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Acoustic behaviour, ecology and social structure of bottlenose dolphins (*Tursiops truncatus, Montagu 1821*) in the North Atlantic

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A thesis submitted in partial fulfilment of the requirements for the degree of

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Declaration

This thesis is my own work and has not been submitted for another degree at University College Cork or elsewhere.

Signed: Anneli Englund

Anneli Englund (PhD researcher)

Date: 24/12/2013

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General abstract

Communication is important for social and other behavioural interactions in most marine mammal species. The bottlenose dolphin (*Tursiops truncatus*, Montagu, 1821) is a highly social species that use whistles as communication calls to express identity and to initiate and maintain contact between socially interactive individuals. Vocalisation behaviour is likely to be influenced by a suite of ecological and environmental factors such as: rates of social contact between individuals and groups, environmental noise, foraging behaviour and habitat. In this thesis, the degree of variability in whistle behaviour was examined between bottlenose dolphins in different habitats. In addition, whistle characteristics and variability were assessed between different areas and populations at a variety of spatial scales in Irish and US Atlantic waters. The whistle characteristics that best discriminated between areas were investigated, along with vocalisation variation in relation to habitat type, levels of social interaction and relatedness. Variations in whistle rates in relation to group size, behavioural state, group dispersion and the presence of calves was also examined. Finally, the use and variation of individually distinctive calls (signature whistles) within and between Irish and US waters were examined. Relatively high levels of variation were found in vocal characteristics within a genetically and socially isolated population of dolphins in the Shannon Estuary in western Ireland, reflecting the need for individual identification and distinctive whistles in a population with long term site fidelity and high levels of social cohesion. At a larger spatial scale, variation between reproductively separate communities in Irish waters was relatively small, with the main variation found between animals in inshore compared with continental shelf waters. The relatively low levels of vocal variation found between inshore communities in Irish waters may be driven by similarities in habitat characteristics, vocal learning and foraging behaviour or social segregation and may reflect that the genetically distinct populations do not interact, at least not during the breeding season. The greatest differences in whistle structure were evident between dolphins using inshore and offshore US waters, likely reflecting social isolation of the two distinct ecotypes inhabiting these waters as well as differences in genetics and morphology, foraging behaviour and habitat conditions. Variation found among inshore communities in US waters likely reflect similarities in habitat use and levels of social interaction between the communities. Whistle rates in the Shannon Estuary varied between encountered schools in relation to group size and group composition but not with behaviour or in relation to the presence of calves. These findings show that vocal variation is likely to be socially mediated, behaviourally maintained and related to levels of social contact between individuals. The findings contribute to our understanding of the interaction of factors influencing vocalisation behaviour in this behaviourally complex and ecologically plastic species.

Chapter 1

General introduction

Contents

1.1 Overview

The overall aim of this study was to examine bottlenose dolphin whistle structure and variation between geographically separated populations, between different habitat types and between adjacent and sympatric communities. A second aim was to describe the whistle characteristics that best discriminate dolphin communities and to examine how these differences relate to habitat use, levels of social interaction and relatedness. The study included sampling vocalisations of bottlenose dolphins in various coastal and pelagic habitats around the Atlantic coasts of Western Ireland and the coastal and offshore waters of North Carolina in the United States.

1.1.1 Bottlenose dolphins

The common bottlenose dolphin (*Tursiops truncatus,* Montagu, 1821) is a medium sized delphinid with colour variations from grey to charcoal and a lighter pigmentation on the ventral side (Figure 1) (Wells & Scott 1999). The species is distributed throughout north-eastern Atlantic coastal waters with established populations in Cardigan bay (Arnold 1993; Baines et al. 2002; Pesante et al. 2007), the Moray Firth (Lewis & Evans 1993; Wilson *et al*. 1997) and the Hebrides in Scotland (Grellier & Wilson 2003; Hastie *et al*. 2003; Mandleberg 2006; Cheney *et al*. 2013), Brittany and Normandy in France (Liret *et al*. 1995; Kiszka *et al*. 2004), northern Galicia (Fernández *et al*. 2011) and the Sado Estuary in Portugal (Dos Santos & Lacerda 1987; Canadas *et al*. 2005). Bottlenose dolphins are also widely distributed in Irish waters (Ingram *et al*. 2001; Mirimin *et al*. 2011) including a seasonally resident population in the Shannon Estuary (Rogan *et al*. 2000; Ingram & Rogan 2003; Englund *et al*. 2007; Berrow *et al*. 2012). Coastal communities are found along the north, west and south coasts of Ireland (Ingram *et al*. 2001; O'Brien *et al*. 2009), and in some areas populated by communities within which some individuals show high levels of local site fidelity (Ingram *et al*. 2003, 2009).

Photo-identification studies indicate large scale ranging patterns and the presence of a relatively small assemblage of at least partly highly mobile bottlenose dolphins in Irish coastal waters (Ingram & Rogan 2003; O'Brien et al. 2009). This is a similar pattern found in the UK where individual dolphins have been found to move between the Moray Firth and the Inner Hebrides in Scotland and Irish coastal waters (Robinson *et al*., 2013). Bottlenose dolphins found in non-coastal waters of Ireland are believed to be genetically distinct from any coastal communities based on genetic analysis of tissue samples collected from stranded or by-caught dolphins (Mirimin *et al*. 2011). Coastal populations tend to have lower levels of genetic diversity than populations further offshore (e.g. Natoli *et al*. 2004; Quérouil *et al*. 2007) and whilst the origin of animals stranded on Irish coasts remains uncertain, high levels of genetic diversity suggest that they may belong to a larger neritic, continental shelf assembly (Mirimin *et al*. 2011).

Figure 1. Bottlenose dolphins in Connemara waters, showing the species characteristic robust body, dark grey colouring and lighter ventral side.

1.1.2 Taxonomy and distribution

Globally, the taxonomy of bottlenose dolphins (genus, *Tursiops*; family: *Delphinidae*) is still unresolved (Committee on Taxonomy 2012). While a species is generally defined as a group of individuals that interbreed or can potentially interbreed under natural conditions, hybridization may still occur and the species definition questioned. For the bottlenose dolphin physiological and morphological variation within the genus distribution has resulted in a number of species being proposed (e.g. Hoelzel *et al*. 1998) and caused debate concerning phylogeographical and phylogenetic relationships within the genus (Curry & Smith 1997). Globally, only two species are currently recognised (Committee on Taxonomy 2012), the common bottlenose dolphin (*T. truncatus*) which inhabits all temperate and tropical ocean basins (Rice 1998) (Figure 2) and the smaller Indo-Pacific bottlenose dolphin *T. aduncus* (Ehrenberg, 1832), which is restricted to the Indian and western Pacific Oceans (Rice 1998; Wang *et al*. 1999; Wells & Scott 2002).

For *T. truncatus*, two different forms or ecotypes are recognised in the western North Atlantic, types whose distribution broadly corresponds with coastal and non-coastal habitat. These are distinguishable on the basis of morphology and ecological markers (Hersh & Duffield 1990; Mead & Potter 1990), are genetically divergent and may eventually be assigned to different species (Hoelzel *et al*. 1998). The taxonomic status of several other subpopulations of *Tursiops* are questionable and the genus may be split further in the future (Natoli *et al*. 2004). For example, bottlenose dolphins in the Black Sea are morphologically different from Atlantic and Pacific bottlenose dolphins and genetically differentiated from bottlenose dolphins in the Mediterranean and the north-eastern Atlantic and therefore considered a subspecies (Committee on Taxonomy 2012).

In some locations, the two ecotypes of *T. truncatus* are sympatric while in others they are parapatric (e.g. Hansen 1990; Torres *et al*. 2003). They are, for example, considered sympatric and share haplotypes within the Gulf of Mexico, although the offshore form here is not panmictic and shows significant genetic differentiation, indicating reduced gene flow (Segura *et al*. 2006). Offshore animals have a higher genetic diversity than coastal animals (Segura *et al*. 2006). In Irish waters, the existence of morphologically different ecotypes of *T. truncatus* has not been established but non-coastal animals show higher genetic diversity than inshore animals (Mirimin *et al*. 2011).

Populations of bottlenose dolphins in the Pacific Ocean are more genetically divergent from all NW Atlantic inshore ecotype populations than they are from populations of the NW Atlantic offshore ecotype (Tezanos-Pinto et al. 2009), suggesting that these inshore populations have relatively recently diverged. The authors suggested that habitat specialization has occurred independently in different ocean basins, possibly with *T. aduncus* filling the ecological niche of the inshore ecotype in some coastal regions of the Indian and western Pacific Oceans (Tezanos-Pinto *et al*. 2009; Fernández *et al*. 2011), where *T. aduncus* are generally only found in coastal areas (Ross & Cockcroft 1990; Rice 1998; Wang *et al*. 1999; Wells & Scott 2002).

There is evidence of resident and transient groups within most of the *T. truncatus* range, with animals inhabiting bays, estuaries or lagoons generally showing high site fidelity but with seasonal migrations regularly occurring (Mead & Potter 1990; Curry & Smith 1997; Ingram 2000). The NW Atlantic offshore type occurs primarily in waters beyond 34 km from the coast and the coastal type is generally found within 7.5 km of the coast (Torres *et al.* 2003). However, basic information on distribution and ranging patterns of offshore bottlenose dolphins are still mainly lacking (Wells & Rhinehart 1999).

T. truncatus occupies a range of habitats across tropical and temperate regions globally (Figure 2). The species shows a high level of plasticity and is well adapted to different habitats in offshore, pelagic and coastal waters where its range often brings these dolphins into harbours, bays, estuaries, fjords and river systems (Shane & Wells 1986; Hansen 1990; Leatherwood & Reeves 1990; Curry & Smith 1997; Wells & Scott 1999, 2002; Ingram & Rogan 2002; Bearzi et al. 2005) and they range as far north as the Faroe Islands (Bloch & Mikkelsen 2000) and as far South as southern New Zealand (Williams et al. 1993).

Most cetacean species, including bottlenose dolphins are strongly influenced by ecological variables, such as the availability of food and the presence of predators (Reynolds *et al*. 2000) and bottlenose dolphins use a range of feeding tactics, some of which are localised and unique (Smolker et al. 1997; Mann et al. 2008)

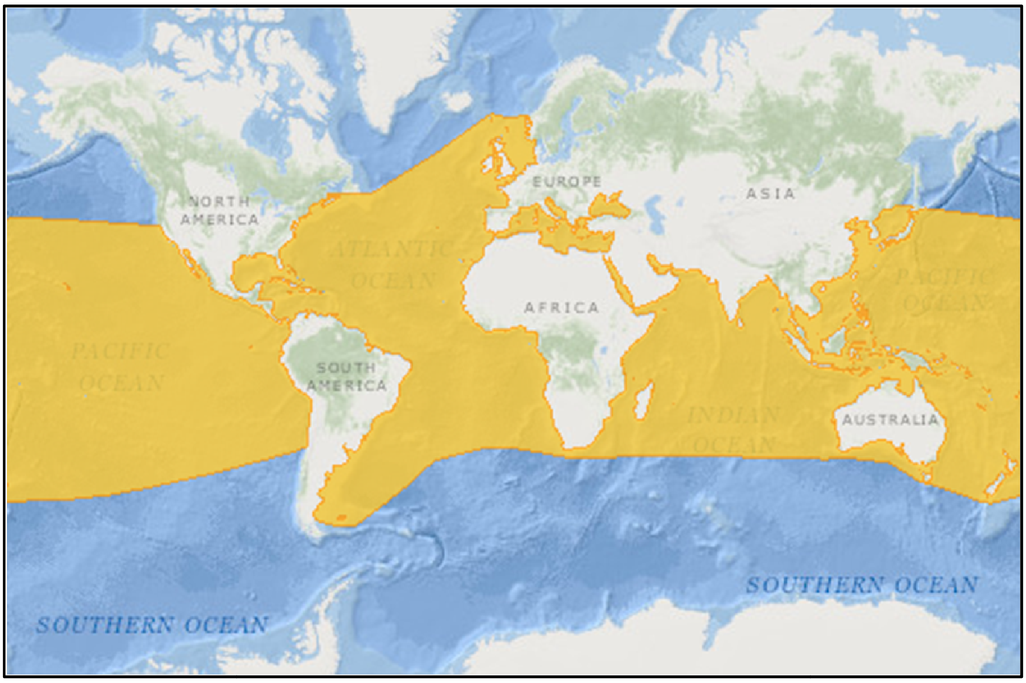

Figure 2. Worldwide distribution of the common bottlenose dolphin (*T. truncatus*), Data for map from IUCN Red List of Threatened Species (www.iucnredlist.org).

Coastal bottlenose dolphins are usually found to live in fission-fusion societies, a social system that is characterised by temporary associations and flexible grouping patterns (Aureli *et al*. 2008). This system is similar to those of terrestrial species such as chimpanzees (*Pan trolodytes*), bonobos (*Pan paniscus*), spider monkeys (genus *Ateles*), some bats and lions (*Panthera leo*).

1.2 Animal sounds and communication

Marine mammals use acoustics for communication, navigation, obstacle avoidance and prey detection (Richardson *et al*., 1995). Odontocetes use sounds actively, such as echolocation, burst pulses, calls and whistles and passively by listening. In such a system, communication is likely to play an important role in social organisation to enable individuals to recognise and find each other when separated over longer or shorter distances. Acoustic signals may be particularly important in the maintenance of group cohesion when visibility is poor or when communication takes place over larger distances. Bottlenose dolphins are more likely to emit individually distinctive calls when isolated which suggests that these are used as contact calls (Caldwell *et al*. 1990; Sayigh *et al*. 1990; Janik & Slater 1998).

In many socially organized vertebrates, the parental care may depend on individual recognition (Thorpe, 1968). In particular for birds that are breeding in dense colonies, the basis for recognition tends to be auditory rather than visual. In the barn swallow (*Hirundo rustica*) and king penguins (*Aptenodytes patagonicus*), the call used by the parent returning with food to the young has the kind of individual differences in acoustic structure on which recognition might be expected to depend and it has been suggested that the young use these calls to distinguish their own parents from others in the colony (Medvin & Beecher 1986; Jouventin et al. 1999)

Elephants (*Lozodonta* spp.) rely on a complex communication system to sustain their clan-based society (Poole *et al*., 1988). Vocal calls are the most common way elephants communicate and they are able to differentiate between the calls of individuals from about 4 km. Such calls are used for a range of purposes, from caring for calves, reconciling differences during disagreements and coordinating the movement of social groups (Langbauer *et al*., 1991).

1.2.1 Variation in animal calls

Geographical variation in acoustic signals occurs in numerous taxa including insects (Simmons *et al*., 2001, Higgins and Waugaman, 2004), frogs (Cockroft and Ryan, 1995), birds (Grant and Grant, 1996, Slabbekoorn and Smith, 2002) and mammals (Peters and Tonkin-Leyhausen, 1999, Bazua-Duran and Au, 2004). This variation is likely driven by a combination of environmental, ecological, biological and cultural factors (May-Collado and Wartzok 2008; Mitani *et al.* 1999; Whitehead 1997). Geographically distinct repertoires have been found between populations of, for example, Weddell seals (*Leptonychotes weddellii*) around the Antarctic continent (Morrice et al. 1994). In long-term social groups, animals may develop behavioural strategies that are based on relationships between group members (Massen & Sterck 2013) and selective pressures may be expected to favour the development of discriminative signals coding for individual or group identity (Sayigh *et al.* 2007; Boughman and Moss 2003; Brown and Farabaugh 1997; Boughman 1997; Boughman 1998). In species living in complex social systems it is sometimes possible to discriminate between individuals, their sex and group using vocal cues. Such individual or group distinctive vocalisations have been found in several social canid species (Tooze *et al*. 1990; East & Hofer 1991; Fromolt *et al*. 1997; Durbin 1998), bats (Boughman 1997; Kazial *et al*. 2008), birds (e.g. Brown & Farabaugh 1997; Wanker *et al.* 1998), cotton-top tamarins (*Saginus oedipus*) (Weiss *et al*. 2001), and seals (Charrier *et al*. 2003). In birds, geographic variation has been partly attributed to genetic differences for populations (Baker and Cunningham, 1985, Catchpole and Slater, 1988) where local dialects may lead to reproductive divergence and speciation.

Acoustic variation may occur on different spatial scales in some dolphin communities and variation in communication calls has been found between geographically separated areas for bottlenose dolphins, spinner dolphins (*Stenella longirostris*), Atlantic spotted dolphins (*Stenella frontalis*) and pilot whales (*Globicephala spp.*) (Wang et al. 1995a; Camargo et al. 2006; Baron et al. 2008), between adjacent populations of bottlenose dolphins (*T. truncatus* and *aduncus*), Tucuxi dolphins (*Sotalia fluviatilis*), estuarine dolphins (*Sotalia guianensis*), common dolphins (*Delphinus delphis*), pilot whales and Atlantic spotted dolphins (Wang et al. 1995a; Bazúa-Durán 2004; Azevedo & Van Sluys 2005; Morisaka et al. 2005; Rossi-Santos & Podos 2006; Ansmann et al. 2007; Baron et al. 2008) and between social units within populations for killer whales (Deecke et al. 2000) or between individuals for *T. truncatus* (Janik et al. 1994) and *T. aduncus* (Gridley et al. 2012). Call repertoires may also be shared by genetically related or socially affiliated groups and result in convergence in calls with similar acoustic properties leading to reduction in individual variability within group and a heightening of group distinctiveness. Such group distinctive calls have been found in greater spear-nosed bats (*Phyllostomus hastatus*), wild chimpanzees (*Pan troglodytes verus*) and orange fronted parakeets (*Aratinga canicularis*) (Boughman 1997; Crockford et al. 2004; Cortopassi & Bradbury 2006).

1.2.2 Cetacean auditory system

The auditory system of cetaceans incorporates special adaptations for underwater life. For example, high frequency sounds (echolocation) are believed to be received through the mandible tissue rather than through the air-filled auditory meatus of terrestrial mammals (Thewissen, 2002). This allows marine mammals to dive to great depths without pressure effects compromising their hearing capabilities (Ridgeway *et al*., 2001). The hearing of cetaceans ranges over a wide span of frequencies, up to 150 kHz with the main hearing sensitivities around 10 to 100 kHz (Au, 1993).

1.3 Vocalisations of cetaceans

Vocal variation between cetacean species tends be related to overall size, with larger species generally using lower frequencies (Richardson et al. 1995; Wang et al. 1995a; Fletcher 2004; Gillooly & Ophir 2010). However, some baleen whales do not follow this general pattern and produce much higher frequency song compared to whales of similar body mass, including humpback whales (*Megaptera novaeangliae*) (Cerchio et al. 2001) and bowhead whales (*Balaena mysticetus*) (Ljungblad et al. 1982; Cummings & Holliday 1987; Tervo et al. 2012).

1.3.1 Odontocete vocalisations

The sounds made by toothed whales (*Odontoceti*) can be divided into two broad categories, including frequency modulated tonal sounds and broadband clicks (Evans, 1967) which also include burst pulse sounds. Whistles and burst pulse sounds appear to be used mainly for communication, whereas broadband clicks are used for echolocation purposes, except in non-whistling species, such as the harbour porpoise (*Phocoena phocoena*) that may also use clicks as a form of communication (Hansen et al. 2008). Some toothed whale species, such as the sperm whale (*Physeter macrocephalus*), have a sound repertoire almost exclusively made up of clicks, but with properties apparently serving the different purposes of communication and echolocation (Madsen *et al*., 2002).

Odontocete whistles are narrowband tonal calls with durations up to a few seconds and fundamental frequencies that can reach 48 kHz for species like *Delphinus delphis, Stenella attenuata, S. coeruloealba, S. longirostris* (Oswald et al. 2004)*, Lagenorhynchus albirostris* (Rasmussen 2002) and *Tursiops* spp. (Boisseau 2005). Recent findings have shown that at least one delphinid species, the killer whale (*Orcinus orca*) emit whistles for which the fundamental frequency is considerably higher than previously assumed and reach the ultrasonic range with the highest whistles reaching frequencies of 75 kHz (Samarra *et al*. 2010). The reason higher frequency whistles have so far gone relatively unnoticed is likely due to the higher absorption of such frequencies and the fact that standard equipment aimed at recording tonal sounds do not normally include such high frequencies.

1.3.2 Variation in odontocete calls

Whistle repertoires of odontocetes vary greatly between different species (Wang et al. 1995b; Rendell et al. 1999), geographically separate populations (Wang et al. 1995a; Camargo et al. 2006; Baron et al. 2008), groups within populations (Janik et al. 1994; Deecke et al. 2000) and between individuals (Smolker et al. 1993; Sayigh et al. 1995, 2007; Tyack 2000).

Graycar (1976) evaluated predominant whistles used by 158 captive Atlantic bottlenose dolphins captured from six different geographic regions off the coast of Florida and found that about half of the whistles were correctly classified to the area of capture, indicating variation which may reflect regional differences.

1.3.3 The role of foraging behaviour in dolphin vocalisations

Foraging specialisation in odontocetes has been shown to affect vocalisation behaviour especially between ecotypes. For example, clear variation in whistle characteristics and use has been shown between sympatric mammal-eating (transient) and fish-eating (resident and offshore) killer whale ecotypes in the north-eastern Pacific (Ford *et al*. 1998; Saulitis *et al*. 2000). Less complex whistles were found for mammal-eating killer whales, which only produced whistles after a kill and during behaviours that did not involve hunting. This suggests that these animals are under strong selection not to alert potential prey (which may have overlapping hearing ranges) by restricting their vocal activity (Barrett-Lennard *et al*. 1996; Deecke *et al*. 2005; Riesch & Deecke 2011).

