to complete the calibration of the array localization accuracy. RMS errors (Figure 4.3) did not show any evident pattern in the distances available at the time of the

calibration. This is mostly because of the few measurement trials for any given distance. As such, I did not take into consideration the RMS error from the calibration.

My confidence in the results relied on the ranges and 3D localization of the phonating dolphins that were cross checked with the visually estimated range and bearings (Figure 4.6)

The click parameters of wild Risso's dolphins were described for the first time in this study, for the population of Gran Canaria.

Risso's dolphins are a very particular species that gathers characteristics from several sub-families within the *Delphinidae* family. Although it is taxonomically under the *Delphininae* sub-family, the species is genetically closer to the *Globicephalinae* sub-family (LeDuc et al. 1999).

With regards to social structure, Risso's dolphins seem to have somehow an hybrid structure between the matriarchal seen in killer whales (Bigg et al. 1990) and the fission fusion characteristic of the bottlenose dolphins (Würsig & Würsig 1977).

Acoustically, Risso's dolphins follow the same ambiguous pattern. Although they are part of the whistling species it seems that they do not prioritize the use of whistles in communication (as shown in chapter 2 and 3). Instead, they also use clicks (as isolated burst-pulses) to communicate, similarly to non-whistling species (Dawson 1991; Lammers et al. 2003).

This study shows that the biosonar behaviour of Risso's dolphins combines characteristics that place them into different *Delphinidae* sub-families, suggesting they may be slightly misplaced under *Delphininae*. Risso's dolphins seem to have their own biosonar adjustments to target range. On one hand, regular (non-burst-pulse clicks) on-axis clicks did exceed the TWTT, but a clear correlation between ICIs and target range could not be found. So, the species do not seem to have range locking behaviour similar to beaked whales that show constant ICIs during the approach phase. On the other hand, and contrary to beaked whales, they adjust the source level of the outgoing clicks with the range to the target in a  $20\log(R)$  fashion presenting an automatic gain control of the biosonar system similar to small delphinids.

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# Chapter 5 : Geographic variation of Risso's dolphins whistles

## Introduction

The study of geographic variation in animal vocalizations might provide information on environmental, ecological, biological and even cultural aspects of a species.

Environmental factors such as ambient noise can affect a species' repertoire. The presence of noise can lead to a shift in frequency (Brumm 2006), amplitude (Lombard effect, see Brumm and Zollinger (2011) for a review for several taxa) and/or duration (Morisaka et al. 2005a), and repetition rate (Scarpaci et al. 2000). Examples of these effects are observed in birds (Halfwerk & Slabbekoorn 2009), whales (Parks et al. 2011), dolphins (Foote et al. 2004) and frogs (experimentally induced noise, (Love & Bee 2010), traffic noise (Parris et al. 2009)). Cetaceans respond in a variety of ways to environmental noise such as changing whistle production rate (Van Parijs & Corkeron 2001b; Buckstaff 2004), signal frequency (Lesage et al. 1999), or increasing the duration of whistles (May-Collado & Wartzok 2008), and even changing vocalization amplitude (Scheifele et al. 2005).

All the aforementioned responses and further adaptations to different environmental conditions can lead to geographic variation of the species repertoire, i.e. if animals change the call types or the choice of call types in order to be better transmitted and received in a specific environment this could lead to permanent (long-term) changes in their repertoire, leading to geographical variation.

Intra-specific geographical variations can also reflect an adaptation to different ecological conditions. Open waters seem to favour the use of higher frequencies in pelagic species (Ding et al. 1995b). Shifts in the minimum frequency of different ecotypes of killer whales, *Orcinus orca*, calls are likely related to the differences of their prey (Foote & Nystuen 2008). Biologically, geographic variation can also reflect isolation and genetic divergence or convergence between populations (Risch et al. 2007). Similarly to what happens between species, genetic differences can result in morphological differences between different populations which, if substantial, may lead to limitations/differences in sound production within the same species. Body size seems to be correlated negatively with maximum whistle

frequency, meaning that the larger the body size, the lower the maximum whistle frequency (Ding et al. 1995b; Matthews et al. 1999; Samarra et al. 2010 as an exception to the rule). These studies were based on comparisons between species. Intraspecific comparisons are far scarcer. Jensen et al. (2012) hypothesized that one of the reasons for the differences found in whistle source levels of two populations of bottlenose dolphins could be due to greater differences in body size for the two populations. In his study bottlenose dolphins from Australia which are smaller than the ones from Moray Firth in Scotland present also lower source levels of their whistles. Body size might reflect the maximum acoustic output for the species and thus cause geographical variation in the whistle characteristics of dolphins.

Geographic variation of a species vocalizations can also reflect its adaptations to the local area in terms of association patterns and social groups (Miller & Bain 2000; Deecke et al. 2010), and even sex differences (Mennill and Rogers (2006) as an example in birds, Sayigh et al. (1995) for marine mammals). Sex roles in a population determine the social structure and, therefore, the association patterns within the same. Moreover, sex differences in dispersal of the vocalizations, learning strategies and even vocalization sounds can lead to geographical variation of the vocalizations of a population. Changes of association patterns over time, for example, accumulative changes in matrilineal units of killer whales over time (Miller & Bain 2000) can lead to pod-specific changes in the calling behaviour in the species through vocal learning (Deecke et al. 2000), and eventually lead to geographical variation.

Intra-specific geographic variation in a species repertoire or acoustic features can be micro-geographic which refers to populations in close proximity. These populations can, therefore, potentially mix (Rossi-Santos & Podos 2006; Hawkins 2010) and lead to the formation of dialects. But intra-specific geographic variation can also be macro-geographic, i.e. between populations that are separated over long distances (Collins & Terhune 2007).

In dolphins, the most common vocalization used for the study of geographic variation is usually a tonal and frequency modulated vocalization: the whistle. Nevertheless, other vocalizations can be used like clicks that form the codas of sperm whales (Weilgart and Whitehead (1997)).

Whistles assume a very important role in a dolphin's acoustic repertoire and biology. These sounds are used in social interactions (Cook et al. 2004), individual recognition (Janik et al. 2006), mediating mother calf reunions (Smolker et al. 1993), group cohesion (Janik & Slater

1998) or sometimes to maintain distance (May-Collado & Wartzok 2007) and recruitment during feeding activities (Acevedo-Gutierrez & Stienessen 2004).

Whistles are suited for comparison amongst different populations of a species due to their frequency modulation and use in several aspects of a dolphin life cycle.

The Risso's dolphin is a cosmopolitan species that can be found in temperate waters around the globe. Despite its worldwide distribution (see Bearzi et al. (2011) for a general review) little is known about the biology, social structure (Hartman et al. 2008) acoustic repertoire (Corkeron & Van Parijs 2001) or conservation (Visser et al. 2011) of this species.

Their acoustic repertoire includes click trains, burst-pulses and whistles (Corkeron & Van Parijs 2001) although the latest are not as frequent as expected from a social species (See chapter two). Whistle descriptions for this species are available from Australian, Scottish and Mediterranean populations (Rendell et al. 1999 and table 5.1).

Given the importance of whistles in a cetacean species' repertoire and the information that can be gathered from the intra-specific comparison of vocalizations I compared the whistle repertoire of wild Risso's dolphins from five different locations around the world. I expect that sampled populations of close locations to share more similarities in their fundamental frequency parameters than the ones of further locations. I also expect to find some variation in the whistles characteristics in relation to potential anthropogenic noise that affect differently the targeted locations.

Table 5.1 - Summary of whistles characteristics from Risso's dolphins from Scotland, Azores and Australia. The authors for the Australian dolphins considered 5 different types of whistles. Values are the mean (Standard deviation).

	Duration (s)	Start frequency (kHz)	End frequency (kHz)	Max. frequency (kHz)	Min. frequency (kHz)	Mean frequency (kHz)	Number of inflection points
Scotland Rendell(1999)	0.53 (0.25)	12.37 (2.63)	10.65 (3.12)	13.44 (2.4)	8.98 (2.68)	11.4 (2.24)	1.38 (1.33)
Azores Rendell (1999)	0.53 (0.39)	8.24 (3.37)	13.41 (4.8)	13.41 (5.3)	6.63 (2.15)	10.4 (2.7)	1.2 (1.31)
Australia Corkeron and Van Parijs (2001)							
Whistle 1	3.2 (1.7)	13 (3)	8.7 (2.1)	13.3 (3)	8.7 (2.1)	ND (no data)	ND
whistle 2	4.1 (8.4)	9.8 (0.9)	11.3 (3)	14.6 (0.6)	9.8 (0.9)	ND	ND
whistle 3	1.6 (0.5)	6.6 (2.3)	10.7 (1.8)	12.6 (4)	6.2 (2)	ND	ND
whistle 4	4.8 (1.1)	7.7 (1)	15.2 (1.8)	15.2 (1.8)	7.7 (1.7)	ND	ND
whistle 5	4.9 (0)	ND	ND	20 (2.2)	3.9 (0.3)	ND	ND

## Methods

Recordings were obtained from several sources (Table 5.2 and Figure 5.1) from hereafter called sampled populations.

Whistles were selected by visual inspection of the spectrograms (Hanning window, FFT size 512, 100% window width) using Adobe Audition 2.0.

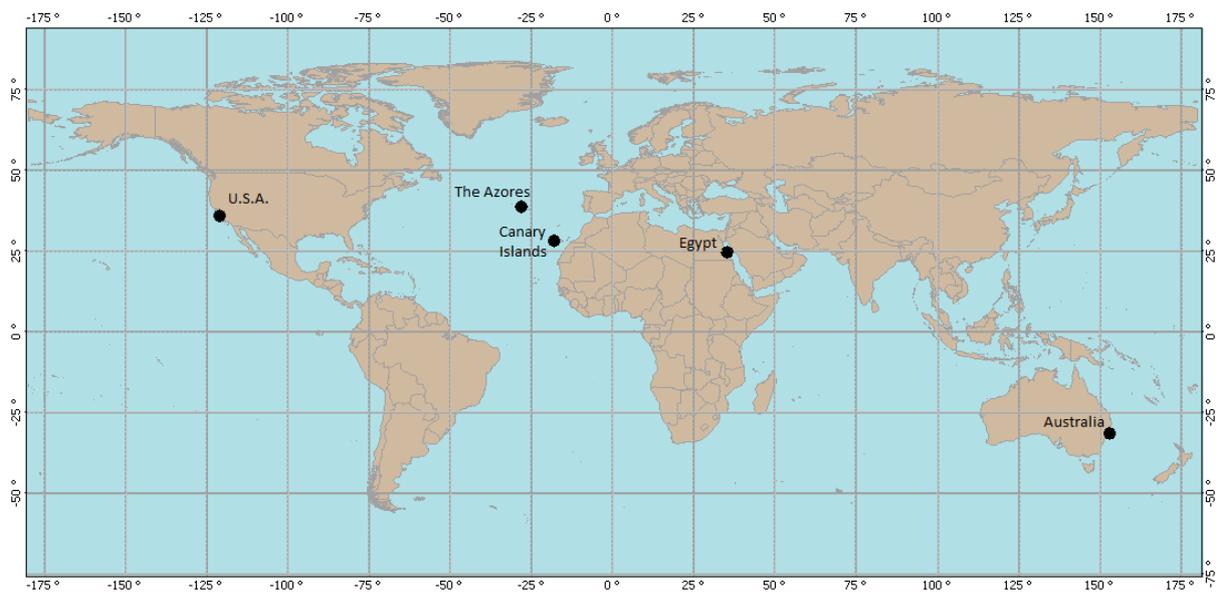


Figure 5.1 - World map with the geographic locations of the whistles analysed in this chapter: Australia, Azores, California (USA), Egypt and Gran Canaria (Canary Islands, Spain).

Table 5.2 - Data source, number of groups of animals, number of hours analysed, and number of whistles analysed.. Types of hydrophones and recording sampling rates are given for each location.

Location	Number of Groups	Number of hours analysed	Number of whistles	Hydrophones used	Sampling rate (kHz)
Australia	1	0.47	21 out of 43	GEC-Marconi SX101 hydrophone (frequency response from 30Hz to 22kHz)	44.1
Azores	Several	8.29	8 out of 839	NO DATA YET	44.1 48 96
California	7 tags	37	335 out of 3492	Dtag2 and Dtag3	120 480
Egypt	Several	1.55	18 out of 33	Towed array with 2 AQ-4 Benthos Hydrophones with frequency response of 1Hz to 15kHz $\pm$ 1dB	96
Gran Canaria	30	45	62 out of 115	An array of 4 hydrophones: 2 HTI-96 MIN and a HTI 94 SSQ, frequency response 2Hz to 30 kHz, $\pm$ 1dB, and a SRD hydrophone HS/150, frequency response 1kHz to 100kHz $\pm$ 1db.	96 and 192

Signal to noise ratio (SNR) was calculated for each whistle. Only whistles with a SNR of at least 12 dB (if recorded with Dtags (Johnson & Tyack 2003)) or 6 dB (for all remaining whistles), were selected for further analysis. These cut-off values were chosen to ensure that only the loudest whistles and, therefore, the ones most likely belonging to Risso's dolphins were used in the analysis.

The time-frequency contour of the fundamental frequency of each whistle was traced from visual inspection of the spectrogram using a matlab routine, Beluga (<http://biology.st-andrews.ac.uk/soundAnalysis/>).

The following parameters were measured from the extracted fundamental frequency contour: start frequency, end frequency, maximum frequency, minimum frequency, and frequency range, mid frequency (the middle sample of the contour), mean frequency and whistle duration.