The risk of alerting prey could also be relevant to variation in bottlenose dolphin populations. However, since bottlenose dolphins generally consume fish and cephalopods, most of their prey does not have critical hearing in the main frequency range of whistles. Thus, adaptations made by dolphins to avoid detection are more likely to be in the use of echolocation or burst pulse sounds. The prey of echolocating bats can respond to the echolocation signals of bats by taking behavioural measures to avoid capture. Some bats therefore hunt without echolocation, using sounds produced by their prey in order to detect and capture them (Ryan *et al.* 1983).

The prey of bottlenose dolphins have traditionally been considered to have relatively poor hearing abilities in the range of dolphin echolocation (Fish and Mowbray 1970). However, sensitivity to some high frequencies and click-like signals has been demonstrated in several fish species (Mann & Popper 1997; Mann *et al*. 1998; Wilson & Dill 2002). Fish have been shown to respond to simulated odontocete echolocation sounds (Wilson & Dill 2002) and dolphins may therefore adapt their use of these sounds accordingly (Nowacek 2005).

Acoustic variation has been related to morphological characteristics in bats (Boughman 1997) and cetaceans (Rendell *et al*. 1999; Gridley 2010). Research investigating the relationships between vocal variation and morphology within dolphin species has so far been restricted to marine and riverine types of tucuxi dolphins (*Sotalia fluviatilis*) (Azevedo & Simão 2002; Azevedo & Van Sluys 2005; Pivari & Rosso 2005), killer whales ecotypes (Foote & Nystuen 2008; Rehn *et al*. 2011; Riesch & Deecke 2011) and offshore/inshore types of bottlenose dolphins (Azevedo *et al*. 2007; Papale 2012).

1.3.4 Individually distinctive calls

Early work on dolphin whistles suggested that highly stereotyped and individualised signals (Figure 3) were used for individual recognition (Caldwell & Caldwell 1965) helping animals to maintain group cohesion and keep in contact over larger distances (Janik & Slater 1998). Dreher (1961) highlighted the dolphins' whistle contours as an important mechanism in this function (Dreher, 1961). Caldwell and Caldwell (1965) recorded whistles from isolated bottlenose dolphins in captivity and found that each dolphin appeared to produce one particular contour that was unique to that dolphin and introduced the term "signature whistle" (Figure 3), suggesting that these whistles were used to convey identity information (Caldwell & Caldwell 1965; Caldwell *et al*. 1990; Janik *et al*. 2006) (Caldwell and Caldwell, 1965, Caldwell *et al*., 1990).

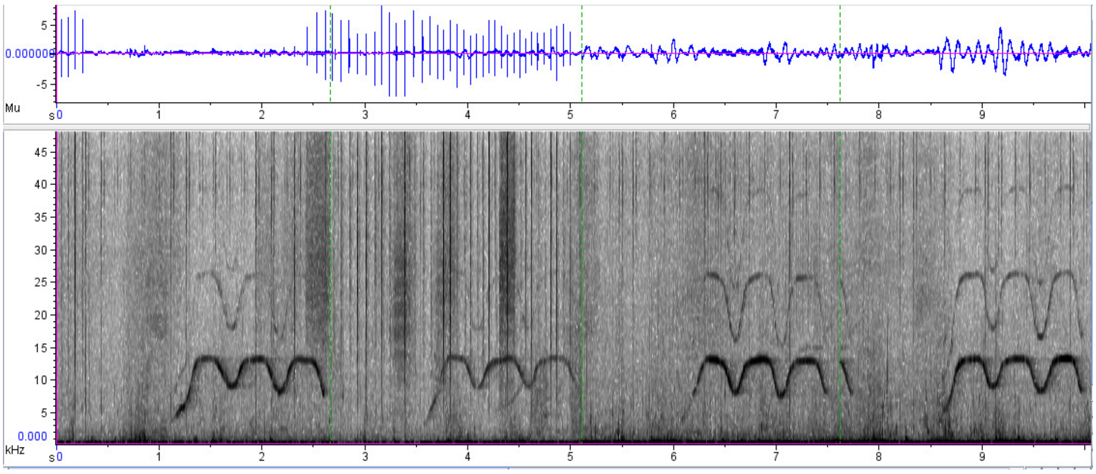

Figure 3. Spectrogram of bottlenose dolphin whistle, showing repetitions of a highly stereotyped whistle. Time is displayed on the x-axis and frequency on the y-axis.

Data collected to date on the ontogeny of whistles, the whistle repertoire and whistle matching suggest that signature whistle contours are learned (Caldwell and Caldwell, 1979, Caldwell *et al.*, 1990, Fripp *et al.*, 2005, Janik, 2000b, Mikisis *et al.*, 2002, McCowan and Reiss, 1995a, McCowan and Reiss, 1995b, Sayigh *et al.*, 1990, Sayigh *et al.*, 1995, Smolker and Pepper, 1999, Tyack, 1986, Watwood *et al.*, 2004). Newborn bottlenose dolphin calves produce a unique contour by the end of their first year (McCowan & Reiss 1995; Tyack & Sayigh 1997) and frequency modulation increases with age. The predominant whistle contours of adults tend to be more complex and often include multi-looped whistles (Caldwell and Caldwell, 1979). Loops are repetitive elements in whistles for which the first (introductory) and/or the last (terminal) loop may vary. Signature whistles generally remain stable over several years, in captivity as well as in the wild (Sayigh *et al.*, 1990, Watwood *et al.*, 2005). Adult male bottlenose dolphins (*T. aduncus*) in some populations form stable long-term bonds or dyads (Smolker and Pepper, 1999, Wells, 1991) for which the rates of association are high and the animals are seen together on most occasions (Owen *et al.*, 2002). The predominant whistle contours of such male partners are more similar than between animals that are not as strongly associated (Watwood *et al.*, 2004).

Since the early work where research was limited to isolated captive bottlenose dolphins, a number of studies have recognised signature whistles in other circumstances, including free-swimming captive dolphins (Tyack, 1986, Janik and Slater, 1998), temporarily restrained wild dolphins (Sayigh *et al*., 1990, Watwood *et al*., 2005) as well as free-ranging wild dolphins (Cook *et al*., 2004b, Watwood *et al*., 2004, Watwood *et al*., 2005). Janik *et al*. (2006) experimentally verified that signature whistles are used to maintain group cohesion and that the dolphins respond to signature whistles produced by familiar conspecifics even after voice features had been removed; thus supporting Caldwells' hypothesis that it is the contour of a signature whistle that carries information about the identity of the caller.

The signature whistle hypothesis has been widely debated (McCowan & Reiss 1995, 2001) although most studies have shown that individualised whistle contours are commonly emitted when dolphins are isolated and that signature whistles are more commonly produced when dolphins are outside of visual contact with each other than when they are together (Janik and Slater, 1998, Cook *et al*., 2004a, Smolker *et al*., 1993, Janik *et al*., 1994). Other species of dolphins appear to have whistles that may function similarly to those of *T. truncatus* signature whistles, including *T. aduncus* (Gridley et al. 2012) *delphinus delphis* (Caldwell & Caldwell 1968; Ansmann et al. 2007), *Stenella frontalis* (Caldwell et al. 1973; Herzing 1996) *Lagenorhynchus obliquidens* (Caldwell et al. 1973; Duarte de Figueiredo & Simão 2009) and *Sousa chinensis* (Van Parijs 2001).

1.4 Recording equipment and methods

Recordings of whistles are often made using single element hydrophones, a technique which accurately records sounds within the sensitivity of the system but which does not enable localisation of the source, unless surface reflection is used (Cato, 1998). Hydrophone arrays on the other hand enable some localisation of the origin of the sound recorded, but with left-right side ambiguity (Miller and Tyack, 1998, Watwood *et al*., 2005) unless a distributed array is used, which then provides greater means for localisation. So far, accurate estimates of range are only obtainable to approximately 10 times the dimensions of such an array, but addition of a depth function increases the accuracy of localisation measurement (Quick *et al*. 2008).

1.5 Whistle contour classification

Categorisation of dolphin whistles is an important part of whistle analysis in order to describe and measure characteristics and variation in an unambiguous way and to enable suitable statistical analysis and evaluation. This requires multiple decisions by the researcher, and where human judges are used to classify contours into categories, detailed instructions are required in order to increase the objectivity and repeatability of the analyses. Computer programmes on the other hand may not perform as well as human observers (Janik 1999).

In earlier studies, descriptive names assigned to different whistle types were commonly used. For example, a whistle that begins at a low frequency and increases continually until ending on a higher frequency is normally referred to as an “upsweep” (Lilly, 1963, Caldwell *et al.*, 1990, Janik *et al.*, 1994). Although this presents an easily understandable way to describe whistles that are common in a population, this qualitative method is open to a large degree of ambiguity, subjectivity and clear guidelines are needed to ensure comparability and the broad whistle categories normally used are limited in the resolution needed to describe a complex whistle repertoire.

Janik (1999) compared four methods for categorising dolphin whistles, one including human classifiers and three using quantitative computer analyses. He found that humans were superior at classifying whistles into categories by whistler and context, using a gestalt sense of the overall contour shape, while the computer methods focused on a variety of individual features that to a larger degree led to categories other than by whistling animal. Another study by Deecke and Janik (2006) showed how a neural network can be used to categorise whistles resulting in categorisation by individual whistles by whistler in over 90% of the cases and thus comparable to human classification (Deecke & Janik 2006).

1.6 Study areas

For the purposes of this study, sampling took place on both sides of the Atlantic Ocean, in Irish estuarine, coastal and continental shelf waters and eastern US estuarine, coastal and offshore waters.

1.6.1 Ireland

Bottlenose dolphins are relatively common in Irish waters where a number of putative populations of are recognised (Ingram *et al*. 2001; Mirimin *et al*. 2011) including a semi-resident population in the Shannon Estuary (Rogan *et al*. 2000; Ingram & Rogan 2003; Englund *et al*. 2007; Berrow *et al*. 2012), a critical habitat for this species (Ingram & Rogan 2002) and a candidate Special Area of Conservation (cSAC) under the European Habitats Directive. The Shannon population has been studied since the mid 1990's (Berrow *et al*. 1996; Ingram 2000; Rogan *et al*. 2000). Research has shown that dolphins are present in the estuary all year around, show seasonal residency and a peak in occurrence in the summer months (Ingram 2000), when most calves are born, and numbers of animals using the estuary decreases during the winter (Rogan *et al*. 2000; Ingram & Rogan 2002). There are few records of Shannon dolphins outside of the estuary and they have never been recorded further away than about 15km from the mouth of the estuary (Ingram *et al*. 2001; O'Brien *et al*. 2009).

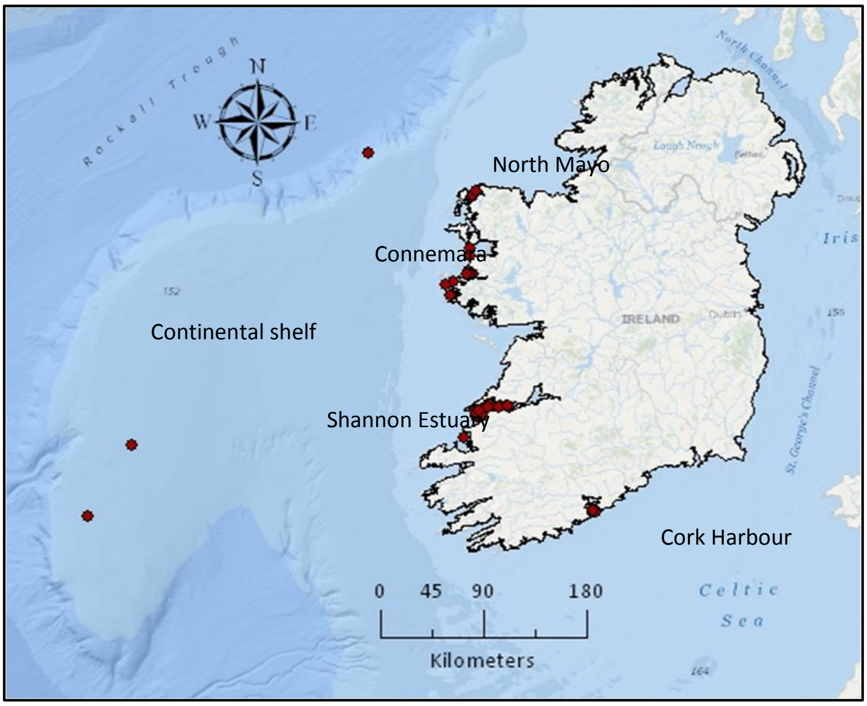

Figure 4. Map of Ireland indicating encounter locations in estuarine (Shannon and Cork Harbour), coastal (North Mayo and Connemara) and continental shelf waters.

There are also far ranging coastal communities of bottlenose dolphins in Irish waters (Ingram *et al*. 2001; O'Brien *et al*. 2009), some of which show inter annual site fidelity (Ingram *et al*. 2003, 2009). The SCANS II survey (Hammond *et al*. in press) reported an abundance estimate for bottlenose dolphins in coastal waters of Ireland of 313 individuals (CV=0.81). Re-sighting rates and large scale ranging patterns found by O'Brien *et al* (2009) and Ingram and Rogan (2003) support the presence of a relatively small assemblage of highly mobile bottlenose dolphins in Irish coastal waters. While few estimates of abundance of these coastal communities have been calculated, the waters of Connemara are estimated to harbour at least 171 (CV=0.28, 95% CI = 100-294) dolphins (Ingram *et al*. 2009), exceeding all previous estimates of the Shannon population (Ingram 2000; Ingram & Rogan 2003; Englund *et al*. 2007, 2008; Berrow *et al*. 2012). However, none of the coastal populations studied here include population sizes anywhere near that of animals living further from the coast where a third, genetically distinct community of bottlenose dolphins have been indicated from strandings data. While the origin of stranded animals remains uncertain, high levels of genetic diversity suggest that they may belong to a larger continental shelf assembly (Mirimin *et al*. 2011). It has been suggested that coastal populations tend to have lower levels of genetic diversity than populations further away from the coast (e.g. Natoli *et al*. 2004; Quérouil *et al*. 2007). Analysis of stomach contents and stable isotope ratios in stranded animals however also indicate that bottlenose dolphins of this third population use continental shelf waters as well as relatively shallow coastal waters but still feed on other prey than inshore communities (Hernandez-Milan, pers. comm.). While estimates for coastal regions are low, offshore surveys have estimated around 7,500 bottlenose dolphins (95% CI: 2,900 - 11,100) in Irish waters north of 53 degrees latitude at depths greater than 200 meters (CODA 2009).

The Shannon Estuary population of bottlenose dolphins is genetically distinct from other coastal as well as from putative continental shelf groups, except for a small group in Cork harbour (n = 8) for which ongoing gene flow or recent dispersal from the Shannon to Cork Harbour has been indicated (Mirimin *et al*. 2011).

1.6.2 North Carolina, U.S.A.

Bottlenose dolphins (*T. truncatus*) occur all along the eastern coast of the United States, in bays, sounds and estuaries as well as in coastal, continental shelf and offshore waters. They range from New York to southern Florida and migrate to southern coastal or more offshore regions during winter months (Rosel *et al*. 2009; Toth *et al*. 2012). One region where the species is common is around Beaufort Inlet in North Carolina, USA which links coastal waters to a complex estuarine system, separated from the continental shelf of the Atlantic Ocean by barrier islands that include Cape Lookout (Figure 5). The Newport River connects with the Neuse River, via Core Creek to the north, where a canal was opened in 1964 allowing contact between Beaufort estuary and Pamlico Sound. Pamlico Sound is a large estuary separated from the Atlantic Ocean by the Outer Banks which are a row of low, sandy barrier islands, including Cape Hatteras.

Photo-identification and telemetry studies have indicated the existence of a northern and a southern grouping (referred to as “stock” for management purposes) of bottlenose dolphins in North Carolina estuarine waters (Read *et al.* 2003) with the population boundary situated at Beaufort Inlet. While animal movements have been reported between the estuaries and adjacent coastal waters (Urian *et al.* 1999), estuarine animals are genetically distinct from migratory animals found in coastal waters (Rosel *et al*. 2009). The Southern North Carolina Estuarine System dolphins include animals occupying estuarine and nearshore coastal waters of North Carolina and South Carolina that do not undertake any large scale migratory movements, but likely overlap with the Northern North Carolina Estuarine System dolphins in the northern portion of their range during late summer and with migratory groups in coastal waters (NMFS 2010) during late Autumn until spring. Northern North Carolina Estuarine System harbours animals that occupy estuarine waters of Pamlico Sound during the summer months and show variation in seasonal ranging patterns (Read *et al.* 2003*)*, genetics (Rosel *et al.* 2009; Caldwell 2001) and stable isotope signatures (Cortese 2000) when compared with more southern estuarine groups.

Offshore bottlenose dolphins are primarily distributed along the outer continental shelf and continental slope with a separation of the inshore and offshore ecotypes across the bathymetry during summer months (NMFS 2008). During winter months, the range of inshore and offshore groups overlaps spatially (Torres *et al.* 2003) south of Cape Hatteras.

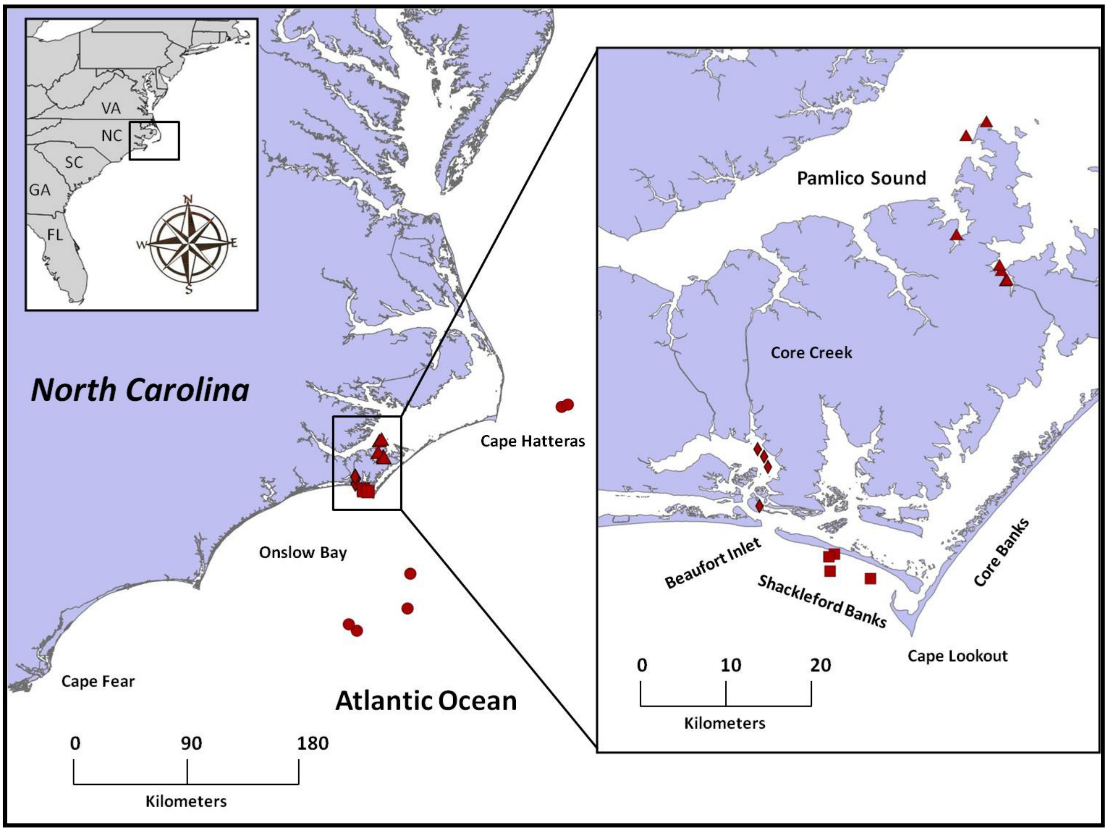

Figure 5. Study area in North Carolina, indicating coastal, estuarine and offshore areas surveyed. Symbols indicate encounter locations, in Beaufort coastal (□) and estuarine waters (◊), Pamlico Sound (Δ) and offshore areas (○).

1.7 Study objectives

For management and conservation of a species to be successful, it is important to determine population boundaries, levels of genetic or social isolation and to understand distribution and ranging patterns and levels of social interaction between and within the communities.

This study used bioacoustics of the common bottlenose dolphin (*Tursiops truncatus,* Montagu, 1821) to investigate aspects of this species' acoustic behaviour in relation to its ecology, relatedness and biogeography. The main focus was on acoustic differentiation through the examination of whistle characteristics, describing variation on different spatial scales. The research chapters included here (Chapter 2-5) detail investigations on a range of scales, starting with the whistle characteristics and acoustic behaviour of a resident population of bottlenose dolphins in the Shannon Estuary (Chapter 2), while exploring variation across social units, behavioural states and group compositions. Whistle differentiation of groups of bottlenose dolphins with a high level of coastal site fidelity along the Irish West coast was then examined and compared with whistles from animals encountered in continental shelf waters (Chapter 3) and communities across the Atlantic Ocean in eastern US waters. Dolphins in US waters (Chapter 3 and 4) were further investigated in more detail (Chapter 4), investigating whistle variability between inshore communities as well as between offshore and inshore ecotypes present in these waters. Finally, the use of individually distinctive calls or signature whistles was examined for both US and Irish waters (Chapter 5) and the thesis concludes with a discussion (Chapter 6) of this research placing it in a larger perspective and providing a discussion of implications, limitations and suggestions for further study.

Each chapter in this thesis was written in a manuscript-style format, appropriate to be published in a peer reviewed scientific journal. All chapters are being prepared for submission to scientific journals and therefore are classified as “in preparation” and while each chapter constitutes a complete study and can be read independently of the others, references to other chapters are included here. Tables and figures appear in the text inside each chapter.

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Chapter 2

Whistle repertoire and acoustic behaviour of a resident population of bottlenose dolphins on the west coast of Ireland

Contents

Abstract

This study examines the use of whistles by a seasonally resident population of bottlenose dolphins (*Tursiops truncatus*, Montagu 1821) in the Shannon Estuary, on the west coast of Ireland. Long term study, including photo identification provides valuable background information against which to assess acoustic variability within this community. In total, 42 hours of boat based survey time and recordings made during 30 encounters resulted in 1,441 whistles logged while in the vicinity of dolphin groups. Whistle rates were examined in relation to behaviour, group size, group composition and level of group dispersion and the complexity of the whistle repertoire was evaluated for the community as a whole and in relation to levels of individual overlap between encountered groups. Overall mean whistle rate was 0.13 (SD±0.19) whistles per minute per dolphin but varied between encounters and in relation to group size (generally increasing with larger group size), group composition (lower rates for tight groups) and also with behaviour (highest rate found for milling and lowest for travelling). Upsweeps were the most observed general contour type recorded and comprised 32.2% of the whistle repertoire, closely followed by convex (27.9%), modulated (19.6%), down-sweep (11.1%), constant frequency (6.7%) and concave (2.4%) contours. The variation found for whistle type use is likely reflecting complex drivers for their use and abundance, but also variation in classification methods of different studies and the varied definitions used in whistle type categorisation. Identification of distinct whistle types (using a neural network approach) showed significant positive correlation between numbers of new individuals and numbers of distinct whistle types. The Shannon population produced a whistle repertoire reflecting the extensive individual mixing evident within this population and characteristic of the fission-fusion society structure of bottlenose dolphins in this region.

2.1 Introduction

The use of sound is important for marine mammals in most aspects of life and in particular for communication, navigation and foraging. Echolocation enables toothed whales to perceive their surroundings and to locate prey even when visibility is poor, while whistles and burst pulse calls provide means of reliable and efficient communication between conspecifics. Acoustic signals are particularly useful for long range communication in water since they propagate faster and attenuate less than in air (Gordon & Tyack 2001). The detection range of common bottlenose dolphin (*Tursiops truncatus*, Montagu 1821) whistles is approximately 750 meters with a maximum communication range of up to 5740 meters (Jensen et al. 2012). Bottlenose dolphin whistles are considered learned signals that are used in the maintenance of group cohesion (Janik & Slater 1998) and individual identification (Janik *et al*. 2006). and may help facilitate important activities such as collaborative feeding, resource defence, breeding and nursing (Norris & Schilt 1988; Gowans et al. 2007).

Since the function of whistles is believed to be primarily social and communicative, some variation would be expected in relation to behavioural context (e.g. Hernandez *et al.* 2010). Some studies have shown that the rate of whistling increases during feeding activities, resulting in other dolphins joining the feeding group (Würsig 1979). Additionally, particular types of calls (e.g. bray calls) have also been associated with feeding behaviour (Janik 2000) and may serve a similar function. While it is not known if this effect results from unintentional advertisement through feeding sounds being overheard by other dolphins (Acevedo-Gutiérrez & Stienessen 2004), dolphins engaged in cooperative feeding may benefit by intentionally attracting other individuals to help in herding of prey and in the defence against potential predators (Acevedo-Gutiérrez & Stienessen 2004). Socialising dolphins tend to increase the rate of whistling while the rate for travelling dolphins is generally reduced (Jacobs *et al*. 1993; Cook *et al*. 2004).

2.1.1 Bottlenose dolphins in Irish waters

The Shannon estuary is situated on the west coast of Ireland (Figure 1) and harbours a seasonally resident population of bottlenose dolphins (Ingram & Rogan 2002). This is one of three known resident populations of this species in the waters of Britain and Ireland with the two others found in Cardigan Bay (Wales), and the Moray Firth (Scotland). The Shannon population has been studied since 1996 (Berrow *et al*. 1996; Ingram 2000; Rogan *et al*. 2000), but records of this species in the Shannon date back as far as 1835 (Knott 1835). The population has been estimated to number between 107 and 140 individuals (Ingram 2000; Ingram *et al*. 2003; Englund *et al*. 2007; Berrow *et al*. 2012) and is considered stable. The available data set gathered over the years now provides a considerable amount of information relating to community structure, detailed history of individual ranging patterns, population trends and information on shared school membership, gender, genetic relationships and social structure.

Although infrequent records of harbour porpoise (*Phocoena phocoena*), and larger baleen whale species such as minke whales (*Balaenoptera acutostrata*) and fin whales (*Balaenoptera physalus*) occur seasonally at the seaward end of the estuary, in particular around Loop Head (www.iwdg.ie), bottlenose dolphins are the only cetacean species resident in the Shannon and the estuary represents the only designated special area of conservation for this species to date in Irish waters.

While bottlenose dolphins are regularly encountered in coastal waters outside of the Shannon, including numerous sightings made along the south, north and west coasts (Ingram *et al*. 2001; Ingram & Rogan 2003; O'Brien *et al*. 2009; Oudejans *et al*. 2010), the Shannon population is genetically distinct from other coastal groups and exhibits low genetic diversity (Mirimin *et al*. 2011). Evidence exist of long range movements for coastal groups and of some levels of site fidelity at other coastal sites (Ingram & Rogan 2002; Ingram *et al*. 2003; O'Brien 2009; O'Brien *et al*. 2009; Robinson *et al*. 2012). Whilst no social interaction has yet been found between the Shannon population and any of the coastal communities (Ingram *et al*. 2003; O'Brien *et al*. 2009), recent genetic work showed that a small group in Cork Harbour (8 animals) and the population in Shannon are genetically similar which likely indicates a recent dispersal event of animals from the Shannon Estuary to Cork Harbour (Mirimin *et al*. 2011).

2.1.2 Study objectives

Although the bottlenose dolphins in the Shannon Estuary have been studied for an extensive period of time, relatively little information exists surrounding the vocal behaviour of this population and of any coupling between their vocalisation rates and social/behavioural factors. This study had two principal objectives; 1) to investigate the relationship between vocal patterns and surface behaviour, group size, group composition and group dispersion and 2) to investigate the complexity of the whistle repertoire of this community.

2.2 Methods

2.2.1 Field sampling

Data were collected during vessel based surveys using a 6m RIB (Rigid hull Inflatable Boat). The Shannon Estuary is the largest estuary in Ireland. It is a busy industrial area with shipping traffic leading into the Port of Limerick as well as smaller local fishing activities and dolphin watching tourism (Berrow & Holmes 1999) taking place in the outer estuary, which is home to a seasonally resident population of bottlenose dolphins. The Shannon is the only designated Special Area of Conservation for this species in Irish waters. Survey work took place in the outer estuary, following a route set up in previous studies (Figure 1a) (e.g. Ingram 2000). Dolphin vocalisations were recorded during all encounters with dolphins, while photographs were taken for identification purposes and when stopped with engine turned off in the vicinity of dolphin groups to collect higher quality recordings. Recordings ceased when dolphins were lost or when all individuals had been photographed. For a more comprehensive description of the standardised photo-identification methods used, see Ingram (2000). All individuals observed were considered part of the group for the duration of an encounter. This approach may have introduced bias by the inclusion of vocalisations by animals outside of visual range (depending on the range of which dolphins could be reliably sighted and heard). To minimise this risk, surveys were only conducted in very good sea and weather conditions (sea state ≤3) and it was therefore assumed that any animals within 750 meters which is the estimated range within which bottlenose dolphin whistles are assumed to be reliably detected (Jensen et al. 2012) were also observed visually.

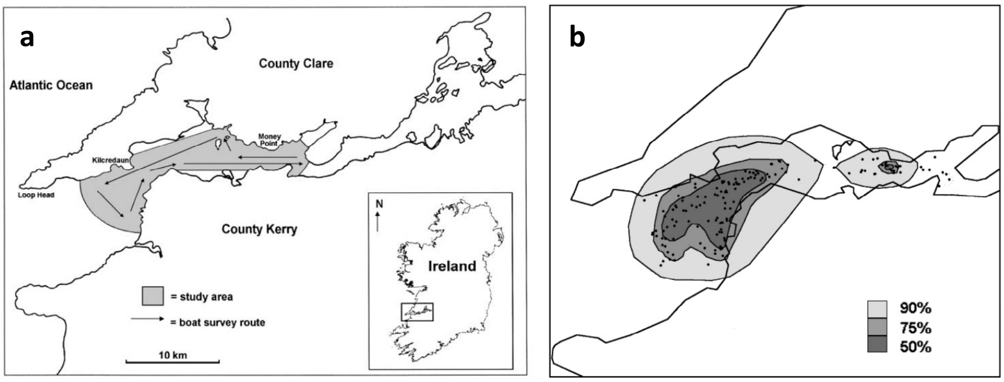

Figure 1. Survey area in the Shannon Estuary, indicating the survey route within the estuary (a) and the outer and inner core areas (b) used by the dolphins (Ingram & Rogan 2002).

Behavioural sampling included documenting the main behavioural state of the group at the onset of each encounter. This was achieved by scanning all individuals of the group for one minute at the onset of the encounter (noting the behaviour of each individual when visible) in order to identify the predominant behaviour (50% group participation). Behavioural states included travelling (directional movement), socialising (physical contact, often including surface events like leaps), milling (non directional movements and dives in one general location, most likely associated with foraging), feeding (events such as fish chase or fish kill observed) and resting (very slow movement or drifting, synchronised breathing) (e.g. Ballance 1992). Any changes in behaviour during the encounter were also noted on an *ad libitum* basis as well as instances of bow-riding, breaching, tail-slapping or other events of a more instantaneous nature. Additionally, group dispersion, categorised as tight (<2 body lengths apart), loose (>2 body lengths apart) or in subgroups (presence of tight groups that were separated by at least 100 meters), group composition, which included number of adults, juveniles and calves and estimated group size (minimum, maximum and best estimate) were also documented.

Acoustic recordings were made using a single channel hydrophone (High Tech, Inc, Gulfport, MS. Model HTI-96-MIN) with a flat frequency response of 5 Hz to 30 kHz ±

1.0 dB, -164.5 dB, *re* 1V/µPa connected to an Edirol digital solid state recorder (R-09-HR). While the upper frequency limit of the recorder was 48 kHz (96 kHz sampling rate) the limit of the system was determined by the 30 kHz upper limit of the hydrophone.

2.2.2 Contour extraction

Sound recordings were analysed using the spectrogram view in RAVEN PRO 1.4 beta version, build 34 (2003-2010, Cornell Lab of Ornithology, Bioacoustics Research Program). Whistles were identified, selected and single whistle files created using the selection table function in RAVEN PRO. While only contours of high quality whistles were extracted (i.e. those that were easily detected aurally and by visual inspection of the spectrogram with minimal interference from noise or overlapping whistles), the occurrence of all whistles was logged for use in whistle rate analysis. Overlap with other whistles was only accepted if whistle contours could be reliably distinguished without any ambiguity. Whistles were considered separate units if separated by a gap of more than 250ms or the difference in frequency was more than 3 kHz (Janik & Slater 1998; Esch et al. 2009).

A spectrogram of each whistle was produced using a Fast Fourier Transform (frame length of 512, 87.5% overlap between frames and a Hanning window) and reproduced using MATLAB, version 7.8.0 (R2009a Student version) and a custom written script “BELUGA” (Deecke and Janik, SMRU, St Andrews). BELUGA is an automated contour extraction program that allows filtering of the signal and facilitates semi-automated contour extraction using a peak-finding algorithm. The resulting traced contour for each whistle was saved in a text file as a list of frequencies with known time and frequency resolution (0.667 ms and 23.438 Hz) and supplied with a unique identifying number so that each whistle contour could be traced throughout the analysis procedure.

The contour files created were opened individually in MATLAB after which the numeric record of every frequency point was exported in batch into MS Excel using another MATLAB script (ctr2excel.m created by Cormac Doherty, University College Dublin) for further analysis and storage in an MS Access database.

2.2.3 Whistle rate analysis

The total number of whistles recorded within each encounter was divided by the recording time and an estimate of group size (based on photo-identification and best estimates in the field) in order to provide a measure of whistle density or whistle rate (whistles per dolphin per minute). Information from visual sightings data included total number of animals, behaviour, presence and number of calves, start and end position (Irish Grid Coordinates) and depth. Spearman's rank correlation test was used to investigate the relationship between whistle rate vs. group size) while a Kruskal-Wallis test was used to investigate the relationship between whistle rate and behavioural context. Chi-squared tests were used to investigate the relationship between whistle occurrence (presence or absence of whistles) in recordings in relation to group dispersion and of whistle rate in relation to presence or absence of calves within the group.

2.2.4 Whistle classification

Whistle contours were classified and the level of complexity within the Shannon community investigated using the proportion of major whistle types, estimated using categories traditionally employed in whistle comparison studies (e.g. Ansmann *et al*. 2007; Bazúa-Durán and Au 2002). Each whistle contour was ascribed to one of these categories, each determined with strict definitions to ensure objectivity and to enable replication. The broad categories created were primarily based on the overall shape of the contour using the presence or absence of inflection points (determined by the use of peakdet.m function in MATLAB and defined as a change in slope direction from positive to negative or negative to positive of at least one kHz). Categories included (for examples, see Appendix II): constant frequency (frequency along the entire contour within 1 kHz, no inflection points), upsweep (start frequency lower than end frequency, no inflection points), down-sweep (end frequency lower than start frequency, no inflection points), convex (one inflection point, at a higher frequency than both start and end frequency), concave (one inflection point, at a lower frequency than both start and end point) and modulated (more than one inflection point). Assigning contours to categories based on contour shape is widely used but tends to make comparisons between studies difficult due to inconsistency of criteria used to define used categories and may result in a high level of subjectivity in assigning whistles to categories (Janik 1999; Deecke & Janik 2006). A number of variables were calculated for each whistle type category including: maximum frequency (MaxF), minimum frequency (MinF), start frequency (SF), end frequency (EF), frequency range (FR, max – min frequency), carrier frequency (CF, median of max and min frequency), number of inflection points (IF, changes between positive and negative slope), presence of harmonics (H) and duration (D).

Another classification method was used to assess the occurrence of signature whistles and how these may be correlated with number of identified individuals present at each encounter. This method is comparable to human classification methods that have been shown to accurately assign whistles to biologically relevant categories of known signature whistles (Janik et al. 2013). Here, a Matlab script, “ARTwarp” (Deecke & Janik 2006) developed for the identification of dolphin signature whistles, enabled comparisons of the complete shape of the contours using a pre-set, critical level of similarity, which is determined by the user. The level of similarity is calculated by the programme by using standardisation of whistle length and by applying dynamic time warping (i.e. local extension and compression of the time axis to maximise frequency overlap for all sections of the whistle contours being compared). The level of similarity between two contours (i.e. how well matched they are) is then given by the average similarity in frequency for all points on the two contours. The application of ARTwarp to extracted contours is fully explained by Deecke and Janik (2006), but the main features are summarised here, along with any modifications.

During the classification process, whistle contours are compared based on the similarity level set and subsequently placed in categories of similar shape. If a contour matched an existing category this contour was added to that category and its reference contour modified to represent an average of all the contours contained within. If a contour was too different from the existing reference contours (based on the similarity level set), a new category was created and that contour then became this new category’s reference. The program iterates through all contours in the data set, opening them in a random sequence for each run until no contour is re-classified or the pre-set maximum number of iterations have been reached (here set at a maximum of 100 iterations).

Information about the resulting categories were exported into MS Excel using a Matlab script (NEToutput.m) that provided the whistle id, category and the similarity (%) of each whistle to the reference contour of its assigned category. A critical similarity of 91% was considered appropriate for the current data set since it has been found suitable for bottlenose dolphin whistles with known function (signature whistles) from captive or temporarily restrained bottlenose dolphins (Deecke and Janik, 2006). The resulting categories were used to compare the number of new identifications of dolphins in each encountered group with the number of distinct whistle types found (using Spearman’s Rank Order correlation) to evaluate the relationship between individual participation and number of distinct whistles that may be potential signature whistles.

2.3 Results

Acoustic surveys took place in the Shannon estuary between June 2008 and August 2010 on 16 days. A total of 13 hours of recordings were made in suitable conditions for photo-identification and other observations (daylight sea state ≤3, good visibility and low swell), while in the presence of 30 dolphin groups. The resulting dataset of 1,442 logged whistles was used for whistle rate examinations and high only quality whistles (n=494) used in detailed analysis of the whistle repertoire.

2.3.1 Whistle rate

Overall average whistle rate was 0.13 (SD±0.19) per dolphin per minute (range 0 to 0.91) and 2.53 (SD±1.88) per dolphin per minute if the 13 encounters that had a whistle rate of zero whistles were excluded. Whistle rates showed a weak positive correlation with increasing group size (Figure 2). However, this was not statistically significant on the $p>0.05$ level. Encounters where whistles were not detected all included less than 15 individuals. Encounters were on average around one hour long, ranging between a few minutes and three hours depending on when all individuals present had been successfully photographed.

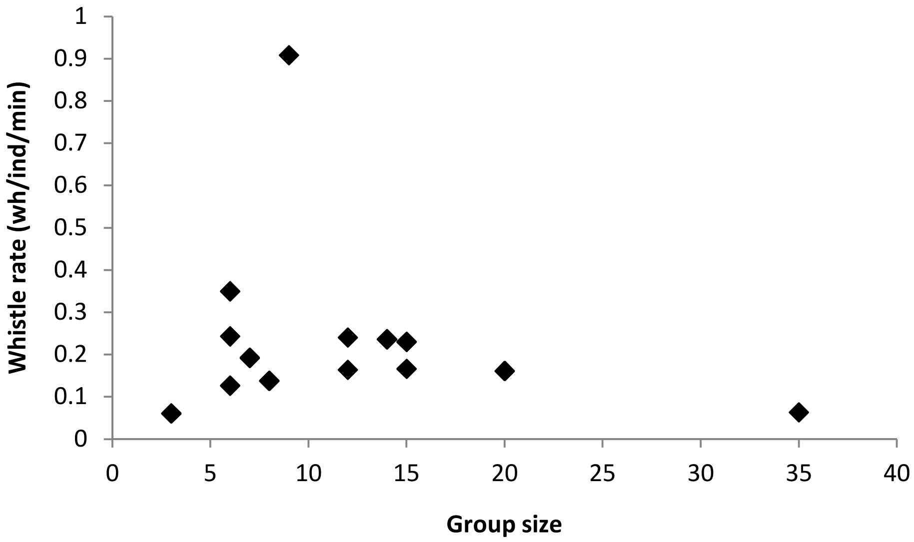

Figure 2. Relationship between dolphin group size and whistle rate (whistles per dolphin per minute of recording) for those encounters in which whistles were detected.

Whistle rate also varied with dolphin activity. Schools engaged in travel behaviour provided the lowest rates. The most common behaviour observed was milling which also provided the highest whistle rates recorded (Figure 3). However, these differences were not statistically significant (Kruskal-Wallis Test, p>0.05).

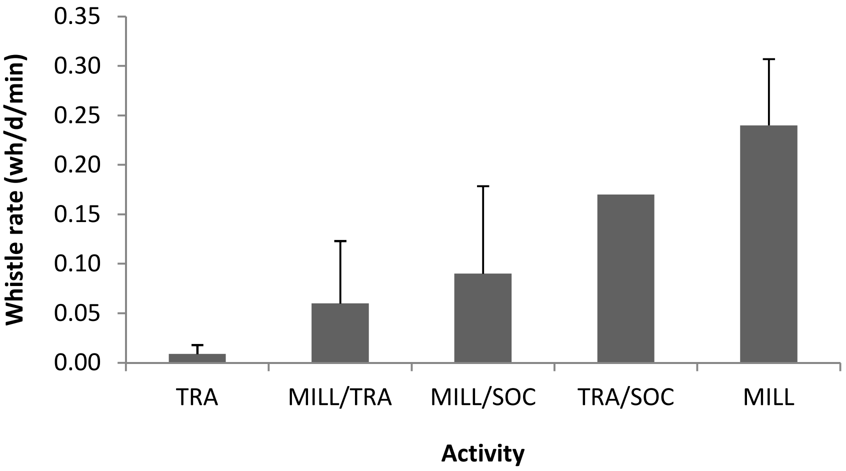

Figure 3. Relationship between dolphin activity and whistle rate (average number of whistles per dolphin per minute of recording) for different behaviours. Error bars indicate standard error and since only one observation of travelling combined with socialising was recorded, standard error cannot be established (TRA=travelling, MIlL=milling and SOC=socialising).