I checked for normality, homogeneity in the variance and correlation between all parameters measured. Although not all the variables assumed a normal distribution and presented no homogeneous variance, I decided to use a Robust Test of Equality of means, included in the one-way ANOVA, to compare the means of each parameter across all geographic locations available. This test is robust to non-normality and it was coupled with a Games-Howell post-hoc test for non-homogeneous variances and non-equal sample sizes (Brown & Forsythe 1974).

To assess the degree of inter-individual variation in whistles parameters I calculated the coefficient of variation for each parameter among individuals of the same sampled population.

To classify whistles from different sampled populations I performed a discriminant function analysis with a stepwise (or jackknife) method on all fundamental frequency parameters.

Although the test for non-normality showed that not all variables had a normal distribution, values for skewness and kurtosis were within acceptable ranges and, therefore, I proceeded with the "raw" variables. Since the Box's test of equality of covariance matrices was also significant, I used separated covariance matrices instead of pooled ones. I used as dependent variable the location and as independent variables minimum, maximum, mean, mid frequency, frequency range and duration of the whistles. Since start and end frequency were highly correlated with minimum and maximum frequency respectively (Pearson

correlation values between 0.61 and 1,  $p < 0.005$ , Figure A. 1 and Figure A. 2), they were not included in the discriminant function analysis.

Finally, since our dataset is highly unbalanced, i.e. one group dominates the dataset (California), the discriminant function analysis may reclassify many whistles correctly by chance even if no real difference exists among locations (White & Ruttenberg 2007). Therefore, I used prior probabilities adjusted to sample size. To address the question of possible bias towards larger sample sizes and non-independence of the population on the whistles from Dtags (California) I sub-sampled the data to a random selection of 20% of the whistles for each tag (ten times) and also removed data of animals producing sequences of the same whistle which could be potentially signature whistles and performed another discriminant function analysis based on that data.

I used binomial tests to test whether the proportion of whistles correctly assigned to each location was higher than expected by chance. Discriminant function analyses were performed separately in all subsamples aforementioned.

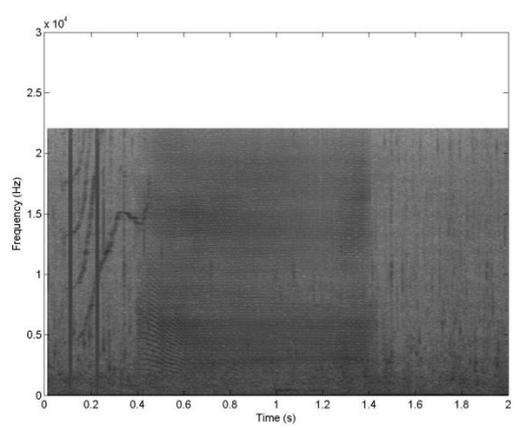
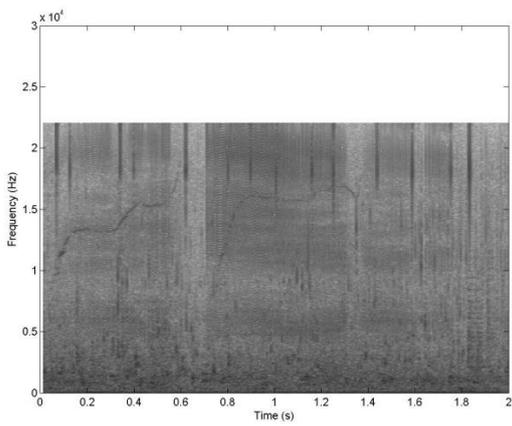
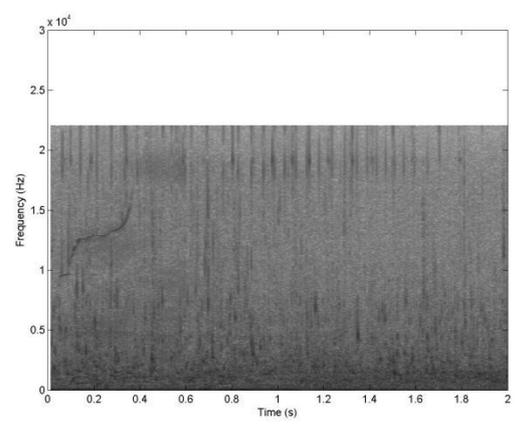
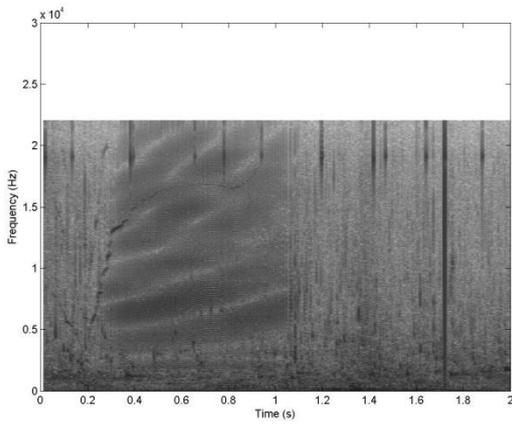
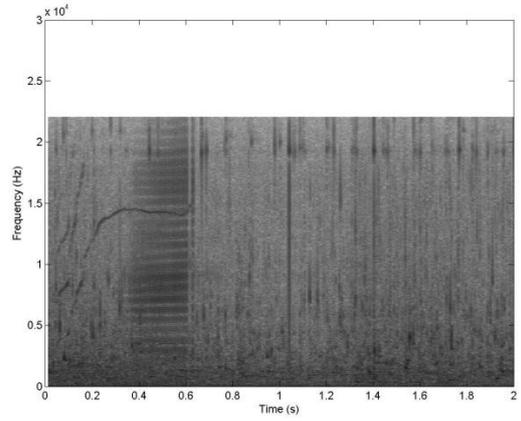
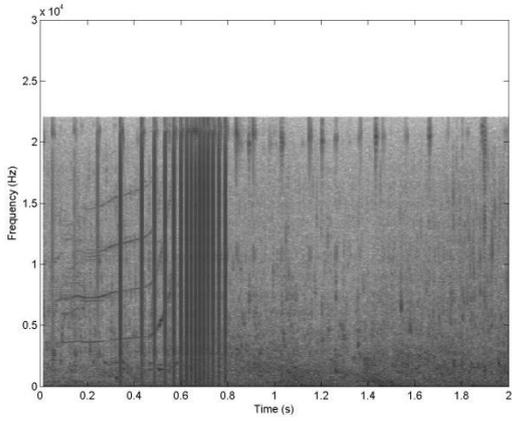
All statistical analysis was performed using SPSS 19 (IBM Inc.).

## Results

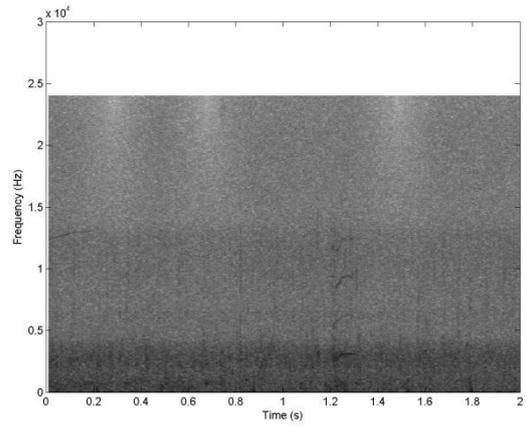
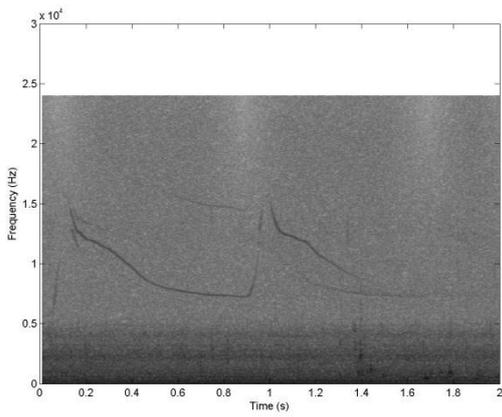
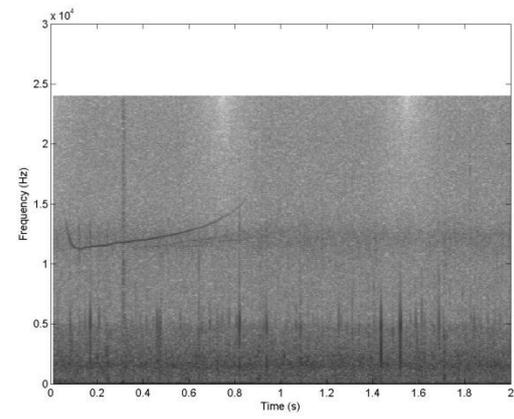
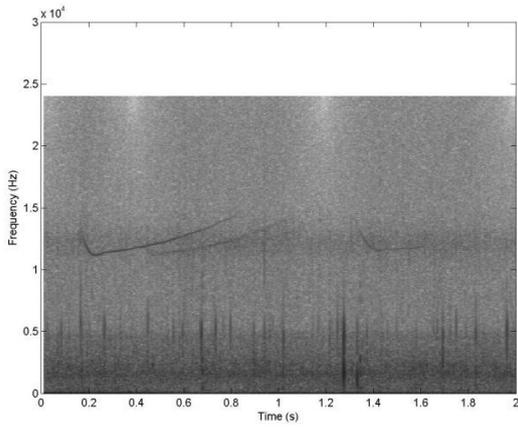
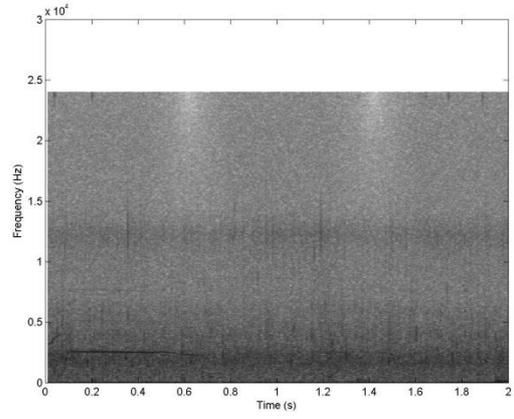
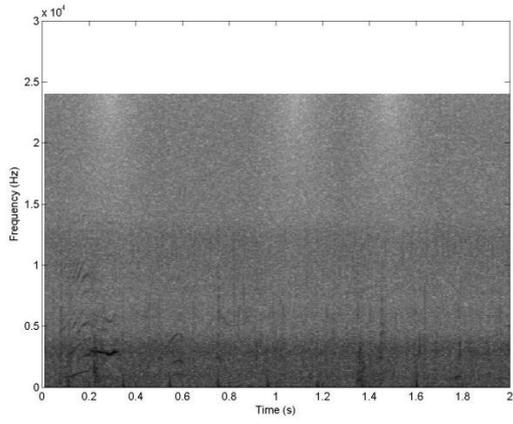
From Table 5.2 we can see that a wide range of equipment and conditions were used. Data on behavioural context and environmental (background noise) were not available. Although a wide range of hydrophone types and sampling rates was used none of the whistles analysed was cut off by a lower sampling rate. It is also worth noticing that data from Australia come from a single encounter of 28 minutes with 6 animals. Data from California was obtained from 6 single animals but with recordings of each animal were longer than the ones single recording of Australian Risso's dolphins. A total of 444 whistles were analysed from five different locations.

Descriptive statistics of Risso's dolphins' fundamental frequency parameters are summarized in Table 5.3. Spectrograms of examples of whistles from each location are shown in Figure 5.2 – For each location I subjectively selected six spectrograms most representative of each whistle repertoire. Figure 5.2