Group composition had an influence on whistle rate, with tightly grouped schools emitting very few or no whistles (Figure 4). For loosely grouped schools, all except one encounter provided whistles (Figure 4) with an average whistle rate of 3.10 (SD±2.48) whistles per dolphin per minute. The difference between presence and absence of whistles for groups with tight or loose composition was highly significant (Chi^2 = 13.6, df = 1, $p<0.001$). When subgroups (tight groups present with ≥100 meter of another groups) were observed the whistle rate varied between 0.06 and 0.17 whistles per dolphin per encounter, however the subset was too small to test for statistical significance (n=3). While whistle rates between groups with and without calves did not vary significantly ($p>0.05$) a slightly higher average rate of 0.15 (n=11, SD±0.25) whistles per minute per dolphin were found for groups with calves compared with 0.11 (n=14, SD±0.12) whistles per minute per dolphin for groups where no calves were observed.

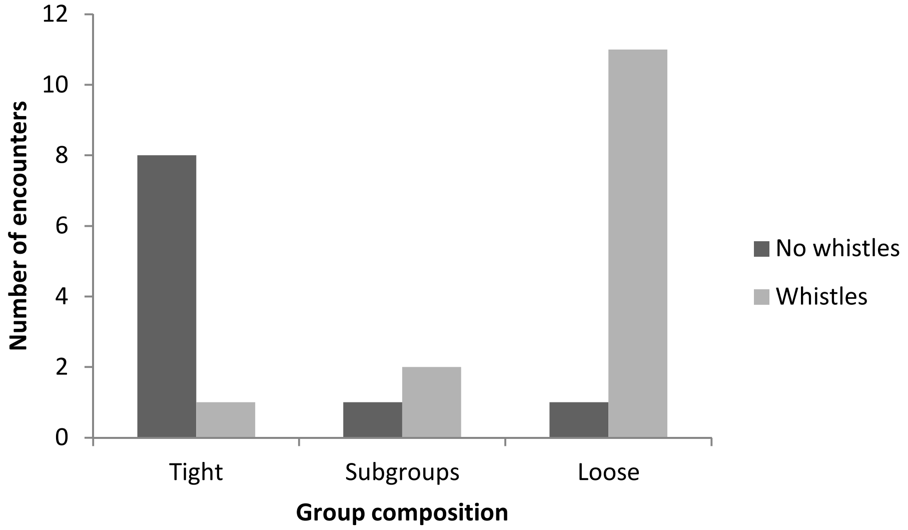

Figure 4. Relationship between dolphin school spacing and presence/absence of whistles for the main categories of group dispersion recorded.

2.3.2 Photo identification

In total, 24 encounters resulted in a set of 76 well marked individuals (with large nicks and/or deep scarring) identified using photo-identification techniques. These individuals were either previously known animals from the Shannon catalogue (maintained by University College Cork) or added to this catalogue if previously unknown. A number of individuals were also recorded for which re-sighting history was unavailable due to insufficient markings for reliable identification. Group size ranged between single animals and 35 with an average of 9.7 (SD±7.3) and included adults, juveniles and young calves. Group composition and individual overlap between groups encountered varied considerably with an array of group member combinations observed and a total of 42 individuals (55%) recorded more than once during the study period.

Calculations of membership overlap between groups were based on total group size with a maximum of 6 individuals shared between any two encounters. The largest group encountered included members from 9 other encountered groups. Investigations into individual use of different parts of the estuary (Figure 1), showed that some individuals (11%) were regularly recorded using both inner and outer areas while others used only the outer part (38%) and some only the inner part (4%). However, acoustic comparisons of whistle similarity between the areas were not possible since groups encountered in the inner parts of the estuary supplied extremely low whistle rates (13 whistles recorded in total, all within one single encounter).

2.3.3 Whistle repertoire

Frequency, time and modulation characteristics of whistle contours were extracted from 494 high quality whistles, of which 64% included harmonics. Whistles with up to 10 inflection points were found and while whistles with more than one inflection point were the most common and corresponded to 54% of all whistles, 17% had 3 or more inflection points.

Manual sorting of contours into five general whistle type categories revealed that the whistle type upsweep, also often named rise or type B whistle in other studies was the most observed contour type recorded and comprised 32.2% of the whistle repertoire, closely followed by convex (D, 27.9%), modulated (F, 19.6%), down-sweep (C, 11.1%), constant frequency (A, 6.7%) and concave (E, 2.4%) contours (Table 1).

Table 1. Summary of the average of acoustic variables for whistle types, with the percentage of all whistles included. Standard deviation and range (min and max) are shown below the standard deviation for each variable. The variables number of inflection points and presence of harmonics are not included in this summary.

Type	**%**	**D (s)**	**MaxF (kHz)**	**MinF (kHz)**	**SF (kHz)**	**EF (kHz)**	**FR (kHz)**	**CF (kHz)**
A	6.7	3.27 ±2.08 0.4-9.6	10.96 ±2.48 6.2-16.3	8.80 ±2.10 5.2-12.3	10.02 ±2.45 5.9-14.9	9.81 ±2.68 6.0-16.2	2.16 ±1.54 0.1-6.5	9.88 ±2.17 5.7-13.7
B	32.2	3.03 ±2.09 0.9-8.7	16.74 ±3.86 8.7-26.5	10.06 ±2.81 5.2-16.9	16.03 ±4.62 5.7-26.3	10.26 ±2.85 5.2-16.9	6.68 ±2.97 2.2-17.1	13.40 ±3.03 7.3-21.1
C	11.1	6.95 ±2.30 2.0-17.4	13.86 ±2.96 8.4-20.9	6.14 ±1.61 2.4-13.1	6.83 ±1.96 2.4-14.4	7.43 ±2.48 4.0-15.4	7.73 ±3.23 2.5-17.2	10.00 ±1.75 6.5-16.5
D	27.9	1.28 ±1.31 0.3-4.0	9.84 ±4.40 6.2-19.0	6.14 ±1.37 4.7-9.2	9.09 ±4.04 5.4-16.3	9.25 ±3.97 6.1-19.0	3.70 ±3.32 0.6-10.3	7.99 ±2.80 5.6-13.9
E	2.4	12.05 ±3.68 4.9-22.1	14.59 ±2.87 9.1-23.3	6.57 ±1.89 1.6-12.3	7.77 ±2.89 1.9-21.0	9.12 ±3.78 3.3-23.3	8.01 ±2.99 2.9-16.6	10.58 ±1.91 5.4-17.8
F	19.6	12.05 3.68 4.9-22.1	14.59 2.87 9.1-23.3	6.57 1.89 1.6-12.3	7.77 2.89 1.9-21.0	9.12 3.78 3.3-23.3	8.01 2.99 2.9-16.6	10.58 1.91 5.4-17.8

Variable codes: D=duration, MaxF=max frequency, MinF=min frequency, SF=start frequency, EF=end frequency, FR=frequency range and CF=carrier frequency.

In total, 145 distinct whistle type categories were created when running ARTwarp using the 494 high quality contours extracted. A total of 62% of these categories included only one (40.7%), or two (20.7%) whistles while 55 categories included at least three whistles and therefore were considered potential signature whistles (at least three whistles required). Only one included a high number of contours of the same distinct type (24 in total).

The cumulative number of new identifications of dolphins in each encountered group was positively correlated ($r_s = 0.652$, $p < 0.05$) with the cumulative number of distinct whistle types found per encounter (Figure 5).

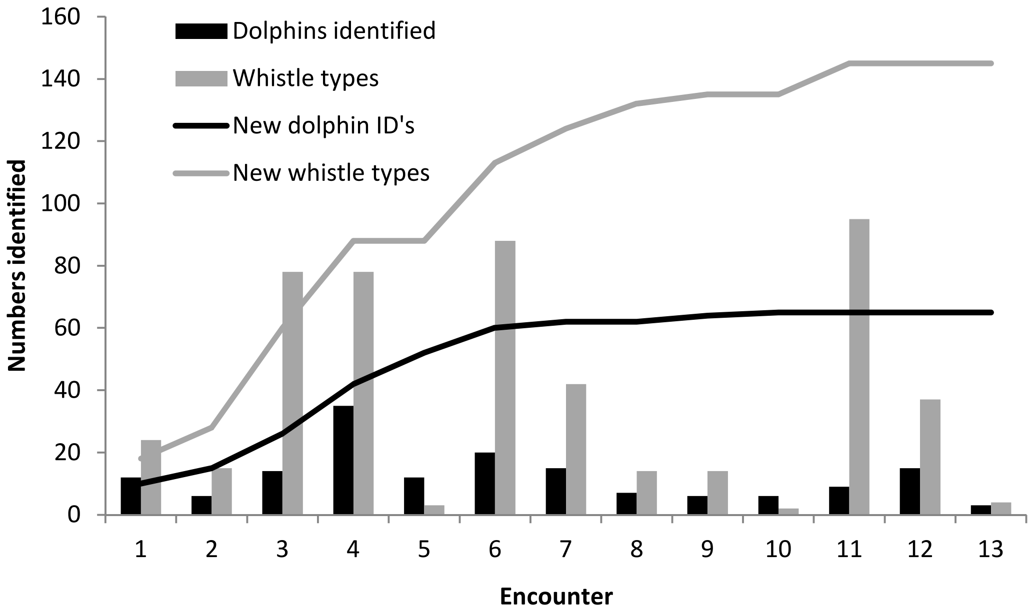

Figure 5. Discovery curves for the cumulative number of new distinct whistle types compared with the cumulative number of new dolphins identified per added encounter as well as the total number of dolphins and distinct whistle types identified during each encounter.

2.4 Discussion

While encounters in the Shannon provided variable whistle rates, it was notable that almost 50% did not include any whistles and in particular that the encounters in the inner parts (Figure 1) of the estuary provided very low whistle rates overall. However, when encountered in the inner Estuary during the study period, groups were generally small and in tight formation which would likely decrease the need for the use of calls that are important for individual recognition and maintenance of group cohesion.

While whistle rate varied with level of group dispersion and although not significantly, with group size and in relation to surface behaviour, the power of these tests is low and more data would be required to confirm or discard patterns found. A number of other studies have shown patterns of positive correlation between whistle rate and increasing group size (Jones & Sayigh 2002; Parijs et al. 2002; Cook et al. 2004), while one study indicated that individual whistle rates initially increased but then decreased when groups reached over 15 individuals (Quick & Janik 2008) and the authors suggested that as the potential of masking increase with an increasing number of dolphins present, individuals may avoid masking effects by reducing their individual whistle rates (Quick & Janik 2008). In this study, only two encounters included group sizes above 15 individuals and while one of these (n=35) did show a comparably low whistle rate more large encounters would be required to explore this further.

The highest rate of whistle production was found for loosely dispersed groups and for milling and socialising behaviour. This is consistent with findings in other areas (Jones & Sayigh 2002; Quick & Janik 2008) and supports the hypothesis that whistles function primarily in social communication (Caldwell *et al*. 1990), are used for maintenance of group cohesion (Janik & Slater 1998) and as contact calls for animals that are temporarily separated. While more dispersed groups tend to provide higher whistle rates (Quick & Janik 2008), group dispersion is also often closely related to behaviour and other factors. For example, travelling or resting groups tend to remain closer together than animals involved in socialising or milling behaviour. While multivariate tests would have been useful to investigate these patterns in greater detail, this was not possible due to low rates or absence of whistles for some combinations of factors.

Whistles may be produced by a nearby group rather than the closer focal group intended by the researchers (Quick & Janik 2008) and whistle rates may be overestimated if not using localising techniques (determining which animal is producing the sound). In this study, a single hydrophone was used and localising was therefore not possible and all animals within view were instead assumed to be part of the focal group. This reduced the risk of incorrectly assigning whistles to specific groups, with the trade-off of reduced subgroup specific information. It is still possible that whistles made by animals that were not within visual view and for which activity or identity was unknown, may have been assigned to the wrong group. This would depend on the range dolphins could be sighted vs. heard. Detection range has been estimated to approximately 750 meters for bottlenose dolphin whistles (Jensen et al. 2012) and since survey work only took place in favourable weather and sea conditions (sea state ≤3), it is likely that animals within this range would have been observed.

Groups with calves did not produce significantly more whistles than groups were no calves were observed. Calf groups of *T. aduncus* have been found to produce lower whistle rates than non-calf groups and this has been suggested to have a function in predator avoidance (Hawkins & Gartside 2010). For the Shannon population the risk of predators is likely absent (Ingram 2000) and such measures may therefore be unnecessary. Terrestrial species that live in fission-fusion societies similar to those of bottlenose dolphins are known to exhibit variation in call rate that may depend on a combination of factors. For example, the call rates of chimpanzees (*Pan troglytes*) appear to depend on the rank of the calling male as well as on the context in which the call is made, with the highest calling rate occurring before and after travelling, suggesting a function in group cohesion and maintaining of contact with group members (Mitani *et al*. 1999). Similarly, calls of baboons (*Papio cynocephalus ursinus*) can be behaviourally specific and influenced by the age and sex of the individuals involved (Rendall *et al*. 2000; Fischer *et al*. 2001).

Social analysis confirmed results from previous studies which consistently showed high levels of mixing and little evidence of group fidelity (Ingram 2000; Miller 2009; Foley *et al*. 2010). This is consistent with the highly fluid and dynamic social structure of a fission-fusion society usually recorded for this species (Connor *et al*. 2000).

The prevalence of certain whistle contour types was similar to earlier studies in the Shannon for which up-sweep was the most observed contour type recorded overall (Hickey *et al*. 2009), in particular during foraging behaviour, while down-sweep was the most common type found during travelling (Berrow *et al*. 2006). The relative abundances of whistle types were different to studies elsewhere (Wang et al. 1995; Oswald et al. 2003; Dos Santos et al. 2005; Akiyama & Ohta 2007; Azevedo et al. 2007; Baron et al. 2008; May-Collado & Wartzok 2008; Gridley 2010; Steiner 2011;

Papale 2012). Bottlenose dolphins in Brazil were shown to produce upsweeps and down-sweeps equally (Azevedo *et al*. 2007), while analyses of the acoustic repertoire of a coastal population of bottlenose dolphins in the West Mediterranean Sea was shown to be dominated by upsweeps (Diaz López 2011). In this study, the second most common type found was convex, which was the least frequently produced whistle type found in a study in North Carolina, USA, accounting for less than 5% of all whistles and being very rare in offshore groups (Keena 2008). The Shannon Estuary population instead appear to produce low numbers of concave type whistles, accounting for 3% (Hickey *et al*. 2009), which was very similar to the proportion found in this study, while in the West Mediterranean, flat or constant whistles were the types least commonly recorded (Diaz López 2011). The results from this study and studies elsewhere show that there is great variation in prevalence and use of whistle types between areas, likely reflecting complex drivers for their use and abundance, but may also be a sign of the substantial variation in classification methods and definitions used in whistle type categorisation in different studies.

The method used for measuring complexity of the whistle repertoire was initially developed to detect signature whistles and may thus not be ideal for this type of investigation. A high number of whistle categories were created with relatively few repetitions of distinct whistle types. This would, rather than supporting the idea of convergence, suggest that dolphin whistles (at least likely signature whistles) in the Shannon are highly diverse. This would in turn reflect that since whistles are learned and culturally transmitted (Janik et al. 2006; Laland & Janik 2006), uniqueness is highly important in a population where levels of social interaction are high. Overall vocal characteristics of the Shannon population may also be due to evolutionary adaptations to environmental factors or reflect physiological limitations that could be driving the overall stability in acoustic parameters within and between populations as have been suggested for *T. aduncus* (Wang *et al*. 1995).

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Chapter 3

The role of vocal variation in maintaining social cohesion and group differentiation in bottlenose dolphin communities.

Contents

Abstract

Several putative populations of bottlenose dolphins (*Tursiops truncatus*) are present in Irish waters, including adjacent communities that are genetically distinct, with no evidence of social interaction but likely overlapping ranges. In waters with poor visibility it is presumed that acoustic signals play an important role in the maintenance of social boundaries. The greatest need for distinct community calls would therefore be expected in the acoustic repertoire of genetically distinct communities that interact socially during the breeding season. Variation in vocalisation characteristics of complex whistles (≥2 inflection points) was investigated by comparing frequency and time variables, prevalence of distinct whistle types and similarity of whistle repertoires of dolphins sampled from five geographic regions in western and southern Irish waters: the Shannon Estuary, Cork Harbour, Connemara, North Mayo and continental shelf waters. Additionally, comparisons of vocal characteristics were also made with communities in eastern US waters. Levels of social interaction were investigated using photo-identification techniques, which supported findings of other studies indicating isolation between all sampled communities except Connemara vs. North Mayo. Using classification tree analysis, frequency and time characteristics of whistles were found to be good predictors of sampling site. High variation were found between continental shelf waters and inshore areas, suggesting that vocal divergence may be due to differences in habitat use and behaviour and indicate social isolation between these areas. In contrast, overall variation between inshore communities was low, even between genetically distinct communities, suggesting that any interaction would be most likely to take place outside of the main breeding season. Comparisons with the western North Atlantic showed clustering of continental shelf whistles with whistles from offshore waters suggesting potential similarities between these populations. MANOVA showed similarities between Irish and US waters inshore, but not between continental shelf and offshore waters, suggesting general species relatedness or habitat driven patterns of similarity. This study illustrates that vocal variation is likely to play an important role in actively maintaining intra-group cohesion and between group-separation in bottlenose dolphins at relatively small spatial scales.

3.1 Introduction

Many animals that live in complex societies are dependent on communication within and between social groups. The formation of social groups has many advantages, including strategies for predator avoidance, for example in schooling fish or grazing mammals (Kie 1999), foraging success in birds (e.g. Krebs, 1974) and reproduction in primates (Struhsaker & Pope 1991). A basic necessity of group living involves the ability to locate and stay in contact with conspecifics. For cetaceans, living in an environment where visual communication is often limited by poor visibility, vocal transmission provides the most effective means to transfer essential information. Acoustic signals are particularly useful for long range communication in the aquatic environment since they propagate faster and attenuate less in water than in air (Gordon & Tyack 2001) and therefore play an important role as contact calls (Janik & Slater 1998).

Group distinctive calls are uncommon and only shown for a few mammal species, including greater spear-nosed bats (*Phyllostomus hastatus*), killer whales (*Orcinus orca*), vervet monkeys (*Chlorocebus pygerythrus*) and chimpanzees (*Pan troglodytes*) (Ford 1991; Boughman 1997; Crockford et al. 2004; Filatova et al. 2012) for which it is possible to recognize social groups based on call characteristics alone.

Geographic variation can occur on a smaller or a larger scale, for example through distinctive dialects. Dialects are common in birds (e.g. Wright & Wilkinson 2001; Loghlen & Rothstein 2010; Yoktan *et al*. 2011), bats (Boughman 1997; Kazial *et al*. 2008), humans (Clopper & Pisoni 2004; Clopper *et al*. 2006) and non-human primates (Green 1975; Mitani *et al*. 1999), but uncommon among cetaceans. Dialects or group specific calls have not yet been determined for any cetacean species other than the killer whale (Ford 1991; Deecke et al. 1999; Filatova et al. 2012) and sperm whale (Weilgart & Whitehead 1997; Rendell & Whitehead 2005).

Dolphins emit sounds that are usually grouped into three types; short pulsed sounds used in echolocation, burst pulse calls and whistles; with the latter two primarily used in communication (Richardson *et al.* 1995). Whistles are frequency modulated, narrowband tonal calls used by most delphinid species with fundamental (dominant) frequencies which generally fall between 5 and 20 kHz, often with harmonic components that may reach up to 100 kHz or more. Higher frequency components of whistles can be highly directional, suggesting that listening dolphins could use this characteristic to facilitate coordinated movements between individuals or groups (Lammers & Au 2003).

Bottlenose dolphins (*Tursiops* spp.) live in fission-fusion societies, a social system where group membership regularly changes and few stable relationships exist between individuals (Wells *et al*. 1987; Smolker *et al*. 1992), except for mother calf pairs and in some areas between males (*T. aduncus*) that form long term alliances (e.g. Connor, Smolker, & Richards 1992; Connor, Heithaus, & Barre 2001; Möller *et al.* 2001; Connor *et al.* 2011). Early studies of bottlenose dolphin whistles highlighted the dolphins' whistle contour as an important characteristic in individual recognition (Caldwell & Caldwell 1965). Bottlenose dolphins use individually distinct, stereotyped whistles (Caldwell & Caldwell 1965) that account for 90% or more of the whistle production in captive or temporarily restrained conditions and around 50% of whistles emitted in free ranging groups (Cook *et al*. 2004). Signature whistles are developed early in life and used to broadcast identity (Caldwell et al. 1990; Janik & Slater 1998), they are made novel by learning and encode identity in their frequency modulation pattern (Caldwell et al. 1990; Janik & Slater 1998; Janik et al. 2006). Since signature whistles are learned signals (Janik & Slater 1997; Tyack & Sayigh 1997; Miksis et al. 2002; Fripp et al. 2005; Janik 2009), dolphins could converge on common whistle structures that are shared between individuals (Watwood *et al*. 2004), within social units or within populations (Tyack & Sayigh 1997; Fripp *et al.* 2005), which may in turn facilitate the development of local dialects (Filatova et al. 2012). Although dialects have not been shown for bottlenose dolphins, recent research on whistle use suggest that stereotypic whistle exchanges occur when groups of bottlenose dolphins (*T. truncatus*) meet and join at sea (Quick & Janik 2012). However, while such whistle exchanges would facilitate discrimination on an individual level they are unlikely to enable group discrimination within a fission-fusion society where group composition constantly changes.

3.1.1 Vocal variation

The structure of dolphin whistles and their vocal repertoires vary within (e.g. Bazua-Duran & Au, 2004) as well as between species (Steiner 1988; Wang *et al*. 1995a; Rendell *et al*. 1999). Phylogenetic studies by May-Collado *et al*. (2007a and 2007b) indicated that the evolution of minimum frequencies used by cetaceans is influenced by body size and group size, while social structure appears to have a greater influence on whistle complexity. Intra-specific variation in whistle structure has been identified between populations that are widely separated (Wang *et al*. 1995b; Camargo *et al*. 2006; Baron *et al*. 2008), between neighbouring populations (Wang *et al*. 1995b; Bazúa-Durán & Au 2004; Azevedo & Van Sluys 2005; Morisaka *et al*. 2005a; Rossi-Santos & Podos 2006; Ansmann *et al*. 2007; Baron *et al*. 2008), among social groups within populations (Janik *et al*. 1994) and between males and females (Sayigh *et al.* 1995). Morisaka *et al* (2005b) found that frequency parameters were the most important variables to consider when discriminating between populations, while other variables such as duration and number of inflection points showed higher within-population variability (Morisaka *et al.* 2005b).

3.1.2 Distribution and habitat use

The common bottlenose dolphin (*Tursiops truncatus*, Montagu 1821) uses a range of habitats including estuaries, coastal areas and oceanic waters. A number of populations of bottlenose dolphins are distributed throughout eastern Atlantic coastal waters including Cardigan bay (Arnold 1993; Baines et al. 2002; Pesante et al. 2007), the Moray Firth (Lewis & Evans 1993; Wilson *et al*. 1997) and the Hebrides in Scotland (Grellier & Wilson 2003; Hastie *et al*. 2003; Mandleberg 2006; Cheney *et al*. 2013), Brittany and Normandy in France (Liret *et al*. 1995; Kiszka *et al*. 2004), northern Galicia (Fernández *et al*. 2011) and the Sado Estuary in Portugal (Dos Santos & Lacerda 1987; Canadas *et al*. 2005).

A number of putative populations of bottlenose dolphins are also recognised in Irish waters (Ingram *et al*. 2001; Mirimin *et al*. 2011) including a semi-resident population in the Shannon Estuary (Rogan *et al*. 2000; Ingram & Rogan 2003; Englund *et al*. 2007; Berrow *et al*. 2012), a critical habitat for this species (Ingram &

Rogan 2002). The Shannon population has been studied since the mid 1990's (Berrow *et al*. 1996; Ingram 2000; Rogan *et al*. 2000) and research has revealed that dolphins are present in the estuary year-round, but show seasonal residency with a peak in occurrence (and calving) in the summer months (Ingram 2000), while numbers decrease during the winter period (Rogan *et al*. 2000; Ingram & Rogan 2002). To date we have no knowledge of where any of the Shannon animals spend time during the winter months and the few records of Shannon dolphins observed outside of the estuary have so far always been within 15km from the mouth of the estuary (Ingram *et al*. 2001; O'Brien *et al*. 2009).

There are also far ranging coastal communities in Irish waters (Ingram *et al*. 2001; O'Brien *et al*. 2009), some of which show local site fidelity (Ingram *et al*. 2003, 2009). The SCANS II survey (Hammond *et al*. in press) reported an abundance estimate for bottlenose dolphins in coastal Ireland of 313 individuals (CV=0.81). Photo-identification studies show that re-sighting rates and large scale ranging patterns found by Ingram and Rogan (2003) and O'Brien *et al* (2009) support the presence of a relatively small assemblage of highly mobile bottlenose dolphins in Irish coastal waters. Few estimates of abundance of these coastal populations have so far been calculated. Connemara waters were estimated to harbour at least 171 (CV=0.28, 95%CI=100-294) dolphins (Ingram *et al*. 2009), exceeding all previous estimates of the Shannon population (Ingram 2000; Ingram & Rogan 2003; Englund *et al*. 2007, 2008; Berrow *et al*. 2012). The Shannon Estuary population of bottlenose dolphins is genetically distinct from other groups in Irish waters, except for a small group in Cork harbour likely representing a dispersal from the Shannon (Mirimin *et al*. 2011). Some range overlap between the Shannon Estuary dolphins and coastal ranging groups have been suggested, and while no records of social interaction have been found, there is documented overlap in area use in Kerry waters close to the mouth of the Shannon Estuary (Ingram *et al*. 2001).

A third, genetically distinct community of bottlenose dolphins has been indicated from genetic analysis of tissue collected from stranded dolphins (Mirimin *et al*. 2011) in Irish waters. Coastal populations tend to have lower levels of genetic diversity than populations further offshore (e.g. Natoli *et al*. 2004; Quérouil *et al*.

2007) and whilst the origin of animals stranded on Irish coasts remains uncertain, high levels of genetic diversity suggest that they may belong to a larger neritic, continental shelf assembly (Mirimin *et al*. 2011). Analysis of stomach contents and stable isotope ratios in stranded animal tissue indicate that bottlenose dolphins of this third population use continental shelf waters in addition to coastal waters and stomach contents suggest that these animals may be foraging on the continental shelf and close to the shelf edge (Hernandez-Milian*, pers comm*). Whilst abundance estimates for bottlenose dolphins in Irish coastal regions measure in the hundreds, offshore surveys have estimated around 7,500 bottlenose dolphins (95% CI=2,900 - 11,100) in Irish waters north of 53 degrees latitude at depths greater than 200 meters (CODA 2009), suggesting that coastal populations represent a fraction of the total of this species in Irish waters. There are currently no management directives taking into account these smaller numbers of coastal dolphins that appear to be separate from larger shelf populations and may be subjective to different threats while genetically and socially distinct.

3.1.3 Aims and objectives

The aim of this study was to investigate the role of vocal variation in maintaining social cohesion and group differentiation among bottlenose dolphin communities in Irish waters. It was hypothesised that the need for community distinction would be higher for adjacent and sympatric communities that are genetically distinct but where social interaction occurs during the breeding season. Also that social isolation between communities and vocal learning within communities would result in increased within-community similarity and elevated between community variations.

In order to achieve these aims, the objectives were to; 1) describe the structural characteristics of whistles from adjacent and sympatric communities, 2) measure the magnitude of variation in whistle parameter characteristics, whistle contour shape and whistle repertoire complexity within and between these communities, 3) to relate any variation found to levels of social overlap, habitat use and genetic similarity and finally, 4) to compare the findings with whistle characteristics among dolphin communities in the North West Atlantic (also, see Chapter 4).

3.2 Methods

3.2.1 Study areas

Dedicated vessel based surveys were carried out in five geographical areas: the Shannon Estuary, Cork Harbour, two coastal sites on the Irish west and south coast (Connemara and Mayo waters) and offshore continental shelf waters. The Shannon Estuary is the largest estuary in Ireland. It is a busy industrial area with shipping traffic leading into the Port of Limerick as well as smaller local fishing activities and dolphin watching tourism (Berrow & Holmes 1999) taking place in the outer estuary, which is home to a seasonally resident population of bottlenose dolphins and the only designated Special Area of Conservation for this species in Irish waters. Survey work took place in the outer estuary, following a route set up in previous studies (e.g. Ingram 2000).

Surveys in North Mayo waters took place in an area where long term marine mammal survey work has been ongoing since 2001 (Anderwald *et al*. 2012). Apart from pipeline construction work, this area has low levels of ship traffic, small scale fishing, sea angling and marine nature tourism. In Connemara waters, the level of commercial traffic is relatively low with recreational (nature tourism, diving) and small scale fishing activities. The final coastal site included was Cork Harbour in the south of Ireland, where a group of six dolphins have showed a high level of site fidelity from 2007 (Ryan *et al*. 2010). Since then, this group has increased in size through the birth of two calves, in 2010 and 2011. Cork Harbour is the largest natural embayment in Ireland at the mouth of the river Lee (the second largest estuary in Ireland), and is a busy port and heavily industrialised site (Minchin *et al*. 1996; Ryan *et al*. 2010).

The island of Ireland is situated on the continental shelf, a shallow water plateau, which slopes down gently towards the continental shelf edge where it drops away rapidly between 200 to 1,500 metres down steep underwater cliffs and canyons to the Porcupine Abyssal Plain, around 5,500 metres below the surface. At its closest, the shelf edge is only about 30-60 km from the northwest coast (Figure 1). The marine shelf area within the 200 m depth contour to the south and west of Ireland covers approximately 200,000 square kilometres. Ocean circulation forces cold and nutrient rich water up to the continental shelf where it mixes with warmer surface waters, promoting phytoplankton production, attracting fish, squid and higher predators. The North Mayo region therefore experiences a rich diversity of marine species and oceanic species of cetaceans are commonly encountered close to the coast (e.g. common dolphins (*Delphinus delphis*), white beaked dolphins (*Lagenorhychus albirostris*) and baleen whales).

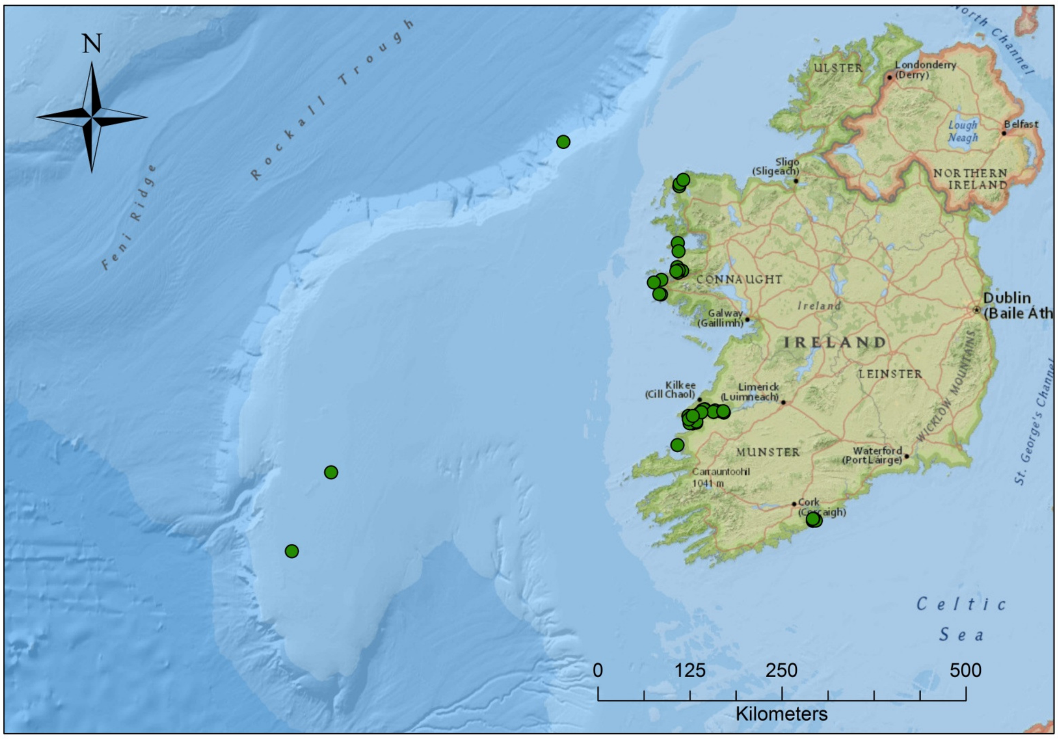

Figure 1. Map of Ireland showing encounter locations in North Mayo, Connemara, Shannon Estuary, Cork Harbour and continental shelf waters.

Outgroup comparisons with bottlenose dolphin communities in US waters included the inshore waters of North Carolina, US (Figure 1 in Chapter 4). These comparisons were based on data presented in Chapter 4 of this thesis where details of sampling areas and methods used can be found.

3.2.2 Recording whistles

Focal group follows (Altmann 1974) using standard photo-identification techniques and acoustic recordings were undertaken from a small boat in Beaufort sea-state 3 or less in fair weather conditions. When dolphins were encountered, the numbers present were estimated and all individuals visible were considered part of the focal group. Recordings were made during and after photo-identification took place. In general, only recordings made when the boat was stationary and engine in neutral or moving very slowly could be used in analysis due to interference from noise created by the boat. The drop-down hydrophone was positioned at 2 meters depth and recordings made onto an Edirol solid state recorder. Notes were taken using a small dictaphone (camera, dictaphone and recorder were time synchronised prior to each survey). For-non coastal surveys, recordings were made continuously using towed hydrophone arrays and recordings linked based on visual records and encounter information supplied by the survey team. The vessel deflected from the survey route during encounters with bottlenose dolphins to approach and acquire photographs and other information.

In order to acquire representative samples of whistles from all areas and habitat types, efforts were made to record a number of groups from each study area, spread over an extended time period. Additionally, recordings were made across a variety of behavioural states, group sizes, group compositions and locations within these study areas. To standardise field techniques, acoustical data were, when possible, collected using the same recording system and deployed in the same manner. However, the suitability of recording systems depended on the survey in question (Table 1) and in particular on vessel types employed. While the upper frequency limit of the recorder was 48 kHz (96 kHz sampling rate) the limit of the system was determined by the 30 kHz range of the hydrophone used in inshore waters.

Table 1. Summary of recording equipment used, including type of hydrophone, recording device and sampling rate for each setup.

Survey	Hydrophone type	Recording device	Sampling rate
All inshore surveys	Single channel hydrophone, model HTI-96-MIN. High Tech Inc., MS, US	Edirol R-09-HR or R-44 digital solid state recorder, Roland Systems Group, UK	96 or 192 kHz 24 bit
Continental shelf - 2009	Four element 200m towed hydrophone array. Seiche Ltd., UK	Magrec HP-27 buffer box through laptop and DAQ-6255 USB NI sound card	192 kHz 16 bit
Continental shelf - 2010	Four element 400m towed hydrophone array. Seiche Ltd., UK	Bespoke buffer box through laptop and, RME Fireface 800 sound card	192 kHz 16 bit

The data collected were standardised when possible, and for analyses purposes, 96 kHz sampling rate was used for all recordings providing an effective band width of 48 kHz. Recordings made with a higher sampling rate were down-sampled using Adobe Audition 3.0© (1992-2007 Adobe Systems Incorporated) to enhance comparability between sampling occasions. Recordings in continental shelf waters took place during larger ship surveys on the R.V Celtic Explorer (Cetaceans on the Frontier Survey II, 18th – 31st August, 2009) and on a sailing yacht R.V Song Of The Whale (Acoustic survey for beaked whales, 15th September – 12th October, 2010). While differences in sample size between the recording systems used could be counteracted by down-sampling, the use of different bit depth for continental shelf compared with inshore recordings may have negatively influenced detection range by reducing the dynamic range of these recordings.

3.2.3 Acoustic analysis

Initial analysis revealed very low levels of variation within the dataset when using all whistles available and therefore, a decision was made to restrict analysis to complex whistles (containing at least two inflection points), based on the assumption that they contain more information than simple whistles (Weilgart & Whitehead 1990; Lindström & Kotiaho 2002). Whistles were identified from recordings by eye using the spectrogram view (Hanning window, FFT resolution 256) of RAVEN PRO v1.4 (Cornell Lab of Ornithology). A whistle contour was defined by its dominant frequency as a function of time and information about patterns of frequency modulation could therefore be preserved while any noise, harmonics or fluctuations in amplitude originally present in the signal could be discarded.

Whistle contours were also quality graded based on signal to noise ratio (SNR) and only those that were clearly visible above background noise, and for which the entire contour could be distinguished from any surrounding whistles, were included in analyses. Start and end points of each whistle were logged together with information on harmonics, whistle quality and any notes and stored in an MS Access database. The selection table function available in RAVEN PRO was used to manually select each whistle contour and to create single whistle sound files. A custom made script was used to extract contour details, BELUGA (Deecke; *unpublished*) in MATLAB (FFT size 4096, frame size 512 with 87.5 overlap and a Hanning window). In BELUGA, the whistles were traced using a semi-automated process where a peak-finding algorithm selects the fundamental (dominant) whistle contour under the supervision of the user who filters and corrects minor mistakes made due to interfering echolocation or high amplitude harmonics falsely selected by the algorithm. The resulting traced contour for each whistle was saved in a text file as a list of frequencies with known time and frequency resolution (0.667 ms and 23.438 Hz).

From these extracted data, ten basic whistle parameters were calculated and exported into MS Excel. These included: max frequency, min frequency, start frequency, end frequency, frequency range (max – min frequency), carrier frequency (median of max and min frequency), initial slope (average slope of the initial 30ms of the whistle), number of inflection points (changes between positive and negative slope), presence of harmonics and duration.

3.2.4 Variation in whistle variables

To explore the relationship between sampling areas and whistle characteristics, classification and regression tree analysis (CART© Salford Systems) was used to evaluate how effective the measured variables were at distinguishing between the communities and to see how well whistles could be classified to community. CART uses an iterative process (Breiman *et al.* 1984) that provides an indication of similarity or dissimilarity between and within communities by recursively partitioning the dataset based on the best predictor variable at each two-way split until all data points are classified. In this case, sampling area was used as the response variable and all whistle variables except frequency range, presence of harmonics and number of inflections as predictor variables. This method does not assume normality, linearity, homogeneity or independence (Venables & Ripley 1997). Branches in the resulting tree output lead to terminal nodes representing the final classification, and the tree can be grown or pruned to explore variation in resulting subgroups. Validation of classification scores was made using 10-fold cross-validation.

In order to visualise the patterns of overall variation among sites and to further investigate which whistle variables best discriminated between groups, discriminant function analysis (DFA) was employed and differences found further explored by multiple analysis of variance (MANOVA) in SPSS (PASW Statistics 18). If variables were not normally distributed they were transformed using a Box-Cox transformation and MANOVA was only performed on successfully transformed variables. Because MANOVA performs multiple univariate ANOVA analyses, type 1 error was controlled using Bonferroni corrections to the significance thresholds.

Univariate and multivariate analysis (ANOVA and MANOVA) provide information about the difference across individual samples and about variability for each given variable (Insley 1992, 2000; Fernandez-Juricic *et al*. 1999; Phillips & Stirling 2000). However, since the assumption of homogenous covariance matrices was violated (Box's M test, $p<0.001$), the univariate Games-Howell post-hoc test for equality of means (Sokal & Rholf 1995) was applied when running the MANOVA. Although this test does not assume equality of covariance matrices it does assume that the data are normally distributed; and therefore only variables that could be successfully transformed were included. A non-parametric alternative approach using Kruskal-Wallis and Mann-Whitney U-test allowed analysis of any non-normalised variables.

3.2.5 Similarity of whistle contour shapes

To investigate similarity of whistle contour shapes within and between sampling areas and to examine any evidence of convergent vocalisations amongst dolphins, a neural network and time warping approach was used in which whistle contours were sorted into categories of similarity. A MATLAB script, ARTwarp (Deecke & Janik 2006) enabled comparisons between the actual shapes of the contours using a pre-set, critical level of similarity, determined by the user. These comparisons between contours were made using standardisation of whistle length and by applying dynamic time warping (i.e. local extension and compression of the time axis to maximise frequency overlap for all sections of the whistle contours being compared). The level of similarity between two contours (i.e. how well matched they are) was then given by the average similarity in frequency for all points on the two contours.

The application of ARTwarp to extracted whistle contours was fully explained by Deecke and Janik (2006), but the main features are summarised here, along with any modifications and for further detail also see the analysis section in the general introduction of this thesis (Chapter 1).

During the classification process, contours were compared based on the critical similarity level set and placed into different categories. If a contour matched an existing category it was added to that category and its reference contour modified to represent an average of all contours contained within. If a contour did not match any of the existing reference contours, a new category was created and the contour then became this new category's reference. The program iterated through the data set repeatedly, in a random sequence until no contour was re-classified. Information about the resulting categories was exported into MS Excel using another MATLAB script that provided the whistle id, category and similarity of each whistle to the reference contour of its assigned category. A critical similarity level of 91% was considered appropriate for the current data set since it has been found suitable for bottlenose dolphin whistles with known function (signature whistles) from captive or temporarily restrained bottlenose dolphins (Deecke and Janik, 2006) and free ranging dolphins (Quick & Janik 2006). The resulting categories were considered a representative set of distinct whistle types for the group or community in question.

To quantify similarity among whistle contours within a sampling area, similarity indices were calculated between whistle pairs. A similarity matrix comprised of all possible pair-wise measures of similarity (n samples generating 0.5 x n x (n-1) similarity values) was then converted to column comparisons in MS Excel. For between community comparisons, the average similarity for each pair of communities was calculated as a set of similarity values between each whistle from the first community and each whistle from the second community. Assuming that all whistles (and therefore any whistle combinations generated) within the same encounter were correlated the analysis was constricted to the mean similarity value for each encounter. Mann-Whitney U-test was used to test the significance of any patterns observed.

3.2.6 Comparison of whistle repertoires

Whistle repertoire similarity between communities was quantified using the outcome from neural network analysis and repertoires compared based on the presence or absence of distinct whistle types in the respective call repertoires. To do this I used a simple matching coefficient S_{SM} (Sneath & Sokal, 1973): $S_{SM} = (a + d)/(a + b + c + d)$, where “a” is the number of distinct whistle types present in the repertoires of both communities, “b” is the number present in the repertoire of the first community but absent in the repertoire of the second, “c” is the number of distinct whistle types present in the repertoire of the second community but absent in the repertoire of the first, and “d” is the number absent in the repertoires of both communities, using as a base list the total number of whistle types present in all communities being compared. This index was chosen over the Jaccard (Real & Vargas 1996) and similar indices of similarity as it can incorporate more information by the inclusion of positive and negative matches as well as mismatches. The number of negative matches can be influenced by sampling effort, a factor that is not often incorporated into other comparable similarity indices.