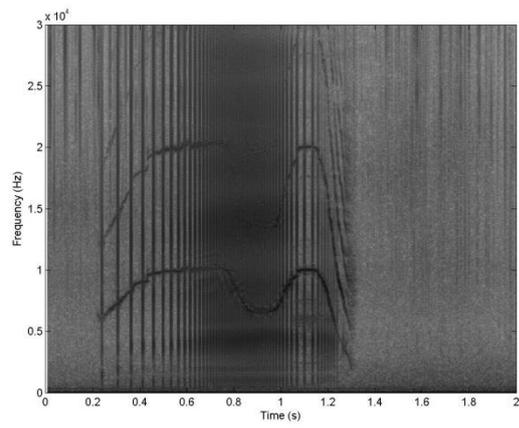
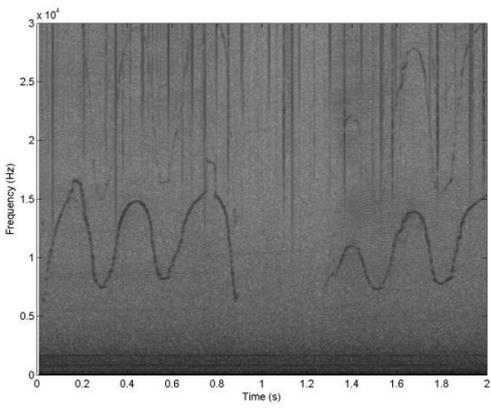
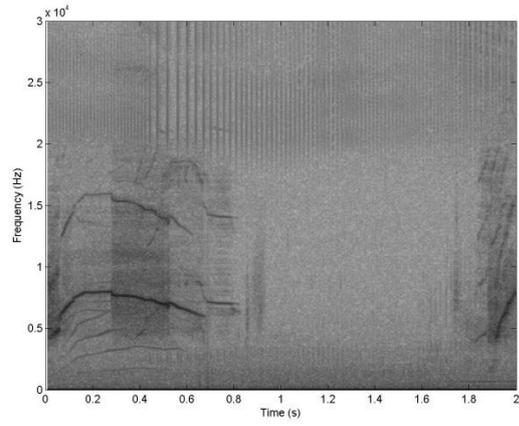
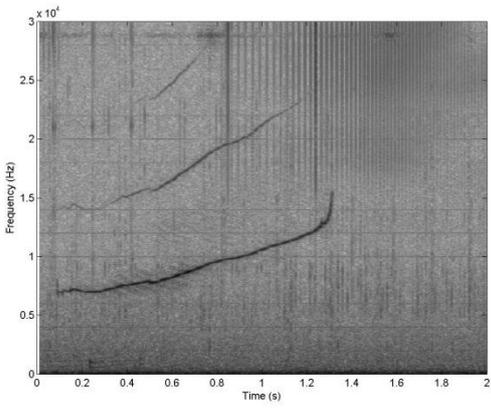
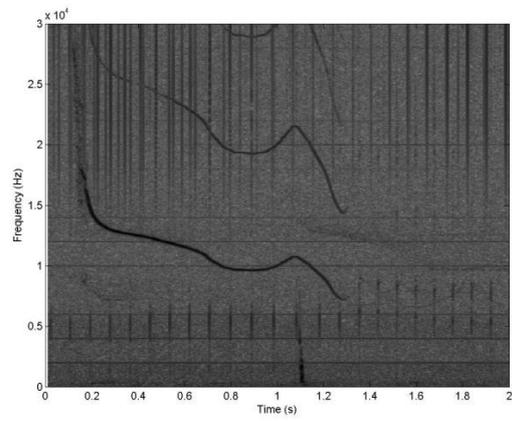
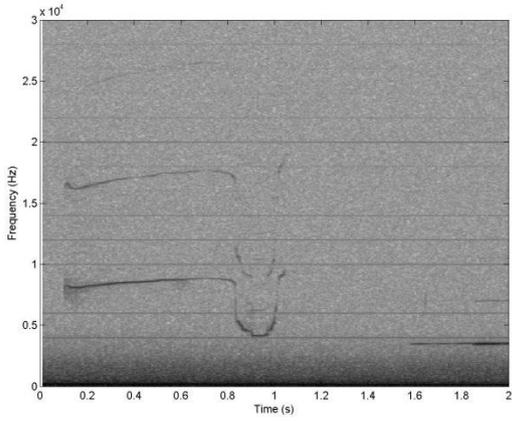
# AUSTRALIA



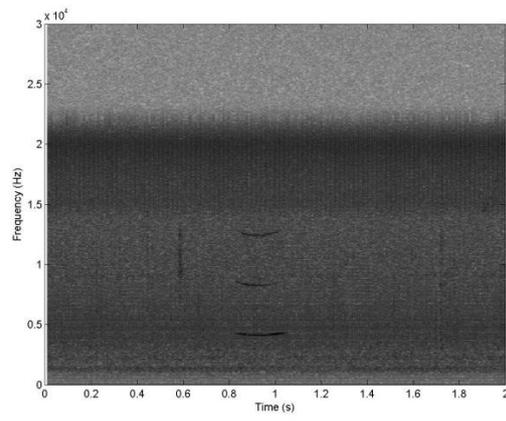
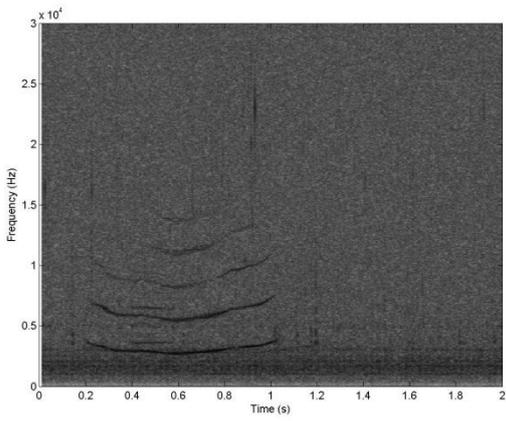
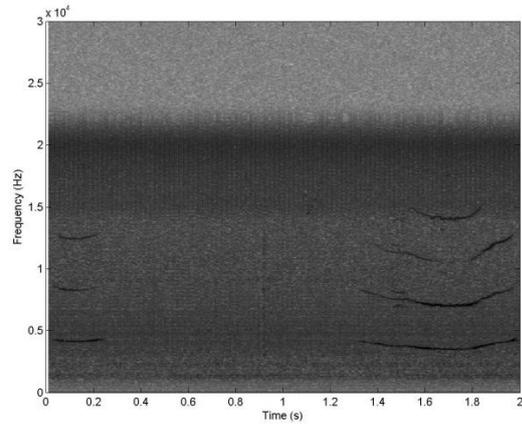
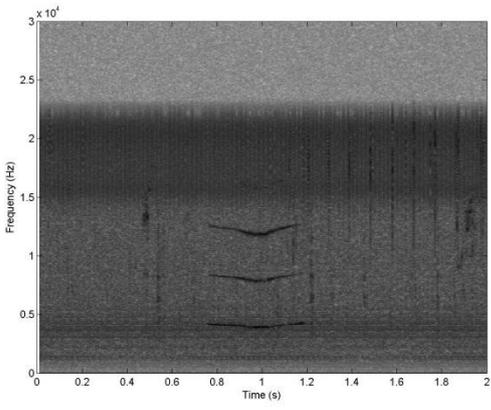
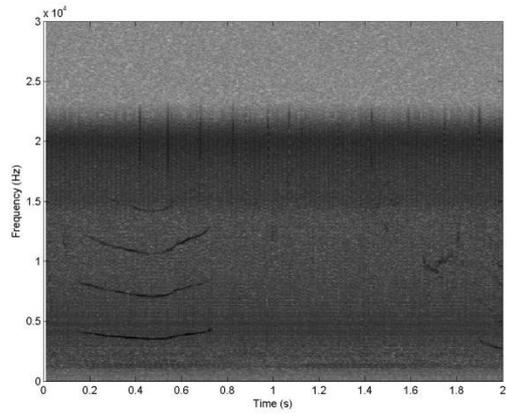
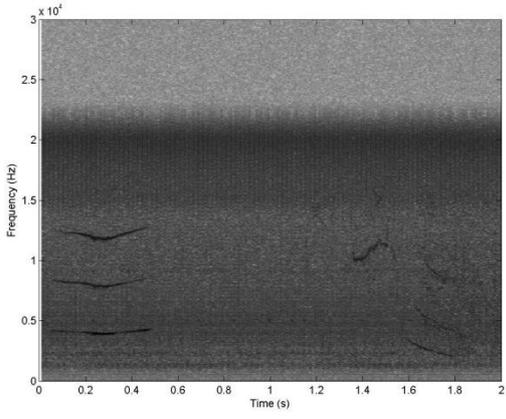
# AZORES



# CALIFORNIA



# EGYPT



## GRAN CANARIA

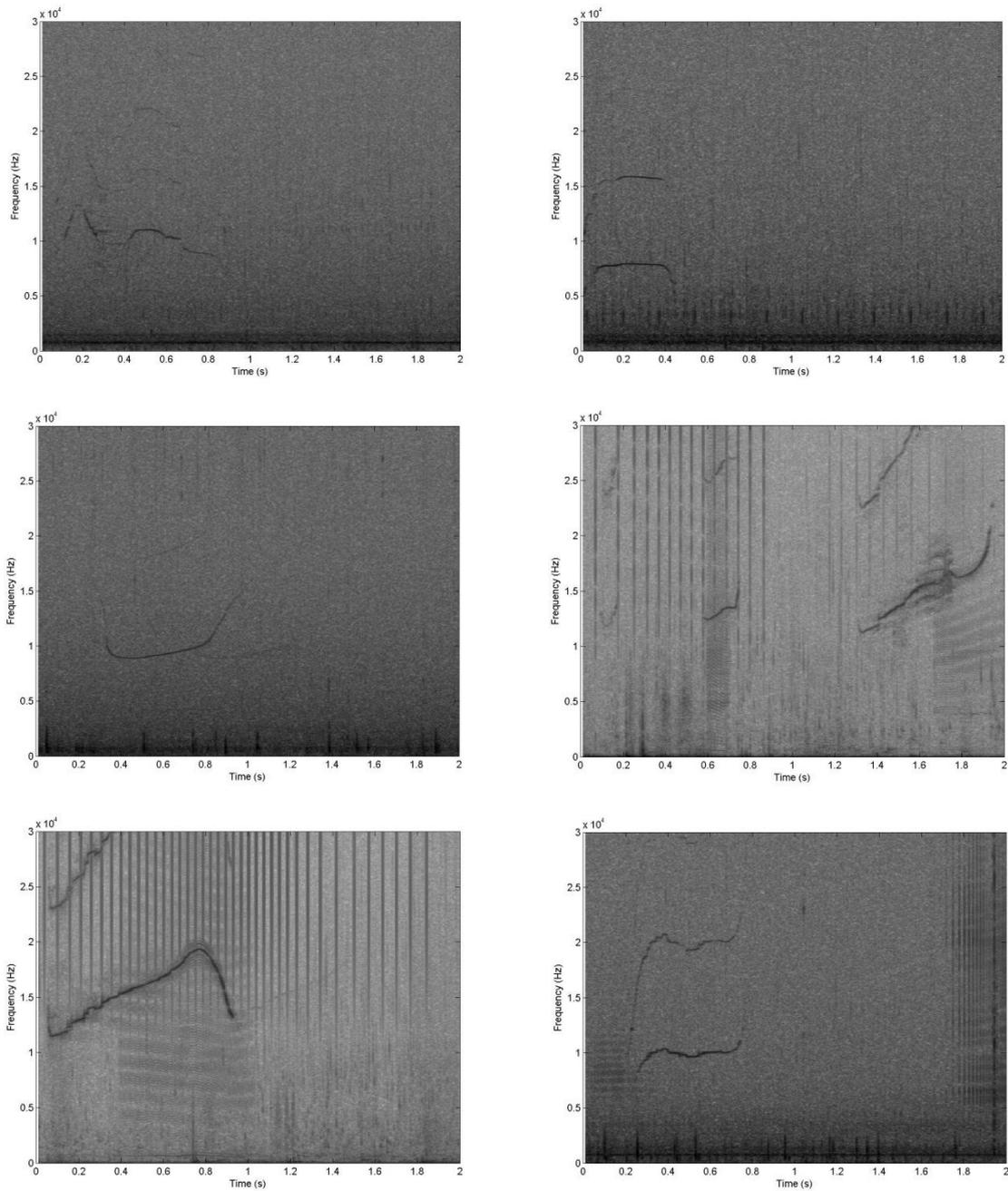


Figure 5.2 – For each location I subjectively selected six spectrograms most representative of each whistle repertoire.

Table 5.3- Descriptive statistics of the fundamental frequency of whistles recorded from Risso's dolphins off Australia, the Azores, California, Egypt, and Gran Canaria. Mean, number of cases, standard deviation and coefficient of variation ((standard deviation/mean)\*100) are presented. Note that descriptive statistics from the Azores sample might not be representative due to the small sample size.

Location		Start frequency (kHz)	End frequency (kHz)	Maximum frequency (kHz)	Minimum frequency (kHz)	Frequency range (kHz)	Whistle duration (s)	Mean frequency (kHz)	Mid frequency (kHz)
Australia	Mean	7.16	16.17	16.20	6.88	9.32	0.45	12.05	12.22
	N	21	21	21	21	21	21	21	21
	Std. Deviation	2.21	2.62	2.63	1.98	2.62	0.21	3.42	4.01
	COV (%)	30.92	16.20	16.25	28.80	28.06	46.08	28.39	32.82
	Maximum	10.88	19.33	19.52	9.76	14.07	0.74	17.20	18.20
	Minimum	3.57	10.32	10.32	3.57	3.57	0.15	4.20	3.75
Azores	Mean	9.38	8.32	9.84	7.22	2.63	0.40	8.11	7.95
	N	8	8	8	8	8	8	8	8
	Std. Deviation	5.62	4.94	5.80	4.13	2.68	0.29	4.51	4.44
	COV (%)	59.99	59.31	58.91	57.22	102.15	72.51	55.55	55.87
	Maximum	14.81	15.00	15.00	11.25	7.31	0.81	12.44	12.19
	Minimum	2.44	2.44	2.63	2.44	0.19	0.07	2.62	2.63
California	Mean	8.62	9.06	13.10	5.96	7.14	0.64	9.31	9.43
	N	329	329	329	329	329	329	329	329
	Std. Deviation	4.47	5.68	4.66	3.08	3.87	0.40	2.97	3.35
	COV (%)	51.83	62.66	35.53	51.59	54.13	62.72	31.89	35.56
	Maximum	29.06	26.25	29.06	23.70	21.00	1.74	24.52	23.70
	Minimum	2.44	1.69	3.38	1.50	0.19	0.03	2.81	2.81

Table 5.3- Descriptive statistics of the fundamental frequency of whistles recorded from Risso's dolphins off Australia, the Azores, California, Egypt, and Gran Canaria. Mean, number of cases, standard deviation and coefficient of variation ((standard deviation/mean)\*100) are presented. Note that descriptive statistics from the Azores sample might not be representative due to the small sample size.