3.2.7 Comparisons with US waters

Comparisons with whistle characteristics in US waters were made using data collected for Chapter 4 in this thesis. However, while Chapter 4 is considering all types of whistles a subset of complex whistles (≤2 inflection points) were used here for consistency. Comparisons were made using discriminant function analysis and multivariate analysis, MANOVA to investigate clustering patterns based on whistle characteristics and the similarity in whistle variables.

3.2.8 Social analysis

Photo-identification of dolphin dorsal fins allows individuals to be identified by unique patterns of naturally occurring marks (Würsig & Würsig 1977). Photographs of dolphin dorsal fins were taken during acoustic recording sessions (using a digital Canon EOS D440 or D1 SLR) in order to study the level of individual overlap between the communities. Photographs were compared between encounters, areas and with identification catalogues maintained by University College Cork. To minimize the risk of misidentification, all included photographs were required to be in focus, well exposed and with the dorsal fin fully visible and oriented in parallel view. Additionally, only dorsal fins with clear and permanent or semi-permanent markings were used, leaving approximately 30% un-identified for Connemara/North Mayo (Ingram et al. 2009), 40-47 % for the Shannon (Berrow et al. 2012) and an unknown number for continental shelf animals (the proportion of unmarked individuals have not yet been estimated for animals using these waters).

3.3 Results

In total, 62 coastal and estuarine surveys were completed between June 2008 and June 2011, resulting in 50 encounters with bottlenose dolphin groups and whistles recorded on 26 occasions (Table 1). Recordings were also made during two continental shelf surveys in 2008 and 2009, which included five encounters (Figure 1), three of which produced whistles. One encounter was located on the shelf edge, 85 km away from the North Mayo coastline, while the other two encounters occurred further south, between 239 and 286 km from the closest Irish coast (Figure 1). Including all recordings, 8,252 whistles were logged of which 1,754 were of high enough quality for frequency contour extraction and 497 complex whistles used in analysis of vocal variation (Table 2).

Table 2. Sampling effort showing number of surveys and encounters in each habitat type and location, total number of whistles logged and number of high quality whistles extracted.

Habitat type	Nr of surveys	Nr of enc	Enc with whistles	Nr of whistles	Whistles	Complex whistles
Estuarine						
• Shannon Estuary	16	27	12	1,441	494	109
• Cork Harbour	14	11	6	393	140	44
Coastal						
• Connemara	21	10	5	1,251	236	108
• North Mayo	11	3	3	2,718	373	126
Continental shelf	2	5	3	2,449	511	110
Total	**64**	**55**	**29**	**8,252**	**1,754**	**497**

3.3.1 Variation in whistle variables

Success of classification by sampling area using the measured variables in CART analysis were relatively high with an overall average of 72.0% (Cork 95.5%, Shannon 56.9%, Connemara 84.3%, North Mayo 72.2% and continental shelf waters 42.7%). These classification results were associated with variation in all frequency parameters for which max and start frequency received the highest scores in the analysis.

In order to visualise any clustering resulting from overall vocal variation among sites, average values for each encounter were used in discriminant function analysis. The results indicate clustering of some of the inshore communities but with a degree of overlap evident for all inshore communities. Whistles from continental shelf waters clustered separately from all inshore samples (Figure 2). The top two ranked discriminant functions explained 90.3 % of the variance (75.4% and 14.9% respectively) and the variables start and end frequency loaded highest on the first canonical discriminant function while minimum frequency and number of inflections loaded highest on the second.

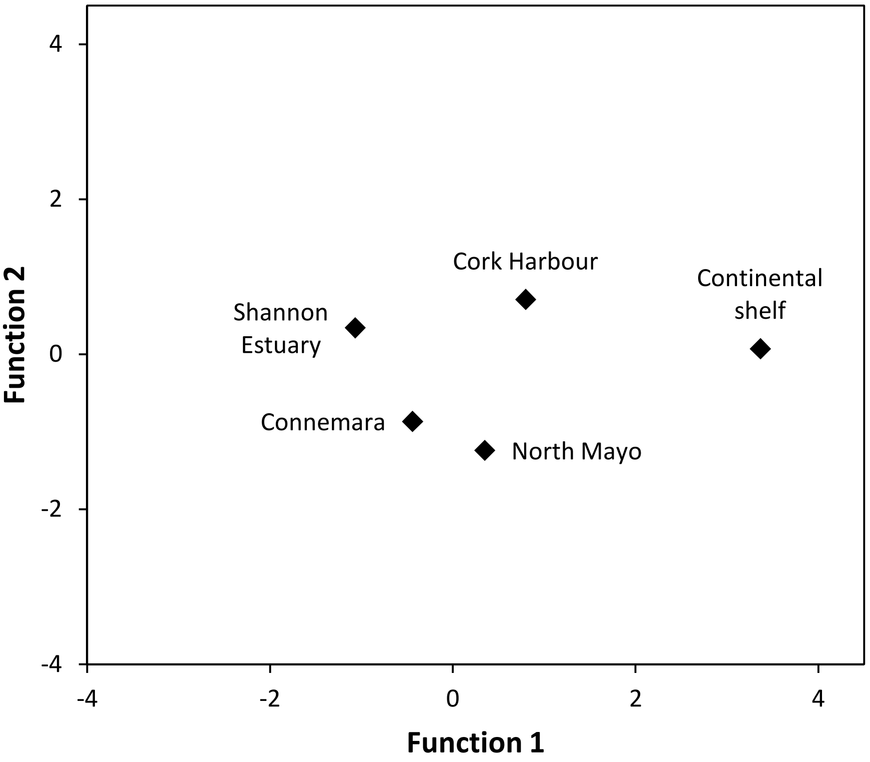

Figure 2. Canonical discriminant function scatter plot of community centroids for the first two discriminant functions, displaying patterns of similarity in whistle characteristics averaged by encounter.

There was a statistically significant difference between whistles from different communities (F (497) = 4.758, $P < 0.001$; Wilk's Lambda = 0.768, partial $\eta^2 = 0.064$) and post-hoc tests showed some variation for all variables except minimum frequency (Table 3). For information purposes I indicate all the probabilities that are less than 0.05, but only those that meet the Bonferroni criterion are considered significant. Significant variation was only found between inshore and continental shelf waters (Table 4).

Table 3. Results of MANOVA and Games-Howell post-hoc test after successful Box-Cox transformation of the first seven variables and results of Kruskal-Wallis and Mann-Whitney U-test for the last three variables. While the level of significance is given for each comparison (NS p>0.01), * p<0.01, ** p<0.001) only comparisons with p<0.005 are considered significant under the Bonferroni correction criterion (10 between community comparisons).

MANOVA	Ck Sh	Ck Ca	Ck Mo	Ck Cs	Sh Ca	Sh Mo	Sh Cs	Ca Mo	Ca Cs	Mo Cs
Max Freq	NS	NS	NS	NS	NS	NS	NS	*	*	NS
Min Freq	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Start Freq	NS	NS	NS	NS	NS	NS	**	NS	NS	NS
End Freq	NS	NS	NS	NS	NS	NS	*	NS	NS	NS
Freq Range	NS	NS	NS	NS	NS	NS	NS	*	NS	NS
Carrier	NS	NS	NS	NS	NS	NS	NS	*	*	NS
Duration	NS	NS	NS	*	NS	NS	**	NS	**	**
Initial slope	NS	NS	*	NS	NS	NS	NS	NS	NS	NS
Harmonics	NS	*	NS	**	*	*	**	NS	**	**
Inflections	NS	NS	NS	*	NS	NS	**	NS	NS	*

Community codes: Ck=Cork Harbour, Sh=Shannon, Ca=Connemara, Mo=North Mayo and Cs=continental shelf)

3.3.2 Similarity of whistle contour shapes

The similarity matrix created using complex whistles (123,256 pair-wise comparisons) between all whistles analysed (n=497) showed that within community variation in average similarity values was similar between the communities, with whistles from continental shelf waters showing the lowest level of within community similarity. Whistles from North Mayo waters had a higher level of within community similarity compared to continental shelf waters but lower when compared with the other inshore communities. Shannon had the highest levels of within area similarity, closely followed by Connemara and Cork Harbour (Figure 3).

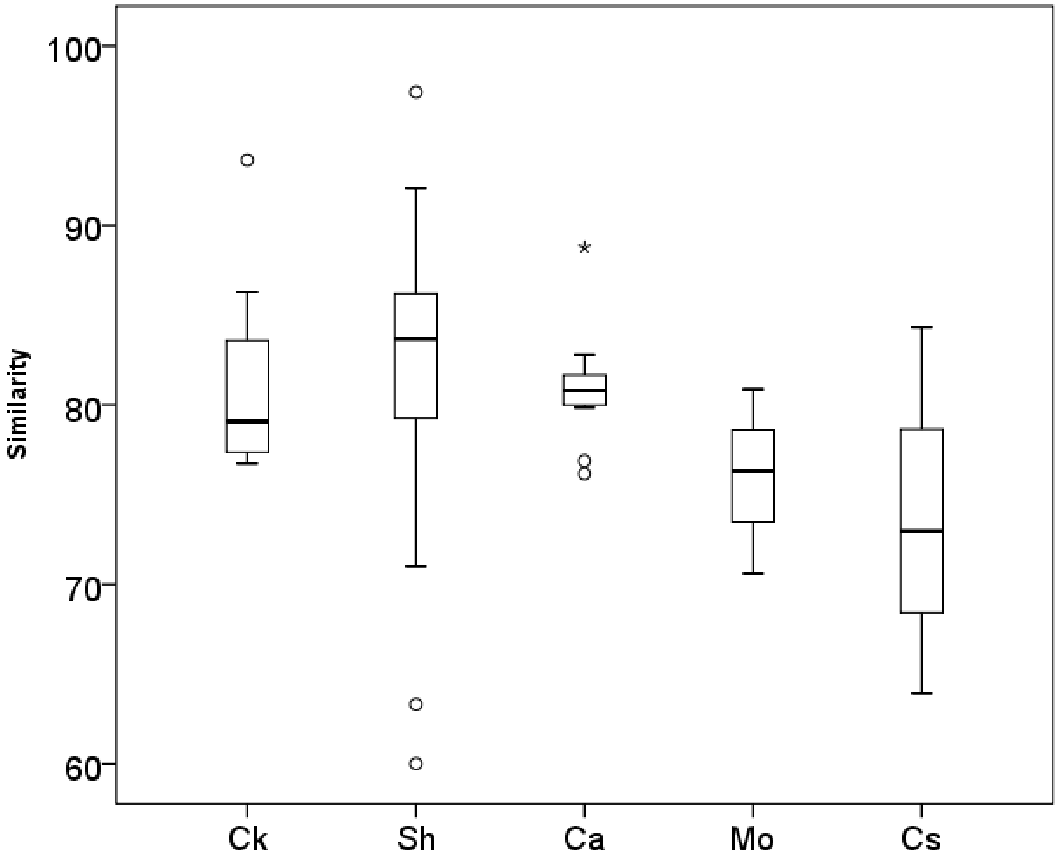

Figure 3. Box plots of average within-area similarity (%) of whistle contour shape between the different sampling areas. Horizontal lines represent mean, boxes interquartiles, whiskers 95% confidence interval and circles outliers.

Regarding between area comparisons, whistles recorded from Cork Harbour and the Shannon Estuary showed the highest similarity in contour shape, closely followed by Connemara/Shannon and Cork/Connemara (Table 5). Three community pairs were significantly different when tested using Mann-Whitney U-test. The largest variation found was between inshore communities and continental shelf waters, in particular for Connemara (Z=-3.554, n=15, p<0.001), followed by North Mayo (Z=-2.828, n=9, p<0.01) and Shannon (Z=-2.598, n=36, p<0.01) while Cork harbour (n=18) whistle shapes were not significantly different from those of continental shelf waters (Figure 4).

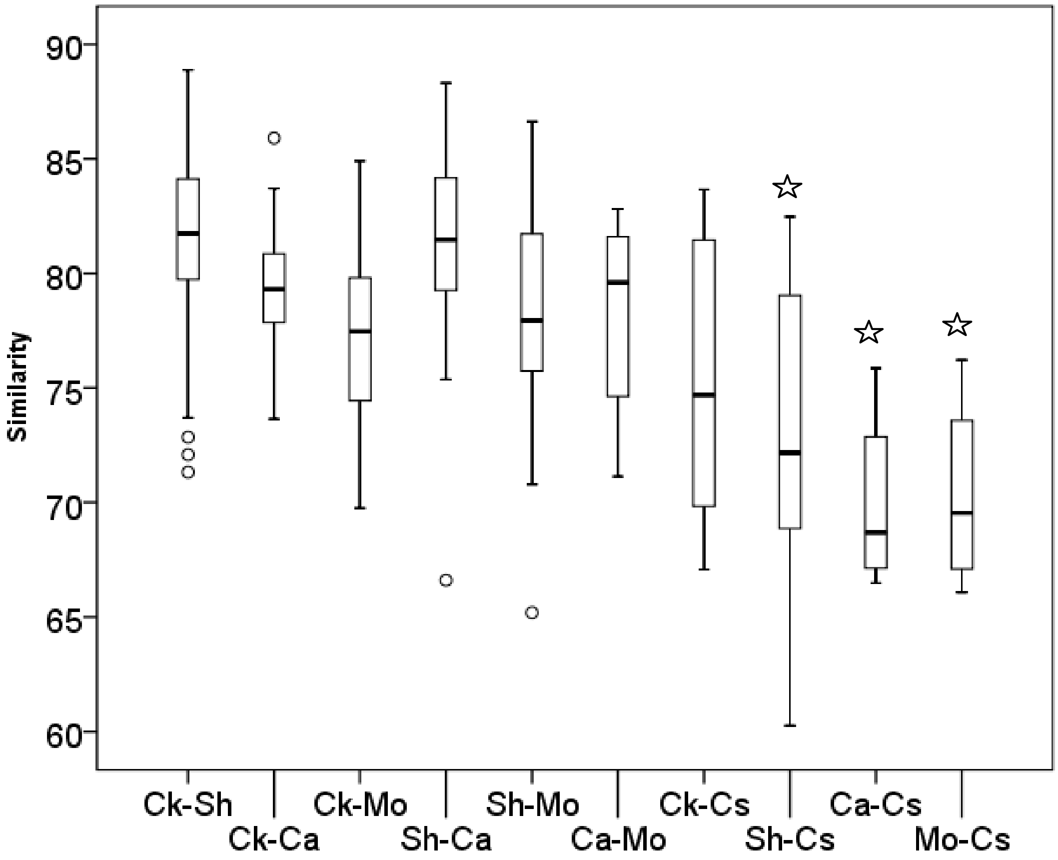

Figure 4. Box plots of average between-area similarity (%) of whistle contour shape for the five areas. Horizontal lines represent mean, boxes interquartiles, whiskers 95% confidence interval and circles outliers. Significant differences between areas are indicated with a star (Mann-Whitney U-test).

3.3.3 Comparison of whistle repertoires

Classification of all complex whistles into categories of similarity resulted in 40 distinct whistle types overall. The number of types created varied between sampling areas, where continental shelf waters provided the highest number (n=22), followed by Shannon (n=20), Connemara and North Mayo (n=19 each), and Cork Harbour (n=14). Out of all distinct whistle types found, 13% were shared between all five areas, 37% were distinct for a single area, and 63.5% were shared between 2 to 4 areas. The highest similarity in distinct whistle types and therefore in whistle repertoires (using the simple matching coefficient), was found between the Shannon Estuary and Connemara (0.73), followed by Shannon/Cork (0.69), Shannon/North Mayo (0.68) and Connemara/North Mayo (0.65). Lowest levels of similarity were found for any combination of inshore compared with continental shelf waters (0.43 to 0.52). Results from comparisons of whistle repertoires are presented in table 5.

Table 5. Overall repertoire similarity between areas, displaying the simple matching coefficient (S_{SM}) on the lower part of the matrix and level of similarity as a gradient of grey on the upper part of the matrix (darker grey symbolise higher similarity).

	CK	SH	CA	MO	CS
CK	-	█	▒	▒	░
SH	0.69	-	█	▓	□
CA	0.62	0.73	-	▒	░
MO	0.62	0.68	0.65	-	□
CS	0.52	0.44	0.52	0.43	-

3.3.4 *Comparisons with US waters*

In order to visualise any clustering resulting from overall vocal variation among sites the average values for each encounter were used in discriminant function analysis. The results indicate clustering of Irish whistles, except for continental shelf samples that clustered closer to US offshore waters (Figure 6). The top four ranked discriminant functions explained 95.4% of the variance (the first two 48.4% and 22.7%). The variables carrier frequency and duration loaded highest on the first canonical discriminant function while max frequency and start frequency loaded highest on the second.

Classification by sampling area for the combined dataset of complex whistles from Irish and US waters when run through CART analysis were relatively low with an overall average of 56.0% and variation between the areas (Irish waters: Cork 77.2%, Shannon 53.2%, Connemara 38.9%, North Mayo 54.0% and continental shelf waters 66.4% and US waters: Beaufort Estuary 66.3%, Beaufort coast 46.5%, Pamlico Sound 58.3% and offshore waters 42.0%). For these comparisons, carrier frequency and start frequency were the most important variables.

Differences were overall also more pronounced between any US communities than for comparisons within Irish waters (except for inshore vs. continental shelf). For the US, the main variation was found between inshore and offshore waters. The most similar areas in US waters were Beaufort Estuary versus Beaufort coast and

Beaufort Estuary versus Pamlico Sound (only one variable varied significantly), showing a similar pattern to what was found in Chapter 4.

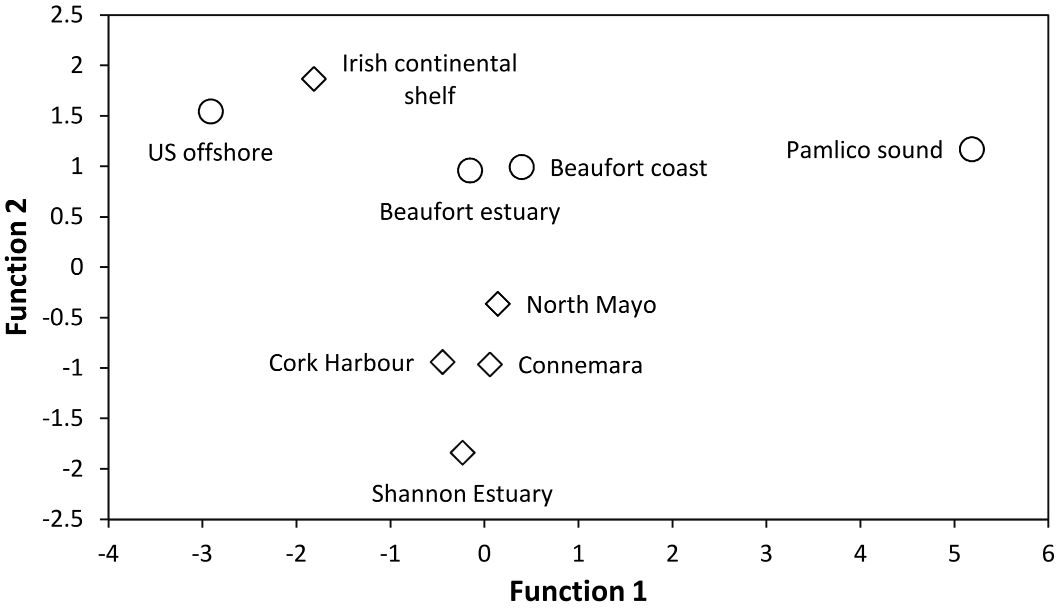

Figure 5. Canonical discriminant function scatter plot of the first two discriminant functions, displaying patterns of similarity in whistle characteristics between communities in Irish and US waters. Symbols indicate sampling country with circles assigned to US and diamond shapes to Irish waters.

3.3.5 Social analysis

A total of 214 permanently marked individuals were identified and matched with UCC catalogues or added to them if previously unknown (Connemara 91, North Mayo 39, Cork Harbour 8, Shannon Estuary 76), while no matches were made with dolphins encountered in continental shelf waters during the study period. While 20 individuals were matched between Connemara and North Mayo, 70 individuals were only seen in Connemara and 19 only sighted in North Mayo waters.

3.4 Discussion

3.4.1 Variation between inshore and continental shelf waters

Significant levels of vocal variation were found between inshore compared with continental shelf waters. It was assumed that the third genetically distinct population indicated from strandings data (Mirimin *et al*. 2011) included the animals encountered in continental shelf waters in this study. This could suggest vocal variation driven by differences in habitat, levels of social interaction and/or by genetics. Even if it is not possible to be certain of genetic distinctiveness for dolphins recorded in continental shelf waters, the groups were in most cases at considerable distance from any coastal sites suggesting low levels of social interaction with coastal communities. However, one encounter occurred relatively close to the North Mayo coast. This encounter included a very large number of individuals (250+) and even if photo identification was only achieved for a very small number of dolphins, no matches have been made between this or any other continental shelf encounter to date. Low levels of social interaction can therefore be assumed between these areas and any vocal variation found is more likely to be reflecting variation influenced by differences in habitat and/or behaviour.