	Location	Start frequency (kHz)	End frequency (kHz)	Maximum frequency (kHz)	Minimum frequency (kHz)	Frequency range (kHz)	Whistle duration (s)	Mean frequency (kHz)	Mid frequency (kHz)
Egypt	Mean	5.35	5.93	6.02	4.91	1.11	0.36	5.21	5.02
	N	18	18	18	18	18	18	18	18
	Std. Deviation	2.72	3.92	3.87	2.75	1.28	0.23	3.04	2.94
	COV (%)	50.82	66.08	64.30	56.07	114.46	62.75	58.28	58.71
	Maximum	12.19	15.09	15.09	12.19	4.88	0.81	13.15	12.75
	Minimum	3.56	3.19	3.75	2.81	0.19	0.03	3.09	2.81
Gran Canaria	Mean	11.46	12.81	15.21	10.09	5.11	0.51	12.47	12.73
	N	62	62	62	62	62	62	62	62
	Std. Deviation	2.78	4.31	3.93	2.48	2.98	0.22	2.82	2.89
	COV (%)	24.26	33.65	25.86	24.53	58.23	43.47	22.64	22.68
	Maximum	19.13	28.88	28.88	19.13	14.63	0.96	22.76	21.38
	Minimum	4.88	2.25	7.13	2.25	0.38	0.08	4.39	4.50
Total	Mean	8.83	9.79	13.20	6.57	6.63	0.60	9.70	9.82
	N	438	438	438	438	438	438	438	438
	Std. Deviation	4.33	5.69	4.82	3.30	3.92	0.37	3.36	3.69
	COV (%)	49.01	58.13	36.50	50.18	59.13	62.70	34.65	37.55
	Maximum	29.06	28.88	29.06	23.70	21.00	1.74	24.52	23.70
	Minimum	2.44	1.69	2.63	1.50	0.19	0.03	2.62	2.63

Although Corkeron and Van Parijs (2001) analysed the same data as presented here, values for the parameters differed. Particularly whistle duration was at least three times longer in Corkeron and Van Parijs (2001) compared to this study. Gran Canaria and Australian whistle samples of Risso's dolphin presented the lowest intra-population variation on all the parameters measured. On the other hand, Egypt and Azores presented the highest coefficient of variation. Overall, across all sampled populations whistle duration provided the highest coefficient of variation.

Results of the comparison of the different fundamental frequency parameters between Risso's dolphin populations showed that Azores' whistles' fundamental contour parameters seemed to be quite similar to the ones of the other populations analysed. The only statistically significant difference was found in the frequency range between the Azores and California and the Azores and Australia.

On the other hand, the Egypt whistle sample seemed to have a quite particular set of whistles parameters. All the parameters with the exception of minimum frequency and frequency range differed statistically from the other locations. Also, no statistical differences between the whistles parameters from the population of Gran Canaria vs. Azores and Gran Canaria vs. Australia (except minimum frequency, and frequency range) were found (see Table 5.4 for statistical and p values).

Table 5.4 - Results of the Robust test for the equality of means for all parameters that were not correlated. Values in the green areas represent the absolute difference between the two means for a given comparison. The green areas represent the statistically significant differences ( $p < 0.01$ ) and the red areas represent the non-significant tests ( $p > 0.05$ ).

		Australia	Azores	California	Egypt
Azores	Max. freq. (Hz)				
	Min. freq. (Hz)				
	Freq. range (Hz)	6695			
	Whistle duration (ms)				
	Mean freq. (Hz)				
	Mid freq. (Hz)				
California	Max. freq. (Hz)	3098			
	Min. freq. (Hz)				
	Freq. range (Hz)	2179	4516		
	Whistle duration (ms)	192			
	Mean freq. (Hz)	2741			
	Mid freq. (Hz)	2796			
Egypt	Max. freq. (Hz)	10180		7082	
	Min. freq. (Hz)				
	Freq. range (Hz)	8206		6026	
	Whistle duration (ms)			282	
	Mean freq. (Hz)	6843		4102	
	Mid freq. (Hz)	7209		4413	
Gran Canaria	Max. freq. (Hz)			2103	9184
	Min. freq. (Hz)	3214		4133	5188
	Freq. range (Hz)	4210		2030	3996
	Whistle duration (ms)			134	
	Mean freq. (Hz)			3160	7263
	Mid freq. (Hz)			3297	7710

Results from the discriminant function analysis are presented in the Table 5.5. I obtained an 82% correct classification of Risso's dolphin whistles to their respective location (Table 5.5). The first two canonical discriminant functions by location combined accounted for 92.8 % of the observed variance (Figure 5.3). The standardized canonical discriminant function coefficients showed that maximum and mean frequencies and frequency range were the most important parameters to discriminate between locations (Table 5.8). Results of the

binomial test revealed that the correct classifications were statistically different from the prior probabilities established based on sample sizes ( $p < 0.008$ ) (Table A. 1).

Table 5.5– Results of the discriminant function analysis among locations using the complete data set. 82% of the cases were correctly classified, highlighted in green.

		Predicted Group Membership						
Location		Australia	Azores	California	Egypt	Gran Canaria	Total	
Original	Count	Australia	11	0	9	0	1	21
		Azores	0	2	2	1	3	8
		California	5	5	292	4	23	329
		Egypt	0	1	1	16	0	18
		Gran Canaria	0	0	23	1	38	62
	%	Australia	52.4	.0	42.9	.0	4.8	100.0
	Azores	.0	25.0	25.0	12.5	37.5	100.0	
	California	1.5	1.5	88.8	1.2	7.0	100.0	
	Egypt	.0	5.6	5.6	88.9	.0	100.0	
	Gran Canaria	.0	.0	37.1	1.6	61.3	100.0	

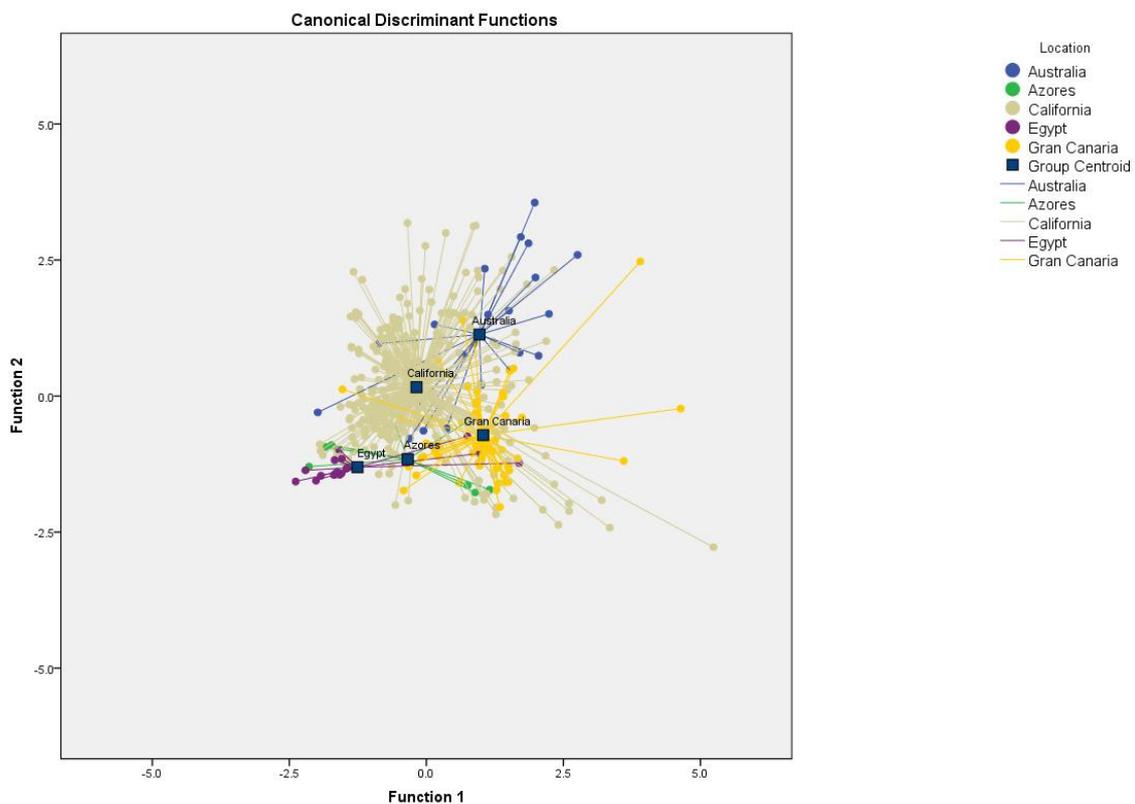


Figure 5.3 - Plot of the first two canonical discriminant functions by location for the complete data set. These two functions combined account for 92.8% of the observed variance.

Table 5.6– Coefficients for the discriminant function analysis based on the complete data set. Maximum, Mean frequencies and Frequency range with the highest scores for the discriminant function 1 and 2, i.e. these are the parameters that mostly influence those two functions and therefore the classification into different locations.

	Function			
	1	2	3	4
Maximum frequency (Hz)	-0.393	-1.736	1.792	-2.306
Frequency range (Hz)	0.126	1.977	-0.979	0.683
Whistle duration (ms)	-0.339	-0.351	0.997	0.461
Mean frequency (Hz)	1.281	0.871	-0.974	1.560

When analysing all whistles from Dtags of California there was some indication of high repetition rates for a type of whistle at least in one of the tagged animals. This could hint at the existence of signature whistles in this species.

When I removed the dtag data deployed on the individual that produced a highly stereotyped and repetitive whistle, that is, a potentially signature whistle, the overall performance of the discriminant function was approximately the same as the one including all the data. On the other hand, when reducing the Californian data to 20% of the original data per tag the overall correct classifications were reduced, but the predicted group memberships per location improved (comparison between Table 5.5 and Table 5.7). The overall correct classification changed from 82% to 80.6% and, for example, the correct classification of Australian whistles as Australian improved from 52.4 to 71.4%. The ten discriminant function analysis yielded a mean correct classification of 72.73% ( $s=5.6\%$ ). From the ten discriminant function analysis performed on the subsample of the dataset available I chose the one with the best overall classification score (80.6%). The first two canonical discriminant functions by location combined accounted for 93.1 % of the observed variance (Figure 5.4). These correct classifications obtained were statistically different from the prior probabilities established based on the sample sizes ( $p<0.005$ ) (Table A. 2). The parameters that mostly contributed to the discrimination between locations were minimum and mean frequencies and frequency range (Table 5.8).

Table 5.7 – Results of the discriminant function analysis among locations. California data was sub-sampled to 20% of whistles from each tag. 80.6 % of the cases were correctly classified, and are highlighted in green.

		Predicted Group Membership						
		Location	Australia	Azores	California	Egypt	Gran Canaria	Total
Original	Count	Australia	15	0	3	1	2	21
		Azores	0	3	1	1	3	8
		California	3	4	52	1	6	66
		Egypt	0	1	0	16	1	18
		Gran Canaria	1	0	5	1	55	62
	%	Australia	71.4	.0	14.3	4.8	9.5	100.0
	Azores	.0	37.5	12.5	12.5	37.5	100.0	
	California	4.5	6.1	78.8	1.5	9.1	100.0	
	Egypt	.0	5.6	.0	88.9	5.6	100.0	
	Gran Canaria	1.6	.0	8.1	1.6	88.7	100.0	

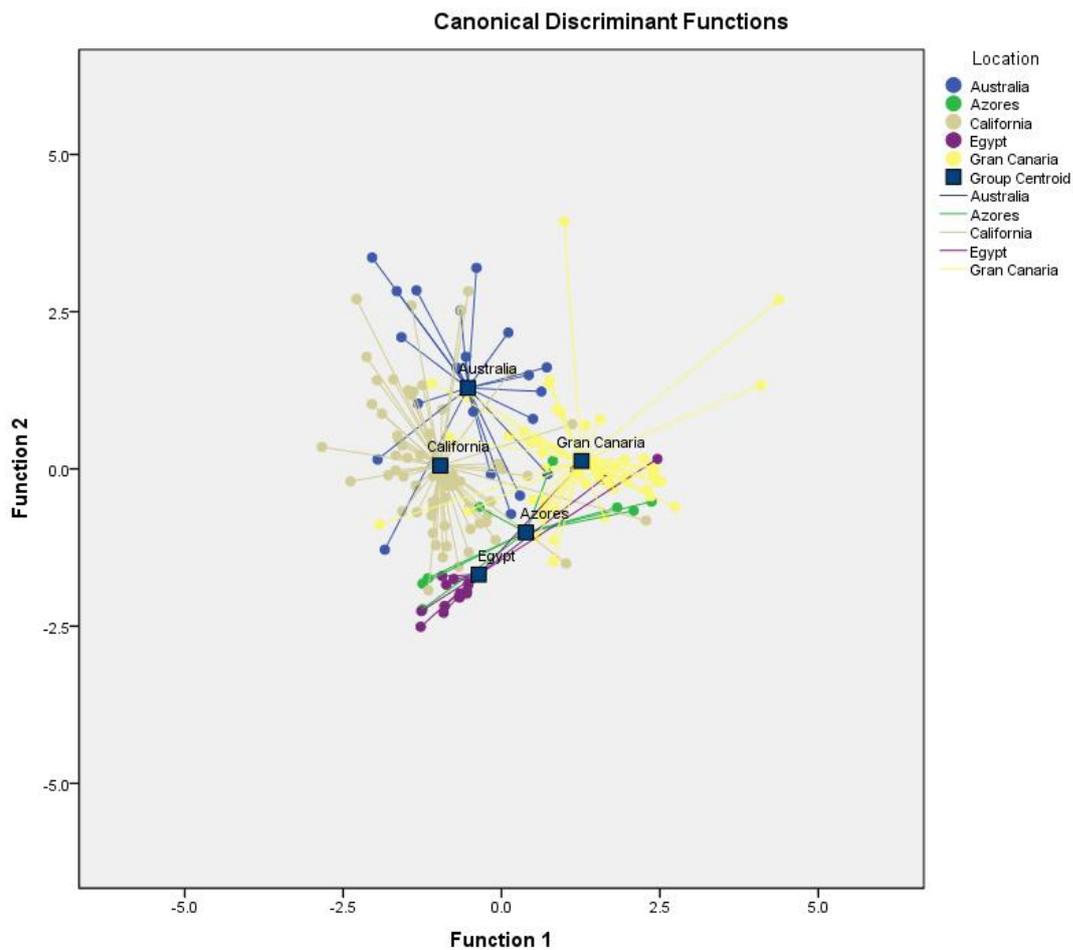


Figure 5.4 - Plot of first two canonical discriminant functions by location from the down-sampled dataset. These two functions combined account for 93.1% of the observed variance.