Within-area variation was highest in continental shelf waters, which is what would be expected considering that groups recorded in this habitat were encountered over a larger geographic area and involve a large number of individuals (Wall *et al*. 2009),. The continental shelf encounter with vocalisations most similar to coastal groups was the one closest to the North Mayo coastline, an area where social overlap with coastal dolphins would be more likely. The other two continental shelf encounters both occurred further to the south, between 239 and 286 km from the closest Irish coast (Figure 1).

I hypothesised that there would be selection for acoustic features that could improve group distinction when needed and therefore predicted that these signals would be most distinctive between genetically distinct sympatric groups that may interact during the breeding season. However, the opposite was found with the genetically distinct dolphins in the Shannon Estuary being acoustically similar to other coastal groups, suggesting that if they do interact this does not occur during the breeding season.

As was observed in comparisons of whistle parameter characteristics, the main differences found in whistle contour shapes were between inshore communities and continental shelf waters, further highlighting the variation that exist between continental shelf and inshore communities. Continental shelf waters also provided the highest number of whistles overall and the highest number of distinct whistle types. This is not surprising since this sampling area also included the largest number of individuals of all areas studied and large numbers of dolphins occurring according to abundance estimates made (CODA 2009).

3.4.2 Variation between inshore communities

Photo-identification results supported earlier findings of social interaction and individually overlapping ranging patterns between Connemara and North Mayo waters (Ingram *et al*. 2009), while no such movements or interactions were detected for dolphins identified in the Shannon Estuary, Cork Harbour or continental shelf waters.

It was hypothesised that social isolation and vocal learning within communities could result in increased within-community similarity and elevated between-community variation for genetically distinct communities that may interact during the breeding season since this would be where discrimination would be required. Dolphins recorded in Connemara and North Mayo waters, two genetically similar communities (Mirimin *et al*. 2011) with overlapping ranges and high levels of social contact (Ingram *et al*. 2001, 2003, 2009; O'Brien *et al*. 2009), were found to be comparatively different acoustically. Further investigation into this variation revealed that within community variation was high for animals using in particular North Mayo waters which could indicate that a larger number of animals are part of this community than have so far been accounted for and it is possible that there is a larger network of resident and other more transient groups or individuals present in coastal waters, as has been indicated by previous sighting records on the Irish west coast (Ingram *et al*. 2009; O'Brien *et al*. 2009; Thompson *et al*. 2011).

It is possible that groups which are known to range along Irish coasts do interact to some extent with the resident community in the Shannon Estuary although this has not been established (Ingram *et al*. 2001; O'Brien *et al*. 2009). The period of likely interaction could occur in the winter months when some of the Shannon population spend most of their time outside the estuary (Rogan *et al*. 2000), perhaps using other coastal sites, continental shelf or offshore waters. This period is outside of the main breeding season, which takes place primarily between July and September in the Shannon (Rogan *et al*. 2000; Miller 2009). If social interactions occur at times when breeding does not take place, genetic distinctiveness would still be maintained and distinguishing vocal characteristics would not be required. Alternatively, dolphins may know the identifying signature whistles of every individual in their population and this could also be sufficient for social boundaries to be maintained.

One example of a similar scenario has been found along the central west coast of Florida, where Sellas *et al* (2005), found strong genetic subdivision between the coastal Gulf and Sarasota Bay populations of bottlenose dolphins, even though geographical distances were short and no obvious geographic barriers were present to prevent gene flow. In these waters, interaction between dolphins from neighbouring areas were not uncommon and mixed groups commonly observed (e.g. Fazioli *et al*. 2006). However, mixing was more frequent outside of the primary breeding season and results of genetic studies indicate that while the opportunity may be present, very little interbreeding occur (Sellas *et al*. 2005).

3.4.3 Variation between Irish and US waters

While not ruled out, so far there is no evidence of morphologically distinct ecotypes in Irish waters as described in other areas between coastal and offshore waters (Ross & Cockcroft 1990; Van Waerebeek *et al*. 1990; Hoelzel *et al*. 1998; Perrin *et al*. 2011). US offshore and inshore ecotypes have been found to differ in ranging patterns (Wells & Rhinehart 1999), morphology (Hersh & Duffield 1990; Mead & Potter 1990), parasite loads (Mead & Potter 1990), feeding habits (Mead & Potter 1990), and haematology (Hersh & Duffield 1990) and now also in vocal characteristics (Chapter 4).

Comparisons with US waters indicated clustering of continental shelf whistles with whistles from US offshore waters suggesting potential similarities between these groupings. CART analysis was a poor predictor of site in comparisons between Irish and US waters, indicating similarity in whistle characteristics and likely reflecting general species related similarities.

3.4.4 Conclusions

Central to successful discrimination of an individual or a group through vocal distinctiveness, is the presence of individual or group specific characteristics in the acoustic repertoire. In order to maintain genetic distinctiveness for communities that interact socially during the breeding season, some means of discrimination to community level would have been expected. However, this may not be required if the dolphins recognise all member of their community individually, something that could be possible through the use of individually distinctive signature whistles.

Overall variation between inshore communities was relatively low and communities with high levels of social interaction and overlapping ranging patterns varied more in their acoustic repertoires than genetically distinct communities with no known levels of social overlap. With similarities in habitat characteristics between coastal sites the low levels of variation found could therefore be a habitat driven effect with a social component, demonstrating how vocal variation can reflect the complexity of bottlenose dolphin social systems.

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Chapter 4

Whistle diversity is coupled to ecotype and habitat selection in bottlenose dolphin populations in the western North Atlantic

Contents

Abstract

Communication through sound is important for social and other behavioural interactions in most marine mammals. Dolphins tend to be highly social and whistles are used to express individuality, initiate and maintain contact between socially interactive individuals, and may have a role in group discrimination. This study presents evidence that whistle variability can provide insights into the structuring of sympatric and adjacent populations, indicating patterns of social interaction between and within discrete groups. The variability of whistles recorded from bottlenose dolphins (*Tursiops truncatus*) in estuarine, coastal and offshore waters of North Carolina, USA were compared. Frequency contours of high quality whistles were extracted from recordings and used to examine vocal variability between sampling areas. Clear clustering was found by location in multivariate analyses and overall correct classification to sampling location was high. Significant variation was found for all parameterized variables, and the greatest differences in whistle structure were found for animals recorded in inshore versus offshore waters. Whistles recorded in offshore waters were of higher frequency, longer duration and had a greater number of inflection points, likely reflecting social isolation between offshore and inshore ecotypes as well as indicating that communication requirements in a more open habitat are different from those of inshore waters. Variation among coastally ranging and estuarine animals were more subtle and reflected overlapping ranging patterns and degrees of social interaction. Vocal variation between sympatric groups of dolphins can be the result of adaptations to particular locations, habitats or feeding strategies and vocal distinctiveness could confer an advantage for group living animals, enabling them to distinguish community members and aid in the maintenance of social boundaries.

4.1 Introduction

Group living requires exchange of information through communication. Acoustic variation in animal communities may be driven by a combination of environmental, ecological, biological and cultural factors (Whitehead 1997; Mitani *et al*. 1999; May-Collado & Wartzok 2008). In long-term or permanent social groups, animals may develop behavioural strategies that are based on relationships among group members and individuals may have preferred associates within the group. Selective pressures would then be expected to favour the development of signals coding for group identity in order to allow discrimination (Brown & Farabaugh 1997; Boughman 1997, 1998; Boughman & Moss 2003). In species that live in complex social systems it is sometimes possible to discriminate between individuals, their sex and group using vocal cues. Such individual or group distinctive vocalisations have been found in several social canid species (Tooze *et al*. 1990; East & Hofer 1991; Fromolt *et al*. 1997; Durbin 1998), bats (Boughman 1997; Kazial *et al*. 2008), birds (e.g. Brown & Farabaugh 1997; Wanker *et al.* 1998), cotton-top tamarins (*Saginus oedipus*) (Weiss *et al*. 2001), and seals (Charrier *et al*. 2003). Bottlenose dolphins live in fission-fusion societies, a complex social system where group compositions often change and few stable relationships exist between individuals. While group specific calls are unlikely in such a system, animals may converge on signals on a community level enabling discrimination of sympatric communities.

Bottlenose dolphins (*Tursiops* spp.) have a worldwide distribution throughout cold temperate and warm tropical seas, inhabiting a range of coastal and offshore habitats (Shane & Wells 1986; Rice 1998). The common bottlenose dolphin (*Tursiops truncatus*, Montagu, 1821) can be found in all temperate and tropical ocean basins, while the Indo-Pacific bottlenose dolphin (*Tursiops aduncus,* Ehrenberg, 1833), the only other species currently recognized in this genus, inhabits the Indian and western Pacific Oceans. Local, morphologically distinct forms of *T. truncatus* have also been described in a number of geographic locations (Ross & Cockcroft 1990; Van Waerebeek *et al*. 1990; Hoelzel *et al*. 1998; Perrin *et al*. 2011). In the western North Atlantic, *T. truncatus* is a widely distributed species and occurs in two ecotypes, ‘coastal’ and ‘offshore’ with differences in geographic ranges (Wells & Rhinehart 1999), morphometrics (Hersh & Duffield 1990; Mead & Potter

1990), parasite loads (Mead & Potter 1990), feeding habits (Mead & Potter 1990) and haematology (Hersh & Duffield 1990). The offshore type occurs primarily in waters beyond 34 km from the coast and the coastal type is generally found within 7.5 km of the shore (Torres *et al.* 2003). Analysis of mitochondrial DNA and nuclear genetic markers have revealed that the two types are genetically divergent (Hoelzel *et al.* 1998) suggesting reproductive isolation (Curry & Smith 1997).

Dolphins of the coastal type exhibit varying degrees of site fidelity, ranging from smaller inshore groupings that may be resident or show seasonal site fidelity, to large migratory coastal groups that appear to move latitudinally on a seasonal basis (e.g. Gubbins 2002; Zolman 2002). Resident estuarine dolphins are present in some areas (Barco *et al*. 1999; Gubbins 2002; Zolman 2002; Mazzoil *et al*. 2008; Waring *et al*. 2009) and the degree of movement and genetic exchange between estuarine systems, adjacent coastal and offshore areas, appears to be limited (e.g. Fazioli *et al.* 2006; Rosel *et al.* 2009; Toth *et al.* 2012).

4.1.1 Dolphin vocalisations

For marine mammals, acoustic signals are presumed to be the most likely means to facilitate identification of an individual (Janik *et al*. 2006; Quick & Janik 2012) Whistles are frequency modulated, narrowband, tonal calls used by most delphinid species and have fundamental frequencies that generally fall between 5 and 24 kHz (Caldwell et al. 1990), often with harmonic components at integer multiples of the fundamental frequency that may reach above 100 kHz (ref). The structure of acoustic signals varies between, but also within cetacean species (Steiner 1988, 2011; Matthews *et al*. 1999; Rendell *et al*. 1999a; Baron *et al*. 2008; Papale 2012). While within species variation on a regional basis is relatively uncommon, variation in whistle characteristics have been studied extensively and found between geographically separated locations (Wang *et al*. 1995a; Rossi-Santos & Podos 2006; Baron *et al*. 2008; Gridley 2010) and adjacent populations (Wang *et al*. 1995a; Rossi-Santos & Podos 2006; Baron *et al*. 2008; May-Collado & Wartzok 2008; Gridley 2010; Hawkins 2010). For the bottlenose dolphin (*Tursiops* spp.) such variation has been identified among social groups (Janik 2000) and between different locations (Ding *et al.* 1995; Morisaka *et al.* 2005a). While vocal variation has been studied extensively between populations and social groups, vocal distinctiveness in relation to phenotypic variation or habitat selection has not been studied in detail.

Bottlenose dolphins use highly stereotyped and individually specific ‘signature whistles’ (Caldwell and Caldwell 1965) which often comprise over 90% of whistles emitted when separated from other individuals in captive conditions (Caldwell and Caldwell 1965) or when temporarily restrained around 40-70% when recorded in the wild (Cook *et al.* 2004; Watwood *et al.* 2005). Signature whistles are believed to be used to maintain group cohesion, have a function as contact calls (Janik & Slater 1998) and to be emitted especially when an animal is separated from other dolphins.

In North Carolina waters, photo-identification and telemetry studies of bottlenose dolphins have indicated the existence of a population boundary for estuarine groups (described as ‘stocks’ for management purposes) situated at Beaufort Inlet (Read *et al*. 2003). While animal movements have been reported between estuaries and adjacent coastal waters (Urian *et al.* 1999), estuarine animals are genetically distinct from migratory animals found in coastal waters (Rosel *et al.* 2009; Caldwell 2001). Bottlenose dolphins that occupy the estuarine waters of Pamlico Sound (North of Beaufort Inlet) during the summer months show variation in seasonal ranging patterns (Read *et al*. 2003), genetics (Rosel *et al.* 2009; Caldwell 2001) and stable isotope signatures (Cortese 2000) when compared with more southern estuarine groups.

Offshore bottlenose dolphins are primarily distributed along the outer continental shelf and continental slope with a separation of the inshore and offshore ecotypes across the bathymetry during summer months (NMFS 2008) while the range of inshore and offshore groups overlap spatially during winter months (Torres *et al.* 2003).

4.1.2 Study aims and objectives

This study aimed to examine vocal variation in the bottlenose dolphin in the western North Atlantic. The objectives were to test whether whistle characteristics vary between groups of bottlenose dolphins using various habitat types, with different levels of social interaction and phenotypic variation. Limited information exists on the level of social mixing of bottlenose dolphins in the western North Atlantic and assessing different aspects of vocal variation could provide insights into local community structure, reveal patterns of social interaction, and indicate geographical and/or social separation.

4.2 Methods

4.2.1 Survey areas

Beaufort Inlet in North Carolina, USA links coastal waters to a complex estuarine system, separated from the continental shelf of the Atlantic Ocean by barrier islands that includes Cape Lookout. The Newport River connects with the Neuse River, via Core Creek to the north, where a canal was opened in 1964 allowing contact between Beaufort estuary and Pamlico Sound. Pamlico Sound is a large estuary separated from the Atlantic Ocean by the Outer Banks which are a row of low, sandy barrier islands, including Cape Hatteras (Figure 1).

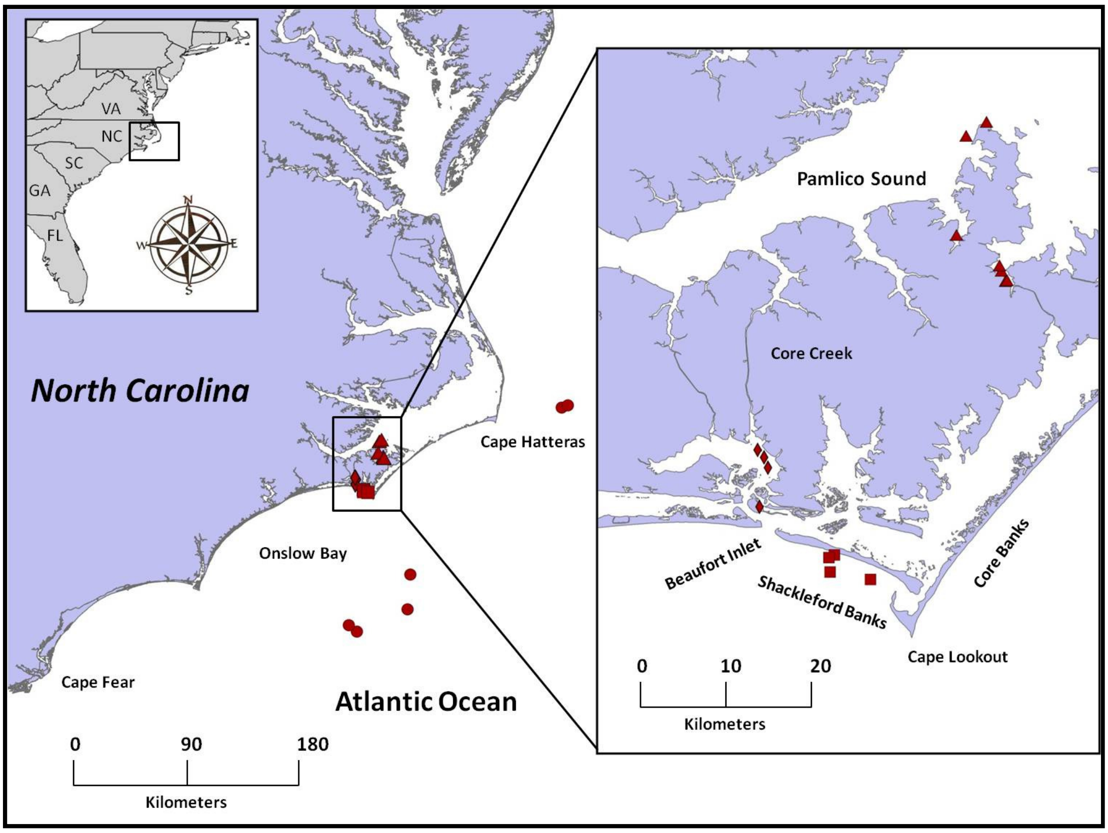

Figure 1. Study area in North Carolina, indicating coastal, estuarine and offshore areas surveyed. Symbols indicate encounter locations, in Beaufort coastal (□) and estuarine waters (◊), Pamlico Sound (Δ) and offshore areas (○).

4.2.2 *Acoustic Sampling*

To standardise field techniques, acoustical data were collected using the same recording system when possible and deployed in the same manner. However, the suitability of recording systems depended on survey vessel used and equipment available and varied between the surveys (Table 1). Recordings of bottlenose dolphins were collected from Beaufort estuarine and coastal waters during small boat surveys in 2010, while recordings from Pamlico Sound were collected in June – July 2007 and in September and October 2008 (Laura 2009). Offshore recordings were collected in July 2008 and in August and September 2009 between 50 and 150 km from the coast (Figure 1), as part of a larger monitoring project (Hodge 2011). For analysis purposes, 96 kHz sampling rate was used for all recordings providing an effective bandwidth of 48 kHz (except for recordings from Pamlico Sound where the sampling rate was 88 kHz and effective bandwidth 44 kHz). Recordings made with a higher sampling rate were down-sampled using Adobe Audition 3.0$^{©}$ (1992-2007 Adobe Systems Incorporated) to improve comparability between sampling occasions. While the upper frequency limit of the recorder was 44-48 kHz (88-96 kHz sampling rate) the limit of the system was determined by the 30 kHz range of the hydrophone. Dynamic range (bit depth) varied between some of the systems which may have influenced the detectability of weaker whistles in offshore waters.

Table 1. Summary of recording equipment used, including type of hydrophone, recording device, frequency response and sampling rate for each setup.

Survey area	Hydrophone type	Recording device	Frequency response	Sampling rate
Beaufort Estuary & coast	Single channel hydrophone, model HTI-96-MIN. High Tech Inc., MS, US	Edirol R-09-HR digital solid state recorder, Roland Systems Group, UK	5 Hz to 30 kHz ± 1.0 dB, -165 dB, *re* 1V/µPa	96 kHz 24 bit
Pamlico Sound	Single channel hydrophone, model HTI-94-SSQ. High Tech Inc., MS, US	Fostex FR-2 field memory recorder, Foster Electric Co., Ltd	2 Hz to 30 kHz ± 1.0 dB, -165 dB *re* 1V/µPa	88 kHz 24-bit
Offshore	Four element towed hydrophone array. Seiche Instruments, UK	Laptop with MOTU traveller interface Mark of the Unicorn, Cambridge, MA, US	2 Hz to 100 kHz ± 1.0 dB, -165 dB *re* 1V/µPa	192 kHz 16-bit

The recorded sounds were visualized using the spectrogram view in RAVEN PRO v 1.4 (Cornell Lab of Ornithology), a Hanning window and Fast-Fourier transforms (FFTs) with 256 points for each analyzed time window. Whistle contours were quality graded based on the signal-to-noise ratio (SNR) and had to be clearly visible above background noise levels to be included in the analysis. This also required that start and end points and the overall shape of whistles were clear and unambiguous so that entire contours could be distinguished from any surrounding sounds. Single whistle sound files were created and time of start and end points of each whistle logged together with information about the presence of harmonics and of whistle quality and stored in an MS Access database.

Contour details for the fundamental frequency contour (lowest frequency) of each high quality whistle were extracted using MATLAB (The MathWorks Inc., Natick, MA) and a custom made script, BELUGA (Deecke; *unpublished*) using FFTs with 512 points for each analyzed time window, 87.5% overlap and a Hanning window. In BELUGA, whistles were traced using a semi-automated process whereby a peak-finding algorithm selects the fundamental whistle contour under user supervision, allowing filtering and manual correction of minor mistakes resulting from interference from echolocation or high amplitude harmonics. The resulting contour was saved as a text file consisting of a list of frequencies with known time and frequency resolution (0.667ms and 23.438 kHz).

Ten basic whistle variables were calculated and exported into MS Excel using another custom written script in MATLAB (Cormac Doherty, University College Dublin, Ireland) and included: maximum frequency, minimum frequency, start frequency, end frequency, frequency range (max – min frequency), carrier frequency (median of max and min frequency), number of inflection points (changes between positive and negative slope, presence of harmonics, duration and initial slope (average slope of the initial 30ms of the whistle). For the variable harmonics, only presence or absence was used as a measure since the upper limit in sampling rate would result in exclusion of any frequencies extending above the effective bandwidth of the system.