Table 5.8 – Coefficients for the discriminant function analysis based down sampled data for California. Minimum, Mean frequencies and Frequency range with the highest scores for the discriminant function 1 and 2, i.e. these are the parameters that mostly influence those two functions and therefore the classification into different locations.

	Standardized Canonical Discriminant Function Coefficients			
	Function			
	1	2	3	4
Minimum frequency (Hz)	0.782	-0.599	1.006	1.323
Frequency range (Hz)	-0.566	0.359	0.520	1.211
Whistle duration (ms)	-0.051	-0.335	0.946	-0.498
Mean frequency (Hz)	0.238	1.181	-1.118	-1.674

## Discussion

Risso's dolphins presented macro-geographic variation in the fundamental whistle parameters across all locations. The whistle parameters that contributed the most to this geographic variation were the minimum and mean frequencies and frequency range.

Egypt seems to be the most differentiated population. Gran Canaria vs Azores and Gran Canaria vs California seem to be the populations with a higher degree of misclassifications among them on the discriminant function analysis and, therefore, share fundamental frequency parameters.

I analysed data that came from a variety of sources. Different recording equipment was used across all different locations and the number of groups and, therefore, individuals recorded was also quite different.

Locations like the Azores yielded a small sample of whistles for the analysis. This may not be representative of the entire population from the Azores but can be used as an indication of the whistle parameters of the area.

Descriptive parameters of whistles such as maximum frequency or end frequency can be tricky to analyse across different locations or different studies when different methods of recording were used. In this study, although this is the case, all whistles used had their full spectra and were not limited by sampling rates. Nevertheless, there is still the possibility that whistles of higher frequencies might not be captured with the lower sampling rates and those frequencies cannot be represented on this study.

Behavioural context can affect the vocal output of a population (Ford 1989), as well as environmental conditions (Lesage et al. 1999). Differences found for the Azores population between our study and Rendell et al. (1999) could be due to the smaller sample size of our study, but also to the reasons aforementioned. Comparisons of behavioural contexts were not possible due to the lack of that data. Environmental data, such as ambient noise were also not available in either study. Nevertheless, considering the time gap between the data collection of the two studies (at least 5 years) and the development of the tourism and whale watching in the area (Visser et al. 2011), it is plausible to assume an increase in ambient noise and it is expected that the ambient noise was highest in the later years represented in the present study.. Dolphins may have produced higher frequency whistles in noisier environments (Lesage et al. 1999; May-Collado & Wartzok 2008) where dolphins were exposed to boat noise. Assuming that the more recent recordings used in this study were the noisiest due to the increase of boat traffic, Risso's dolphins could be expected to produce higher frequency whistles relative to what was reported by Rendell et al. (1999), but that is not the case.

As for the differences found between our analysis and the one in the Corkeron and Van Parijs (2001) study of the same encounter of Risso's dolphins in Australian waters, none of the above explains the differences found between the two studies since these used the same animals in the same encounter of Risso's dolphins. An error in the digitization speed was made at the time and, therefore, duration and frequency parameters are incorrect (Michael Noad, personal communication).

Analysing data from a single group can lead to lack of independence of the data, as well as an under-representation of the targeted population. Repetition of whistles by the same individual is quite common on dolphins, like in the signature-whistle of bottlenose dolphins (Janik 2000b). Similarly, simultaneous repetition of whistles by several members of the same group can occur as in chorusing (Janik et al. 2011). Non-independence of the data can be caused by such repetitions. The existence of signature whistles for Risso's dolphins has been previously suggested (Caldwell et al. 1969; Favaro et al. 2011). Corkeron and Van Parijs (2001) did not find the presence of signature whistles in the Australian population studied. I also did not find any indication of signature whistles for the same population. Albeit from different encounters, the data used from California was based on the deployment of only 6

Dtags. Only the loudest whistles were selected for analysis (>12dB of SNR) giving me some confidence that I was using whistles from the tagged animal. Therefore, I assume that only six animals were sampled for this location. The potential existence of a signature whistle in at least one tagged animal could also lead to a potential bias for the California population, despite the larger sample size (335 whistles). When the data from that Dtag was removed no differences on the results could be found. The coefficient of variation for the extracted whistle parameters (Table 5.3) for this population showed that start, end, minimum frequencies, frequency range and whistle duration all present a coefficient of variation higher than 50%. Even considering the existence of signature whistles and the fact that the data originate from 6 animals these parameters show considerable variance and might, therefore, be representative of the population. When I addressed the question of bias by a larger sample size by sub-sampling the data from California to a random selection of 20% of the whistles from each tag, I obtained an improvement on the correct classification per location, but not for the overall correct classification. So I decided to sub-sample the California whistles and proceed with the analysis based on that decision. When I checked if the classifications obtained were significantly different from random I obtained the same results as from the analysis considering the whole data set. Nevertheless it is important to consider that, even taking into account differences in sample sizes for each location, a highly unbalanced dataset can bias the results. So, depending on the data set used, this could be the reason for the important discriminant whistle parameters change. In this study the exclusion of repetitive data led to one of the main predictors to determine location for Risso's dolphins' whistles changing from maximum to minimum frequency.

Footo and Nystuen (2008) found that minimum frequency in killer whales changed significantly with their ecotype and hypothesized that this could be to reduce detection by their prey. Up until now there is not enough knowledge about Risso's dolphins prey preference across all locations to be able to link any shifts in the minimum frequency to prey taxonomic differences. On the other hand, ambient noise can lead to shifts in both minimum frequency and frequency range (Lesage et al. 1999) which can explain some of our geographical differences as mentioned before.

Intraspecific variation of dolphin whistles can be used to communicate information about identity or emotional state; variation in whistle duration in bottlenose dolphins supports

this hypothesis (Janik et al. 1994) but for Risso's dolphins we don't have information on dolphin behaviour or identity (with the exception of the Dtag data), during recordings to judge that. Whistle duration across all locations studied presented the highest coefficient of variation of all the parameters. In bottlenose dolphins long durations of whistles were associated with areas with high background noise, particularly with a high number of boats in the surrounding areas (May-Collado & Wartzok 2008). Killer whales and belugas, *Delphinapterus leucas*, also increase the duration of their calls (Lesage et al. 1999; Foote et al. 2004) in the presence of boats. On the other hand in another study where background noise was measured, whistle duration did not differ with different background noise levels (Morisaka et al. 2005a). The high variability I obtained in whistle duration can be a reflection of the environmental conditions such as ambient noise of the locations studied. My results show that whistle duration was statistically longer in the Californian whistle sample when compared to Gran Canaria, Australia and Egypt which showed shorter durations in this order.

Similar to other dolphin whistle comparisons, frequency parameters had the lowest coefficients of variation of all whistle parameters used, i.e. lower intraspecific variation for our populations of Risso's dolphins (Wang et al. 1995; Morisaka et al. 2005b; Camargo et al. 2006). As Morisaka et al. (2005b) suggested these frequency parameters could be related to factors such as body size and therefore, the size of the sound production organs, and/or ambient noise levels but we do not have access to any of that information.

Nevertheless, the low variation observed was still sufficient to permit differentiation of wild Risso's dolphin whistle samples (Table 5.5).

The population from Egypt seemed to have distinctive acoustic features in comparison to the other populations, making it almost isolated from all others. Almost all frequency parameters of whistles from this population were statistically different from those of the other populations. On the other hand I found the Azores population did not differ from the other populations in frequency parameters (except frequency range for two locations). All these differences and similarities were reflected in the results of the discriminant function analysis performed where 82% of the whistles analysed were correctly classified to their location and the proportion of correct classifications was statistically different from the scores obtained by chance.

Geographical variations in this study are considered macro-geographic due to the larger distances between the five locations (Figure 5.1). The geographically closest locations were Gran Canaria and the Azores. Photo ID studies so far, revealed no re-captures between both archipelagos (Karin Hartman personal communication). There have been recaptures of a genetically closer species (LeDuc et al. 1999), the short-finned pilot whale, between Gran Canaria and Madeira (Servidio et al. 2007). The movements of a rehabilitated Risso's dolphin were satellite tracked and showed a 3300Km path travelled by one animal (Wells et al. 2009) which is more than double of the distance between the Azores and the Canary Islands. Although capable of physically moving between the archipelagos the two populations seem not to be mixing. The populations might have a high degree of site fidelity and residency (Hartman et al. 2008). Nevertheless there is some overlap between the whistles of both archipelagos: 37.5% of Azorean whistles were misclassified as belonging to the Gran Canaria repertoire. On the other hand none of the whistles from Gran Canaria were misclassified as belonging to the Azores. This result could be due to chance since the Azores only contributed eight whistles to the overall classification. In fact, the Azores got the lowest correct classification result of all locations. I conclude that individual movements to other populations are unlikely to be one of the factors promoting the geographical variation observed.

As mentioned before, geographic variation can reflect the isolation and genetic divergence between populations. For example, the comparisons of the two pairs of most distant populations, Egypt vs California and California and Australia showed statistically significant differences in all whistle parameters except minimum frequency. On the other hand, for the closest populations of the Azores and Gran Canaria none of the whistle parameters differed. Currently we do not have any information on gene flow, individual movements, and genetic relationships of the target populations. Therefore, further research is needed to understand how these may relate to the geographic variation found in their whistle repertoires.

Adaptation to different ecological environments could lead to geographical variation in the acoustic properties of the repertoire of different populations. Ding et al. (1995b) found that offshore or clearer water species had relatively higher frequency ranges than coastal or riverine species. Foote and Nystuen (2008) suggested that differences in the minimum frequency of calls of different ecotypes of killer whales were an adaptation to different prey

targeted by the two ecotypes. Risso's dolphins are pelagic with a preference for water between 500-1000m (Baumgartner 1997). In Egypt, Gran Canaria and the Azores the species is considered pelagic, inhabiting zones with depths between 500-1000m. In California, detection of Risso's dolphin clicks were obtained in areas of 500-1000 m but dolphins were also seen feeding in much shallower areas (Shane 1995). If considering a coastal type of Risso's dolphin in California, the values for whistle frequency range from this location are amongst the two highest for all five locations. So, at least the Californian population of Risso's dolphins does not fit the above theory.

In conclusion, the five locations targeted by this study showed macro-geographical variation of Risso's dolphin whistles. The causes of such variation are still unclear and further research is needed to fill the gaps in our knowledge of the following:

- ambient noise levels for all locations;
- genetic studies of the populations;
- habitat and social structure studies of all populations;
- movements of populations;
- behavioural studies of the species concurrent with acoustic sampling;
- and, yearly sampling of vocalizations.

Further information on any of these topics would allow an investigation of correlations with the vocal variation described here and help to improve our understanding of the reasons for geographical variation in the whistle parameters of Risso's dolphins.

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## Chapter 6 : General discussion

Risso's dolphins are a cosmopolitan species, distributed worldwide. Nevertheless, it is still greatly understudied. In my study I shed some light on this enigmatic species, looking at their acoustic behaviour.

The species presents a range of particular characteristics that makes them unique and an interesting study case.

Risso's dolphins seem to gather a mix of characteristics which links them to both the *Delphinidae* family and also to the *Ziphiidae* family. The "mixed-taxonomic" characteristics begin with the species social structure. Risso's dolphins form a stratified community based on highly associated social units grouped by age and sex classes (Hartman et al. 2008). They combine the fission-fusion social structure typical of bottlenose dolphins (Würsig & Würsig 1977) with a more stable matriarchal social structure found in pilot and killer whales (Bigg et al. 1990).

Risso's dolphins also combine a variety of unusual features in their acoustic faculty. Firstly they produce highly stereotyped burst-pulsed sounds that can be isolated or combined with whistles in a highly synchronized way (Corkeron & Van Parijs 2001); this places them closer to killer whales (Miller & Bain 2000; Miller 2002) than to any other dolphin species. On the other hand similarly to pilot whales Risso's produce isolated burst-pulses that can be used in maintaining group cohesion after a deep dive (Jensen et al. 2011a). They also resemble beaked whales (Madsen et al. 2005) in the sense that they don't seem to employ range locking behaviour in target approach. Conversely, the likely presence of signature whistles in Risso's dolphins (Caldwell et al. 1969; Favaro et al. 2011) places them closer to bottlenose dolphins. The fact that Risso's dolphins have an automatic gain control on the transmitting side of their biosonar also brings them closer to smaller delphinids (Au & Benoit-Bird 2003). Once more, the species seems to be combining features of very different odontocete species as in its social structure.

## **The Risso's dolphin vocal repertoire and its behavioural context**

Describing a species vocal repertoire is the first step to understanding its communication network; the second step is to contextualize and validate the categorization done.

Therefore, in chapter two I described the basic vocalizations found in the vocal repertoire of the population of Gran Canaria and placed them in a behavioural, group size and habitat context. The Risso's dolphin population from Gran Canaria produce mainly three types of sounds: whistles, isolated burst-pulses and click trains.

### **Whistles**

Whistles assume a very important role in a dolphin's acoustic repertoire and biology. The most studied whistles are the signature whistles, highly stereotyped frequency modulated whistles. Caldwell and Caldwell (1965) suggested the existence of these whistles for the first time. They defined them as the individually distinctive signal that bottlenose dolphins use when in isolation (Caldwell & Caldwell 1965; Caldwell et al. 1990). Studies of dolphin whistles focus mainly in the fundamental frequency of the whistle, which, in the case of the signature whistles is where the identity information is encoded (Janik et al. 2006). However, dolphins seem to use information also on the harmonics of the whistles (Lammers & Au 2003).

Despite of the extensive use of whistles by some species, not all delphinid species use whistles. Species like the Hector dolphins, and harbour porpoises, do not whistle and use clicks to communicate instead (Dawson 1991; Clausen et al. 2010).

Risso's dolphins although capable of whistling, seem not to use whistles as the main communicative vocalization. The 45 hours of recordings analysed in chapter two only yielded 115 whistles. Risso's dolphin produced more whistles while socializing than in any other behaviour context indicating that their role is in communication. Just like bottlenose dolphins (Quick & Janik 2008), Risso's dolphins seem to avoid masking by conspecifics and save energy by reducing their whistle rate (whistles per individual per minute) when groups are large. In these cases a short-range communication sound is used instead such as the burst-pulses.

Despite the limited use of whistles by Risso's dolphins, these sounds are still a good trait for comparison of vocalizations amongst different populations due to its frequency modulation

and its use in the communication system of the species. Therefore, in chapter five, I compared the whistle repertoire of different populations of Risso's dolphins.

The study of geographic variation in an animal vocalization might provide information on environmental, ecological, biological and even cultural aspects of a species. Risso's dolphins present macro-geographical differences in the whistle repertoire. The whistle parameters that mostly contributed for this geographic variation were minimum and mean frequencies, and frequency range. I found that Egypt seemed to be the most differentiated population. In contrast, Gran Canaria and the Azores as well as California, seemed to have a high similarity in their whistle parameters.

The differences found could be due to evolutionary divergence caused by geographic isolation, but there is no current knowledge to justify that or any other cause. Data from the deployment of Dtags (Johnson & Tyack 2003) in California suggested that Risso's dolphins might have signature whistles which brings them closer to other delphinids such as the bottlenose dolphin.

Despite the little use of whistles by Risso's dolphins it seems that these vocalizations still play an important role on their acoustic repertoire. Further studies on their whistle repertoire are needed such as the study of the species acoustic adaptations to anthropogenic noise, whistles active space, the presence/absence of signature whistles and its function, and the role of harmonics on Risso's dolphins whistles.

### **Isolated burst-pulses**

Burst-pulses have been reported to be communicative in other species (Janik 2009). Northern right whale dolphins produce stereotyped sequences of burst-pulsed sounds that seem to have a communicative function similar to whistles of bottlenose dolphins (Rankin et al. 2007). Other dolphin species that do not produce whistles also rely on clicks to communicate. Among those are the Hector's dolphins that produce "cries" which are high repetition series of clicks, highly associated with excitement such as aerial and aggressive behaviour (Dawson 1991). Harbour porpoises also use click trains to communicate employing stereotyped aggressive click patterns (Clausen et al. 2010). Sperm whales, use codas, a temporal sequence of clicks in a click train with a stereotyped pattern of ICIs, which are used for communication conveying clan affiliation (Rendell & Whitehead 2005).

Nevertheless, depending on the ICI and the physical properties of their click trains, sperm whales can use click trains for communication or echolocation (Madsen et al. 2002).

In spinner dolphins pulsed sounds seem also to be communicative and could be a more intimate and directional form of communication when animals are close together as opposed to whistles that play an important role in dispersed groups maintaining group cohesion (Lammers et al. 2006). Similarly, when groups of Risso's dolphins are numerous and with low dispersion, the burst-pulses will assume a highly directional and more intimate form of communication; this will avoid masking since these animals decrease whistle rates and increase burst-pulses rates when groups are larger. Besides being produced by socializing groups, isolated burst-pulses were also highly common in deeper waters when dolphins were foraging. These were isolated sounds and did not constitute the terminal part of a click of a foraging sequence (Verfuss et al. 2009). It is unlikely that these burst-pulses were used in target approaches (Madsen et al. 2005). Risso's dolphins might use burst-pulses in a foraging context in the same way as pilot whales do. Pilot whales, when in the ascent phase of their deep dive use "rasps" which are short click series, maintaining short range communication (Jensen et al. 2011a).

In chapter three, when focusing only on the click trains produced by Risso's dolphins I found, once again, that the isolated burst-pulses were associated with foraging and socializing. The highest rates of burst-pulses occurred during foraging and socializing, behaviour patterns in which the animals were spread out over a large area and may, therefore, need to facilitate and or mediate reunions. Also, an increase of the burst-pulse rate could be seen when animals were socializing when compared to slow traveling.

Moreover, when dolphins were engaged in socializing behaviour 25% of burst-pulses were produced by more than one animal at any given time and 55% while foraging which is consistent with a communicative function for this type of sounds. This production of overlapped burst-pulses by more than one animal at a given time could indicate an exchange of these signals among Risso's dolphins either in a social context to communicate or in a foraging context maintaining short distance communication after a long dive similarly to what happens with short finned pilot whales.

## Click trains

In chapters three and four I showed that click trains dominated the vocal repertoire of Risso's dolphins in Gran Canaria.

Risso's dolphins in Gran Canaria are considered an oceanic species and have a particular echolocation behaviour that once again combines characteristics of different odontocete families. This echolocation behaviour seems to be adapted to an oceanic environment with few landmarks or structures.

Firstly, Risso's dolphins do not seem to use a particular type of click train for a given activity. Rather, it seems that the species uses a wide range of click trains types in its activities.

Bottlenose dolphins use not only echolocation but use also passive listening to detect prey. Once the prey is detected they use echolocation to investigate the sound source (fish vocalization) (Gannon et al. 2005). Even though Risso's dolphins use echolocation in several contexts, they do not seem to use the same strategy as bottlenose dolphins. This could be due to ecological differences like the different type of prey targeted by Risso's dolphins (Wurtz et al. 1992). While foraging more than one Risso's dolphin was echolocating at any given time. Risso's dolphins, like pilot whales (Jensen et al. 2011b) seem to forage solitarily. This is consistent with the type of prey targeted by both species (Wurtz et al. 1992) and also with my visual observations in the field; when engaged in foraging behaviour, Risso's dolphins were seen to spread out over large areas. When distant, eavesdropping can be harder and therefore animals echolocate for themselves, which would explain the overlapped production of click trains in this context. Conversely, while slow traveling only one animal echolocated at a time; no overlapped click trains were found. This could be an indication of fewer animals echolocating per group. Rough tooth dolphins combine highly synchronous swimming with echolocation by only one animal when traveling. This suggests eavesdropping behaviour in this species (Götz et al. 2006). Eavesdropping helps other members of a synchronized group to get information on potential targets ahead by listening to the echoes from the sonar of conspecifics (Dawson 1991). In this sense, Risso's dolphins could be eavesdropping on conspecific sonar echoes when traveling or when slow traveling with higher group cohesion (less than one body length) and with high synchrony.

When echolocating, dolphins produce a click that aims at a given target and is reflected back to the animal; the animal then processes the echo for some time (lag time) before

producing the next click. This pulse mode of echolocation allows us to determine the distance that the dolphins are echolocating at. As such, the lag time of the dolphin and the inter click intervals of a click train reflect the distance that an animal echolocates on (Au 1993). That distance could be a reflection of the behavioural state of the animals. Risso's dolphins did not show any differences in the mean ICI across group behaviour patterns. These animals use a wide range of ICIs across and within all behaviours.

Since dolphins use echolocation for navigation and foraging, this variety of ICIs is most likely the result of animals having to perform various echolocation tasks within a certain behavioural category. For instance, foraging behaviour can have several stages such as search, approach, and terminal phase; prey capture, re-unions, after capture dives, and surface resting after a dive or traveling. During all of these activities of foraging, dolphins assess different distances, explaining the wider range of mean ICIs observed. In this aspect Risso's dolphins differ from beaked whales that use stable ICIs while foraging (Madsen et al. 2005). A mean distance of 128 m was estimated for potential targets when dolphins were foraging. This seems to agree with the distances found by Madsen et al. (2004).

Despite differing from beaked whales in the use of non-constant ICIs while foraging, the Risso's dolphin sonar resembles in part that of the beaked whales in that neither species seem to have range locking behaviour. Perhaps, similarly to beaked whales (Madsen et al. 2005), Risso's dolphins navigate through an environment of very deep waters, with few landmarks to lock on to (Baumgartner 1997).

All potential on-axis clicks of Risso's dolphins were found to have ICIs higher than the TWTT, which could mean that the dolphins were in fact targeting the array or a target further away. The only exceptions are the clicks that formed the isolated burst-pulses. Most likely these clicks were not being used in target detection but instead in communication (as discussed in chapters two and three).

The relationship between the target distance and ICIs seems to be controversial even within a given species. Wild finless porpoises, seem to decrease their ICIs over time during prey approaches (Akamatsu et al. 2005). Verfuss et al. (2005) showed that captive harbour porpoises have a distance dependence decrease in the ICI, proportional to the decrease in the TWTT to the potential target with the lag time remaining constant. Conversely, other studies seem not to have found an ICI range adjustment by captive harbour porpoises. Both captive (Au 1993) and wild (Linnenschmidt et al. 2012) bottlenose dolphins present a

reduction in ICI with decreasing target range. Additionally, both beaked whales and sperm whales, seem to have constant ICIs during the search phases of the prey (Madsen et al. 2005). Occasionally, even for beaked whales, during the buzz phase of a target approach/capture, the ICIs measure at the start of a buzz are correlated with the TWTT (Johnson et al. 2008).

In Risso's dolphins, even though all regular click ICIs exceed the TWTT, ICIs did not correlate with the distance to the target; also, the lag time had a great variance and a standard error of the order of the lag time of the delphinids that have range locking behaviour (Au 1993; Verfuss et al. 2005).

In chapter four I could not find evidence that Risso's dolphins had range locking behaviour. The fact that the lag time is not constant and that there is no correlation between ICIs and the target range, lead me to corroborate the hypothesis proposed in chapter three. Therefore, Risso's dolphins, like beaked whales, might not range-lock on targets and instead might include echoes from far distances keeping a "window" open for possible detections in between. Animals inhabiting open waters might as such, adjust their click interval to a specific search range, most likely their maximum perceptual range (Verfuss et al. 2009).

Contrary to beaked whales and more similar to other dolphins from the *Delphinidae* family, Risso's dolphins have an automatic gain control of their biosonar system. Risso's dolphins from Gran Canaria decrease the source level of their on-axis clicks significantly as a function of  $20.8\log(R)$ . This source level compensation on the emitting side of the Risso's dolphin's biosonar agrees with the automatic gain control found in other delphinids (Au & Benoit-Bird 2003; Jensen et al. 2009).

In conclusion, Risso's dolphins have proven to be an interesting and peculiar species to study. The species gathers acoustic characteristics that simultaneously place it in two different families of odontocetes, suggesting the need for a revision of its taxonomic classification and maybe placed them together with another genetically related (LeDuc et al. 1999) deep diver such as the pilot whales.

The following points summarize the main findings of Risso's dolphin acoustic behaviour in Gran Canaria. Risso's dolphins:

- are not only capable of whistling, but also use burst-pulses for communicative purposes;
- have a whistle repertoire with presents geographic variation;
- might have signature whistles in their repertoire;
- use a wide range of click trains under several behavioural contexts;
- might eavesdropping while slow travelling or resting;
- and have a biosonar system that seems to employ gain control on the outgoing part of the sonar, although they do not seem to employ range locking behaviour while navigating or foraging.

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## Appendix

Table A. 1 - Results from SPSS for the binomial test of the correct classification of whistles for each location against the prior probabilities bases on the sample sizes for each location (Test proportion on each table).

**Binomial Test for Australia data**

		Category	N	Observed Prop.	Test Prop.	Exact Sig. (1-tailed)
binomial_test	Group 1	correct	11	.524	.048	.000
	Group 2	incorrect	10	.476		
	Total		21	1.000		

**Binomial Test for Azores data**

		Category	N	Observed Prop.	Test Prop.	Exact Sig. (1-tailed)
binomial_test	Group 1	correct	2	.250	.018	.008
	Group 2	incorrect	6	.750		
	Total		8	1.000		

**Binomial Test for California data**

		Category	N	Observed Prop.	Test Prop.	Exact Sig. (1-tailed)
binomial_test	Group 1	correct	292	.888	.751	.000
	Group 2	incorrect	37	.112		
	Total		329	1.000		

**Binomial Test for Egypt data**

		Category	N	Observed Prop.	Test Prop.	Exact Sig. (1-tailed)
binomial_test	Group 1	correct	16	.888889	.041000	.000
	Group 2	incorrect	2	.111111		
	Total		18	1.000000		

**Binomial Test for Gran Canaria data**

		Category	N	Observed Prop.	Test Prop.	Exact Sig. (1-tailed)
binomial_test	Group 1	incorrect	24	.387	.858	.000 <sup>a</sup>
	Group 2	correct	38	.613		
	Total		62	1.000		

a. Alternative hypothesis states that the proportion of cases in the first group < .858.

Table A. 2 - Results from SPSS for the binomial test of the correct classification of whistles for each location against the prior probabilities bases on the sample sizes for each location (Test proportion on each table). These results are for the discriminant function analysis based on the down sampled data for California.

**Binomial Test for Australia data**

		Category	N	Observed Prop.	Test Prop.	Exact Sig. (1-tailed)
binomial_test	Group 1	Correct	15	.71	.12	.000
	Group 2	Incorrect	6	.29		
	Total		21	1.00		

**Binomial Test for Azores data**

		Category	N	Observed Prop.	Test Prop.	Exact Sig. (1-tailed)
binomial_test	Group 1	Correct	3	.375	.046	.005
	Group 2	Incorrect	5	.625		
	Total		8	1.000		

**Binomial Test for California data**

		Category	N	Observed Prop.	Test Prop.	Exact Sig. (1-tailed)
binomial_test	Group 1	Correct	52	.788	.377	.000
	Group 2	Incorrect	14	.212		
	Total		66	1.000		

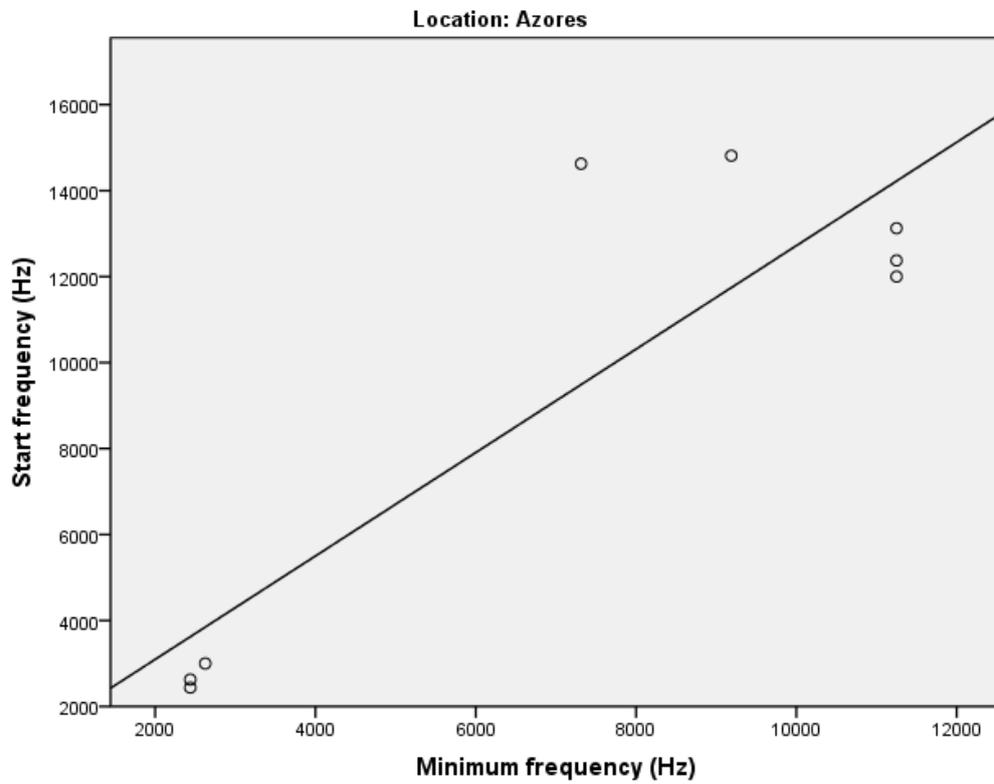
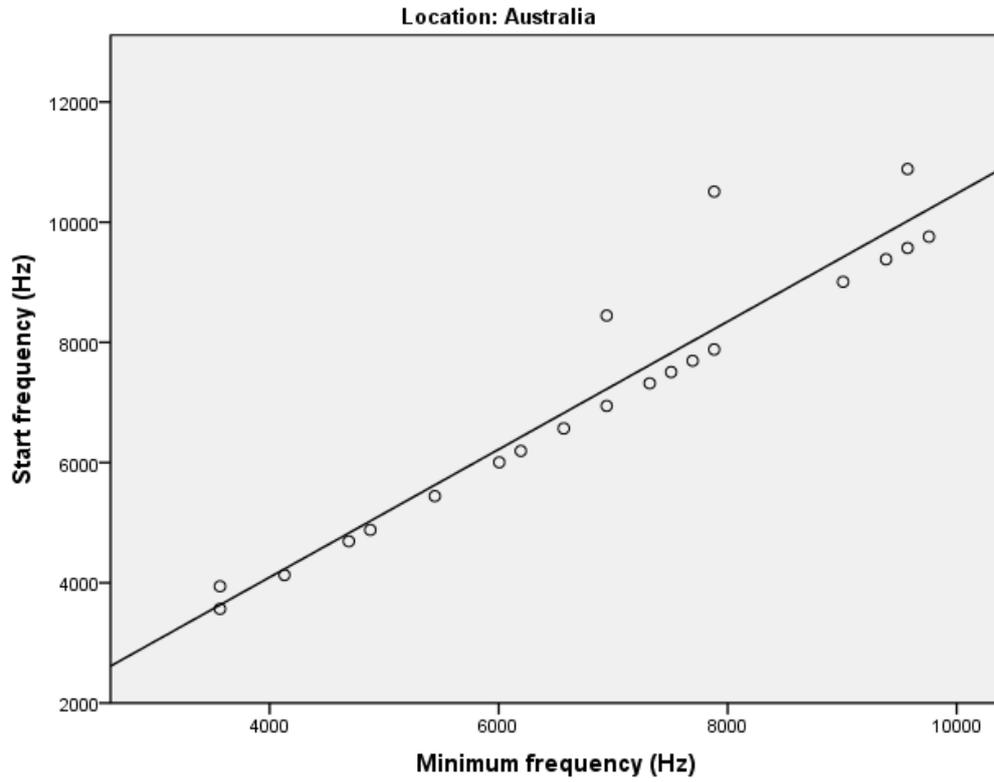
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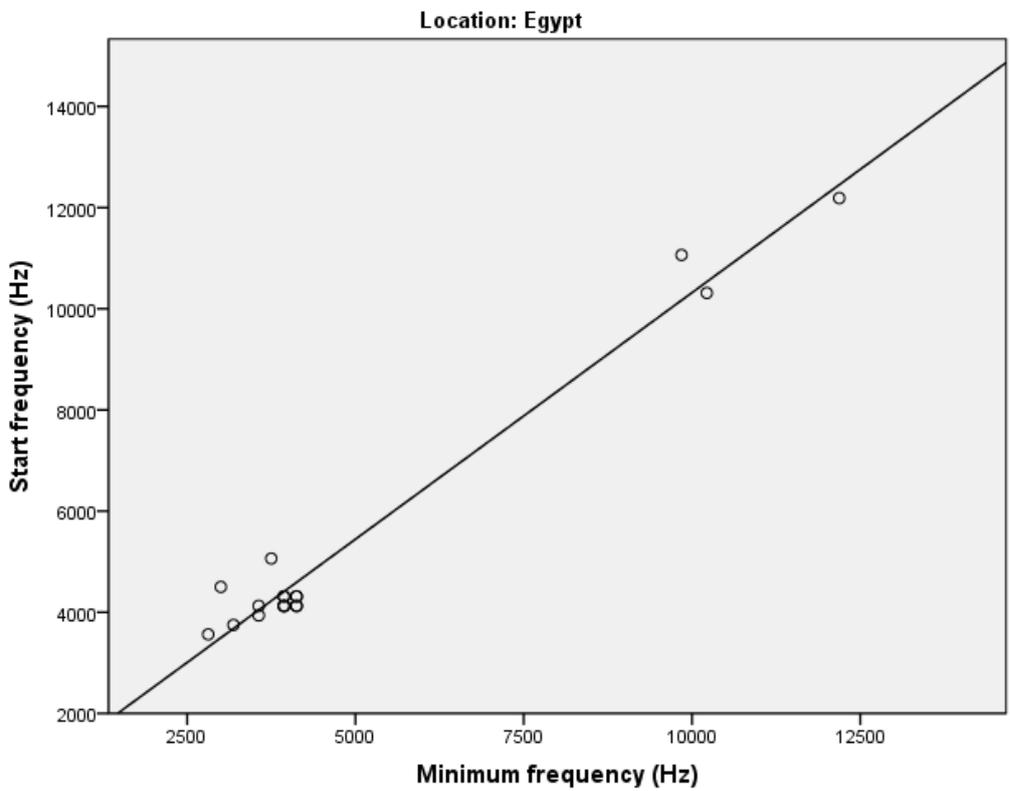
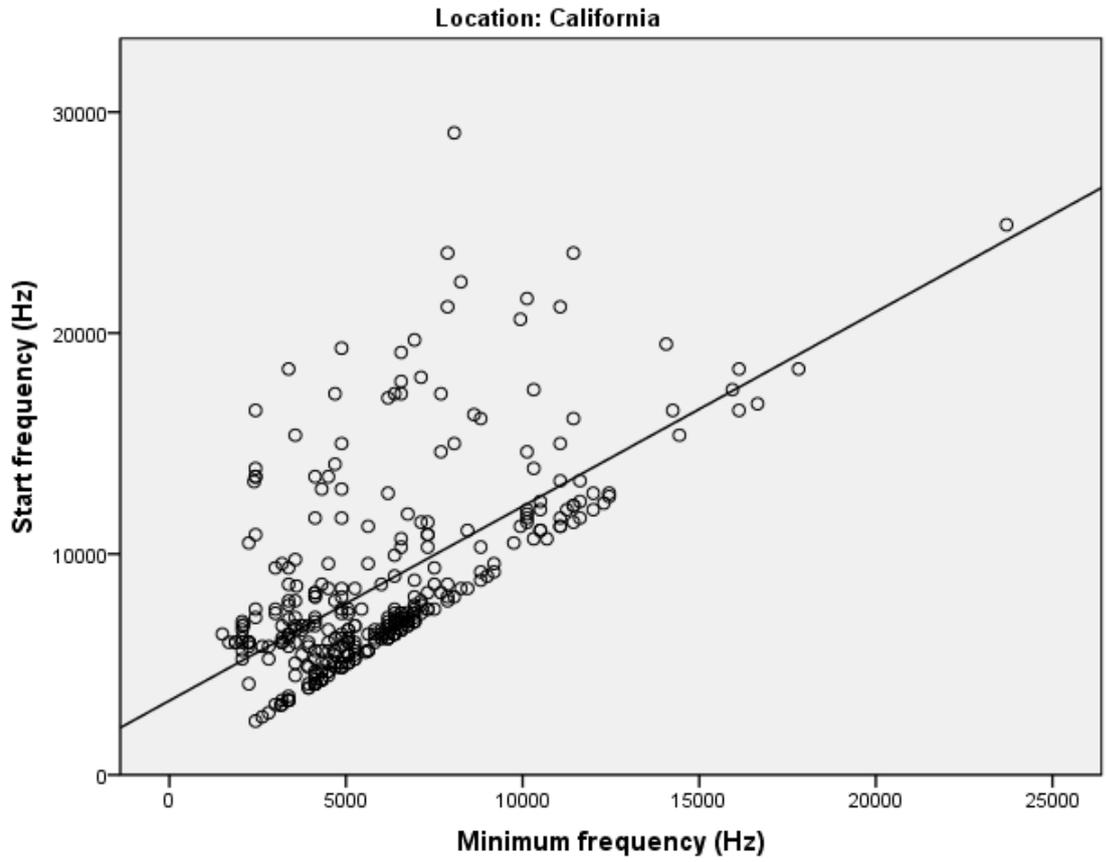
		Category	N	Observed Prop.	Test Prop.	Exact Sig. (1-tailed)
binomial_test	Group 1	Correct	16	.889	.103	.000
	Group 2	Incorrect	2	.111		
	Total		18	1.000		

**Binomial Test for Gran Canaria data**

		Category	N	Observed Prop.	Test Prop.	Exact Sig. (1-tailed)
binomial_test	Group 1	Incorrect	7	.113	.646	.000 <sup>a</sup>
	Group 2	Correct	55	.887		
	Total		62	1.000		

a. Alternative hypothesis states that the proportion of cases in the first group < .646.





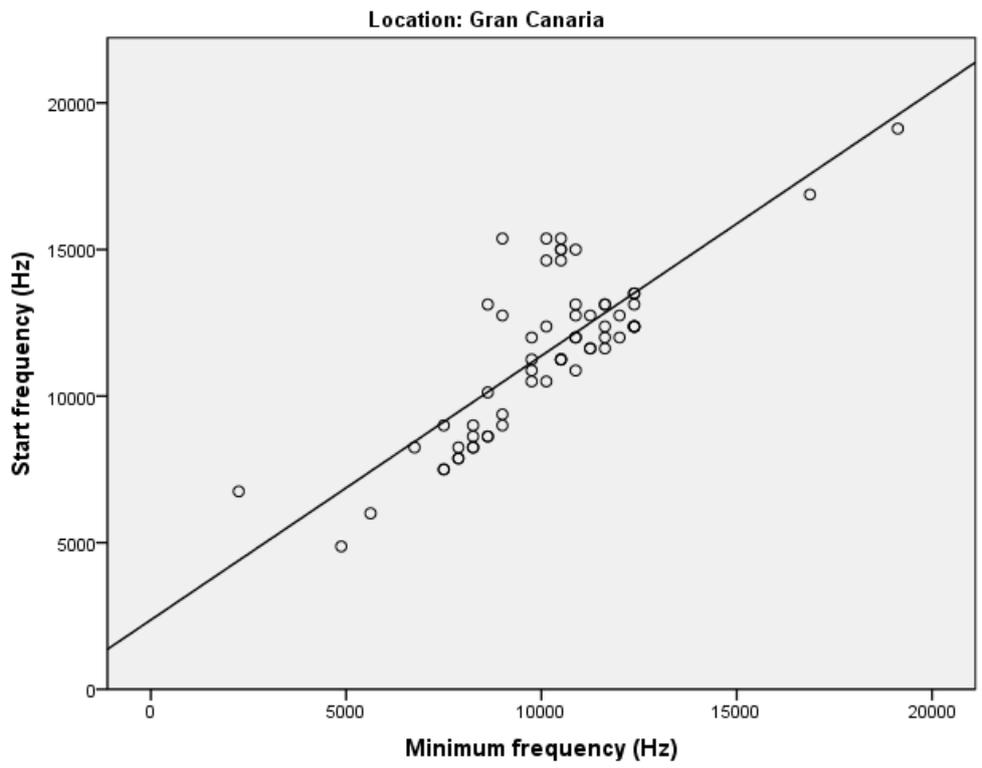
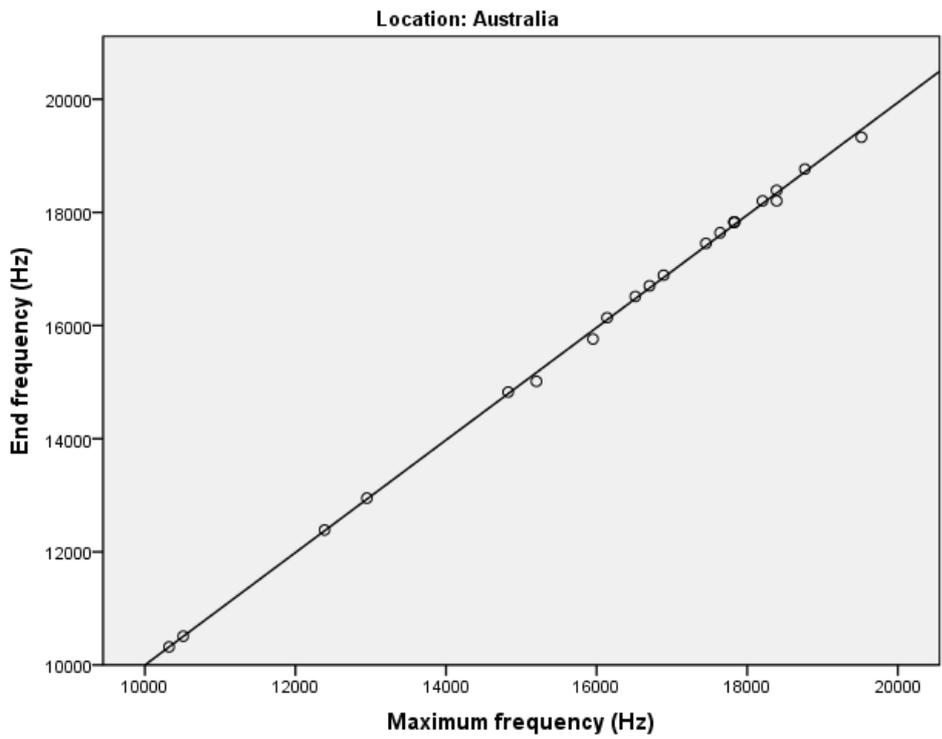
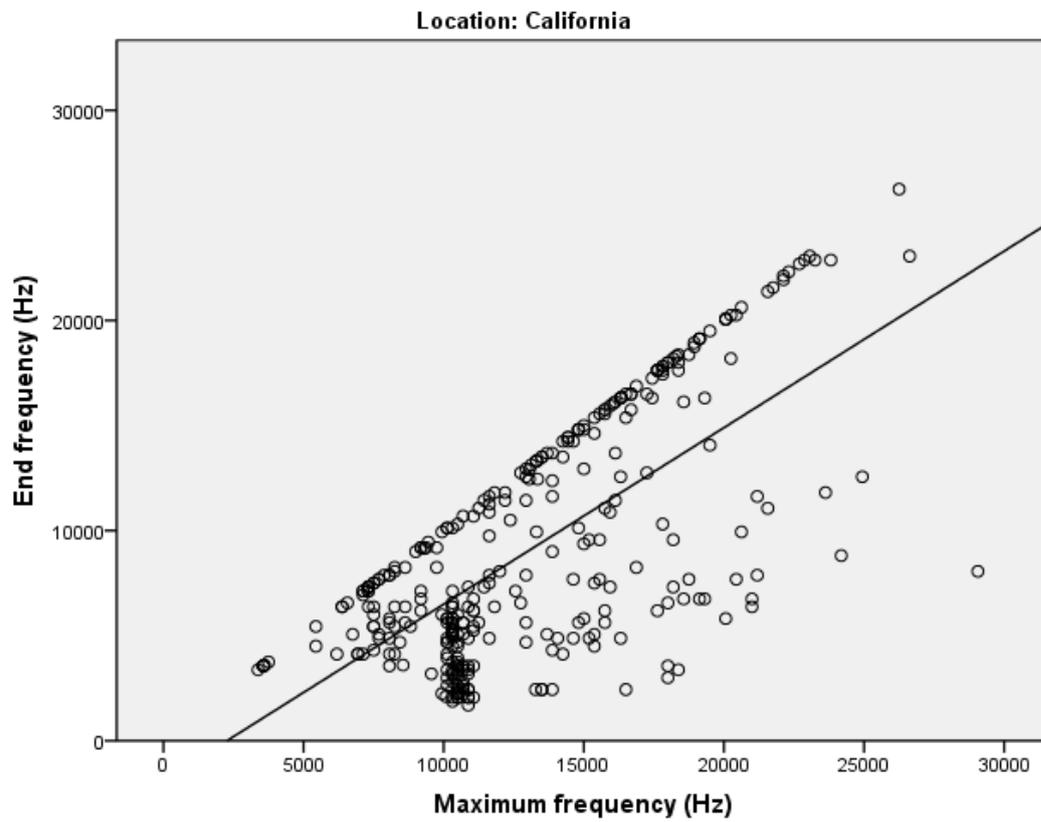
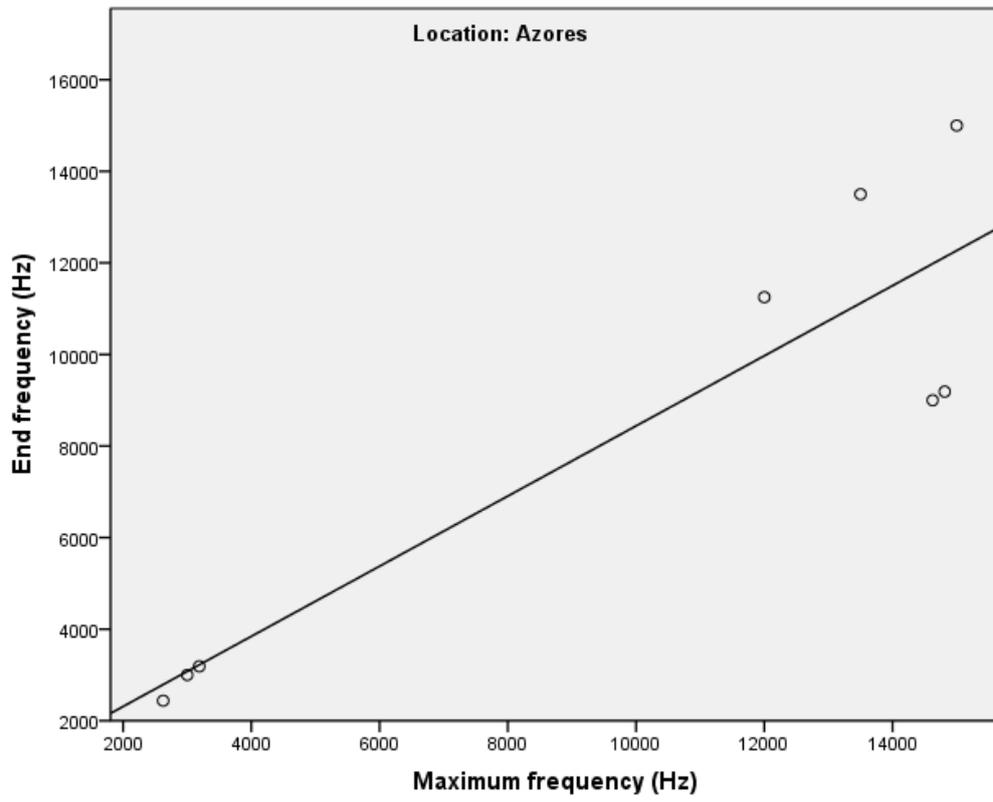


Figure A. 1 – Relationships between start and minimum frequency for each location.





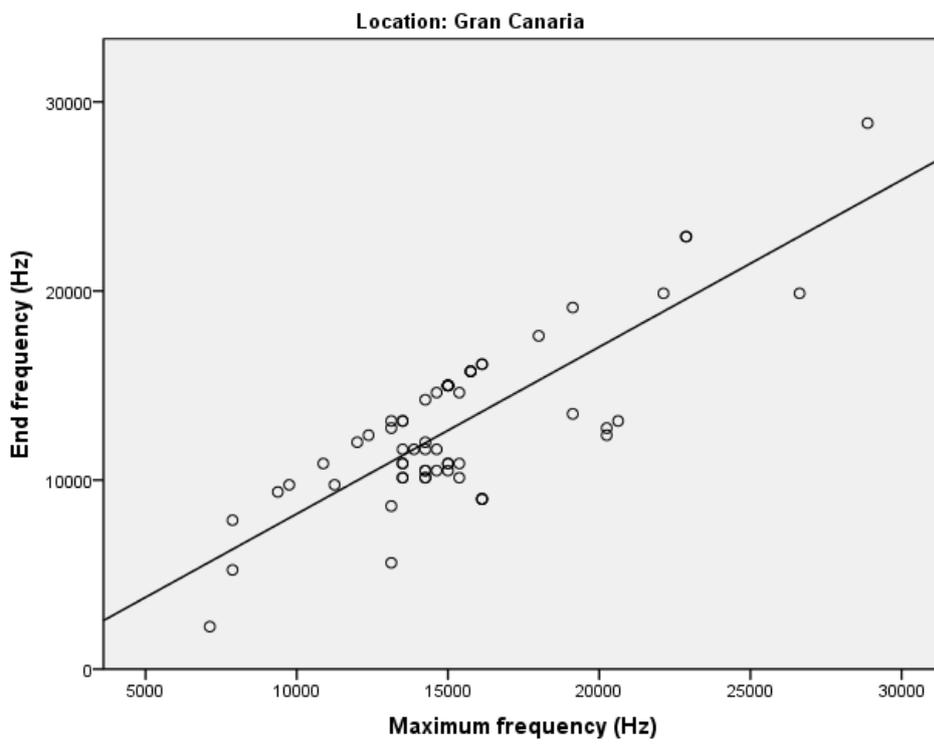
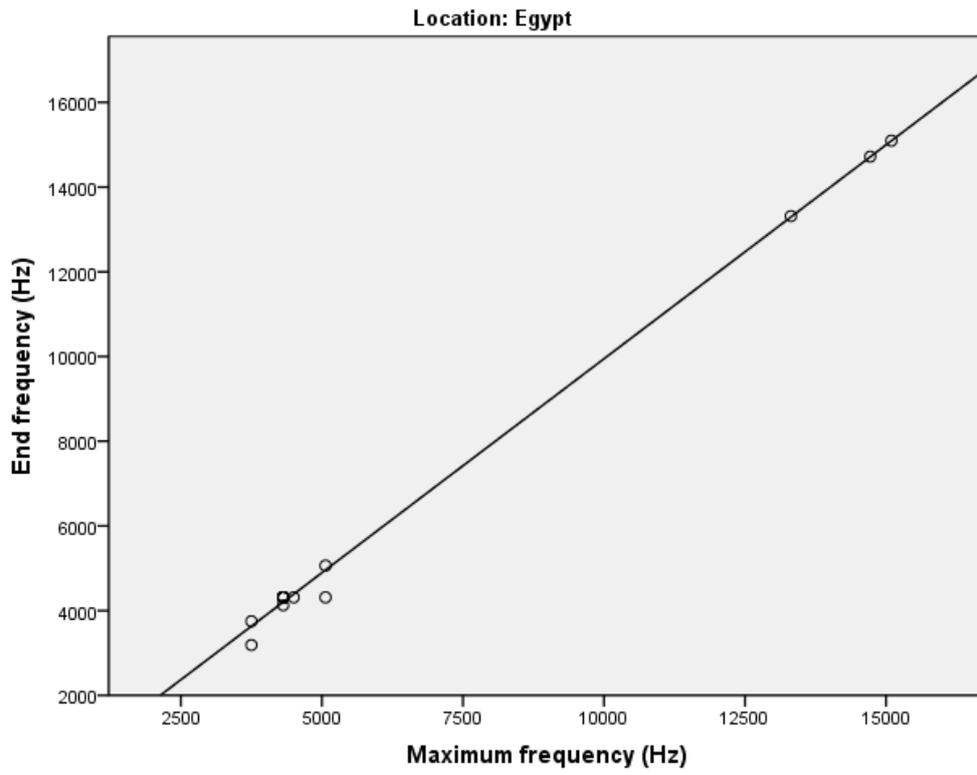


Figure A. 2 – Relationships between end and maximum frequency for each location.