4.2.3 Photo identification

Photographs of dolphin dorsal fins were taken during acoustic sampling sessions to investigate ranging patterns of individuals and levels of social interaction between the different sampling areas. The results were used to investigate the potential for whistle sharing and the likelihood of convergence on similar whistle characteristics based on preferred associations and overlapping ranging patterns. Photographs were compared between encounters and with existing id-catalogues maintained by Duke University Marine Lab, Beaufort and the University of North Carolina, Wilmington. To reduce identification errors only high quality (entire fin visible, in perpendicular view, focus and good light) photographs of dorsal fins with clear and permanent (e.g. large nicks) or semi-permanent markings (small nicks and rakes) were used. Additionally, the presence of the commensal barnacle (Xe*nobalanus globicipitis*) attached to the fins and flukes of dolphins were noted and the prevalence (number of dolphins with at least one barnacle attached) within groups determined. The presence of these barnacles has in combination with information on group size, avoidance behaviour, colouration and distance from the shoreline (Toth *et al*. 2012).been used to distinguish between nearshore and offshore dolphin populations in US Atlantic waters.

Social structure among North Carolina inshore groups was investigated using SOCPROG 2.4 (Whitehead 2009), a series of MATLAB programs that are designed for social analysis, population structure analysis and the study of movement patterns of individuals. Network analysis was performed within SOCPROG (using the half weight index of association) to examine relationships between associates and the program NETDRAW 2.123 (Borgatti 2002) was used to visualize these relationships. NETDRAW allows manipulation regarding groupings and the resulting nodes (which each represent one individual) can be coded by colour or shape, based on varying attributes relating to the individual in question.

4.2.4 Analysis of whistle variation

Statistical analyses were conducted using PASW Statistics 18 (SPSS) and R statistical software (R version 2.8.1. The R Foundation for Statistical Computing, 2008). Descriptive statistics including the coefficient of variation (CV) were calculated for all whistle variables and a number of multivariate methods were used to investigate and test for variation within and between the sampled areas. Clustering resulting from combined measures of similarities and dissimilarities of duration and frequency variables was investigated using hierarchical cluster analysis based on mean values for each encounter (using between groups linkage, Euclidean distances and standardization through z-scores). Discriminant function analysis (DFA) was used to provide a visual representation of the pattern of similarity between and within sampling areas and to evaluate which variables best discriminated between naturally occurring groups.

To further explore the relationship between sampling areas based on whistle characteristics, classification and regression tree analysis (CART) was used within the Salford Predictive Modeller Builder v 6.6 ($^{©}$Salford Systems). CART was applied primarily as a descriptive technique to further assess which variables best discriminate between naturally occurring groups, but also to generate predictive classification scores which measures how effectively whistles are classified to sampling location. CART uses an iterative process (Breiman *et al*. 1984) that recursively partitions the dataset based on the best predictor variable at each two way split until all data points are classified. In this case, sampling area was used as the response variable and eight whistle variables (excluding frequency range and presence of harmonics) used as predictor variables. This method does not assume normality, linearity, homogeneity or independence (Venables & Ripley 1997). Branches in the resulting tree output lead to terminal nodes representing the final classification, and the tree can be grown or pruned to explore variation in resulting subgroups. The CART method has been used in a number of other ecological studies (e.g. Torres *et al.* 2003; Goetz 2005; Friedlaender *et al.* 2006) including work on the spatial distribution of coastal and offshore ecotypes of bottlenose dolphins (Torres *et al.* 2003) and vocal differentiation between dolphin species (Gannier *et al*. 2010). A fraction of the dataset (2%) was used for auto validation and priors were set to match sample frequencies in order to accommodate differences in sample size. Finally, to account for the potential lack of serial independence within the whistle samples due to recordings of multiple similar whistles from the same individual, differences in whistle variables between sampling areas were averaged per encounter and tested using the non-parametric Kruskal-Wallis test and Mann-Whitney U test with Bonferroni corrections for pair-wise post-hoc comparisons .

4.3 Results

Recordings were made during 30 dolphin encounters in which duration varied between 7 minutes and 2.16 hours with a median of 1.23 hours (total recording time 14.8 hours) and of which six did not include any whistles and a further four contained only poor quality whistles that were excluded from further analysis. The contours of a subsample including 2 829 high quality whistles were extracted out of a total 10 216 whistles recorded (Table 2).

Table 2. Sampling effort showing number of encounters in each sampling area (number of encounters with whistles within brackets), total recording effort in minutes, total number of whistles logged and number of high quality whistles extracted.

Area	Number of encounters	Recording effort (minutes)	Number of whistles	Extracted whistles
Beaufort estuary	10 (5)	259.7	1 255	368
Beaufort coast	6 (4)	277.1	4 277	1 245
Pamlico Sound	7 (5)	205.0	1 571	538
Offshore waters	7 (6)	148.8	3 113	678
Total	30 (20)	890.6	10 216	2 829

Whistles recorded in Beaufort coastal waters exhibited the lowest mean values for duration, number of inflection points and all frequency variables except start frequency for which Beaufort estuary whistles had a slightly lower value (Table 3). Whistles from offshore waters provided the highest mean values for all frequency variables except frequency range for which Pamlico Sound had the highest value. Harmonics were present for approximately half of all whistles with small variation between sampling areas. Coefficients of variation (CV) values were consistent between different sampling areas and frequency variables (except frequency range and initial slope) exhibited the lowest CV values, while duration, number of inflection points and initial slope had higher CV values for all four sampling areas (Table 3).

Table 3. Descriptive statistics including the coefficient of variation (CV) for nine whistle variables measured from the four areas (harmonics excluded here since only presence or absence was used for this variable). Frequency components are measured in kHz, initial slope in ΔkHz/s and duration in seconds.

		Frequency (kHz)								
Area		MaxF	MinF	SF	EF	CF	FR	IS	D	I
Beaufort Estuary	Mean	14.8	6.6	8.3	11.3	10.7	8.3	0.9	0.5	1.3
	S.D.	5.1	2.6	3.7	5.8	3.3	5.0	1.0	0.4	1.6
	CV	0.34	0.45	0.45	0.50	0.31	0.61	1.19	0.82	1.07
	Low	1.9	1.0	1.0	1.8	14.2	0.1	-8.0	0.03	0
	High	41.0	34.4	35.0	41.0	37.7	30.8	4.5	2.3	8.0
Beaufort coast	Mean	12.8	6.5	8.4	9.7	9.7	6.3	0.9	0.4	0.8
	S.D.	4.9	2.8	3.8	5.4	3.6	4.3	1.1	0.3	1.3
	CV	0.38	0.43	0.45	0.56	0.37	0.69	1.23	0.79	1.19
	Low	1.3	0.3	1.0	0.3	12.0	0.1	-12.0	0.01	0
	High	42.4	22.8	27.1	30.9	25.9	34.3	6.9	2.3	9.0
Pamlico Sound	Mean	14.8	7.3	9.7	11.3	8.2	10.4	1.2	0.4	1.2
	S.D.	4.8	3.3	4.0	5.5	4.4	4.0	1.7	0.4	1.5
	CV	0.32	0.44	0.41	0.49	0.54	0.35	1.40	0.89	1.02
	Low	3.2	1.9	1.9	2.6	0.1	0.5	-15.5	0.02	0
	High	37.0	29.4	30.8	32.9	29.3	30.4	15.5	2.3	14.0
Offshore	Mean	17.3	8.0	10.6	11.5	12.7	9.5	0.7	1.0	2.0
	S.D.	4.2	2.3	4.0	5.3	2.6	4.5	0.9	0.6	1.9
	CV	0.24	0.29	0.37	0.46	0.20	0.47	1.22	0.66	0.98
	Low	7.1	2.8	2.8	3.6	6.1	0.8	-7.4	0.02	0
	High	42.1	29.2	29.2	34.9	32.0	36.1	5.7	4.5	11.0

Variable codes: MaxF=max frequency, MinF=min frequency, SF=start frequency, EF=end frequency, FR=frequency range, CF=carrier frequency, D=duration, H=harmonics, I=inflection points.

Whistles from Beaufort Estuary and Beaufort coastal waters clustered closely together while Pamlico Sound and offshore groups clustered further apart when results from discriminant function analysis were plotted. One exception was one of the Pamlico Sound encounters which clustered with Beaufort Estuary whistles (Figure 2). The most important variables for discriminating between the communities were carrier frequency and duration for the first discriminant function and max frequency for the second function.

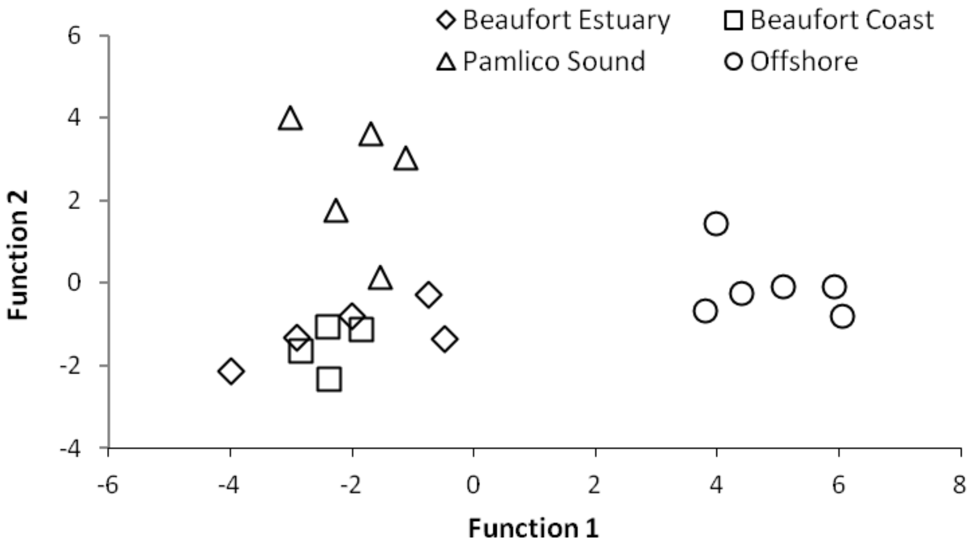

Figure 2. Canonical discriminant function scatterplot of the four study areas using the first two functions, which combined accounted for 98% of the observed variance.

Further multivariate analysis showed a clear division between offshore and inshore groups (using Hierarchical cluster analysis) and divided the dataset into four main clusters, which included: two offshore clusters, one cluster for Pamlico Sound (including one encounter from Beaufort estuary), and all other Beaufort estuarine and coastal whistles grouped together forming a fourth cluster (Figure 3). Finally, one encounter from Pamlico Sound (P10) did not cluster closely with any other inshore groupings (Figure 3).

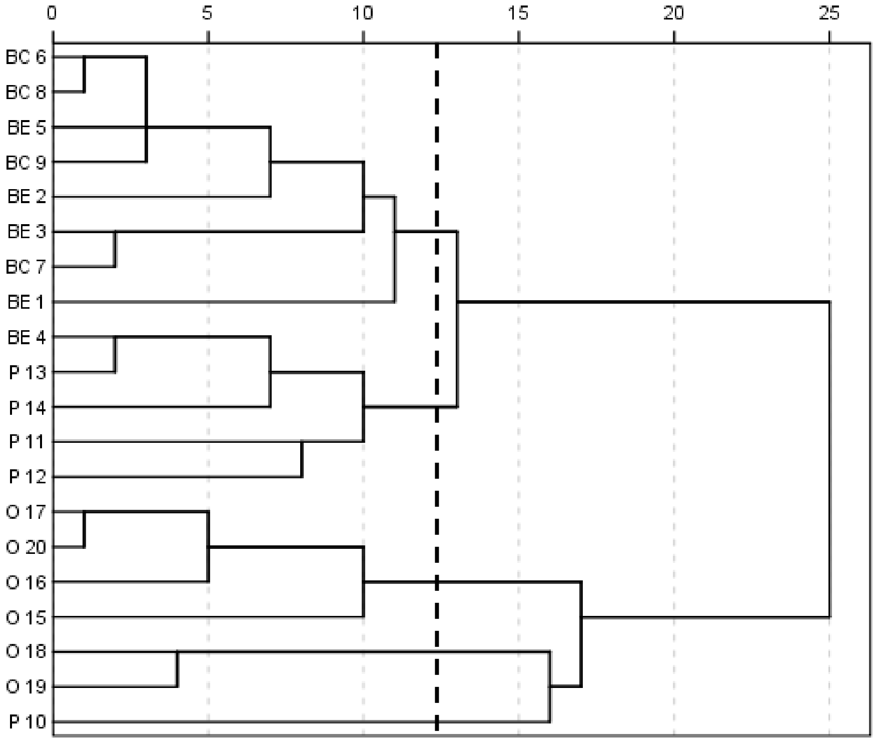

Figure 3. Dendrogram from agglomerative hierarchical cluster analysis derived using mean values of whistle variables for each encounter (BE = Beaufort estuary, BC = Beaufort coast, P = Pamlico Sound and O = offshore waters). Numbers along the vertical axis represents scaled squared Euclidean distance. Dashed line indicates the main clusters found.

4.3.1 Analysis of social structure

Estimated group size ranged from one to 92 with largest groups encountered in Beaufort coastal waters and smallest groups in Beaufort estuarine waters. Dolphins were matched with existing catalogues (Table 4) providing details of movement patterns and associations between individuals, both during this study and from historical records.

Some of the individuals matched with previous records were well known from Beaufort Estuary, with 10 dolphins previously sighted between eight and 51 times and four individuals first recorded in 1995 indicating a high level of site fidelity. For animals encountered in Pamlico Sound in 2007/08, the majority (65%) had previously been recorded around Pamlico Sound or Beaufort Estuary and some also in estuaries around Wilmington in the South, suggesting large home ranges. Complex ranging patterns were found with individual preferences for either

Beaufort Estuary or Pamlico Sound, for a combination of these two areas, or a preference for Beaufort Estuary, southern estuaries and nearby coastal areas. None of the dolphins photographed in Beaufort coastal waters in 2010 had ever been recorded in estuarine waters.

Investigations into individual overlap between groups in relation to similarity in whistle characteristics (based on squared Euclidean distance values from hierarchical cluster analysis) revealed higher levels of acoustic similarity for encounters that had individuals in common. Network analysis further illustrated how these high levels of association highlight the close relationship between Beaufort Estuary and Pamlico Sound. However, high acoustic similarity was also found between Beaufort Estuary groups and one of the groupings in Pamlico Sound which did not contain any individuals known to use Beaufort estuarine waters but was part of the overall network that links Beaufort Estuary and Pamlico Sound. While acoustic similarity was also evident between Beaufort Estuary and Beaufort coastal waters there was a complete lack of association between any estuarine and coastal dolphins encountered (Figure 4).

Table 4. Summary of photo-identification results including total number of photographs taken, number of individuals identified (best estimate) and number of individuals matched with local catalogues.

Area	Year	Number of photographs	Total individuals	Matched individuals
Beaufort Estuary	2010	1 795	70	13
Beaufort coast	2010		184	3
Pamlico Sound	2007/08	965	90	44

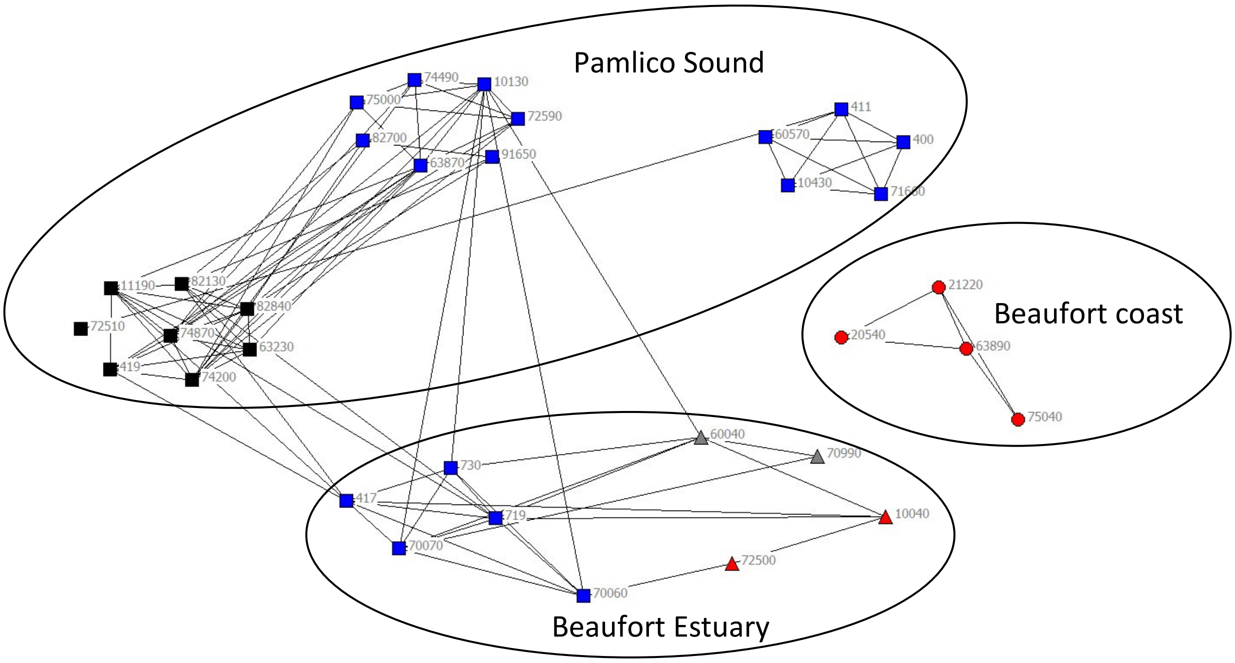

Figure 4. Photo identification results combined with acoustic findings in network analysis. Each node represents an identified individual (catalogue-id numbers in grey) and lines between nodes indicate associations between individuals. Individuals are grouped according to encounter and colour coded by acoustic similarity (based on squared Euclidean distance values). Symbols indicate likely stock membership (Δ=Southern North Carolina Estuarine System stock, □=Northern North Carolina Estuarine System stock and ○=Southern North Carolina Migratory stock).

4.3.2 Xenobalanus load

As an additional indicator of habitat use, the occurrence of the barnacle *Xenobalanus spp. was examined* from identification photographs. A larger number of dolphins were found with the barnacle in Beaufort coastal waters, where 78% of all individuals had at least one barnacle attached to its fins or flukes. In contrast, the prevalence of barnacles was low in estuarine groups with the barnacle only present on 14% of dolphins in Beaufort Estuary and on 1% of dolphins in Pamlico Sound. The difference in presence and absence of *Xenobalanus spp.* between estuarine (Beaufort Estuary and Pamlico Sound combined) and coastal dolphins (Figure 5) was highly significant (Chi^2=169.7, df=1, p<0.001), suggesting a relatively high degree of habitat fidelity.

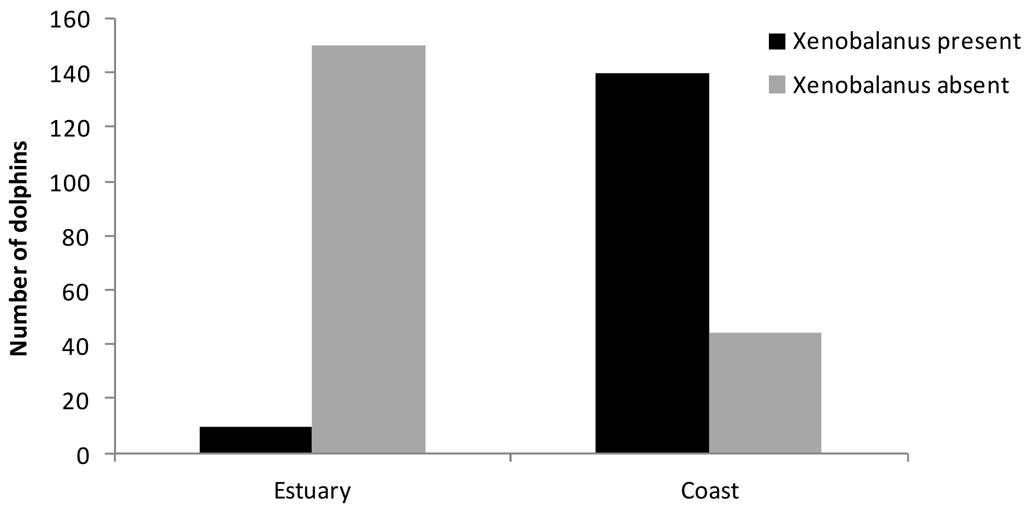

Figure 5. Presence and absence of the barnacle Xenobalanus spp. on number of dolphins encountered in estuarine (Beaufort Estuary and Pamlico Sound) and coastal waters.

4.3.3 Community predictions based on whistle characteristics

The results of CART analysis showed that whistles recorded in inshore waters were rarely classified with those recorded from offshore groups. A total correct classification score of 78% for offshore groups and an 85% correct score for Beaufort coastal whistles indicate that whistles from these areas can be reliably identified to area by basic whistle characteristics alone (Table 5). In contrast, correct classification rate for whistles from Beaufort estuarine waters was low and whistles from this area were likely to be classified with whistles from either Beaufort coastal waters or from Pamlico Sound (Table 5). Beaufort coastal whistles were also occasionally assigned to Beaufort estuary and rarely to Pamlico Sound. Carrier frequency, followed by duration and max frequency were the most important discriminating variables included (when considering primary splitters only) while number of inflection points and start frequency were the least important discriminating variables.

Table 5. Results from classification of whistles using CART analysis showing percentage of whistles classified to the various sampling areas for the test sample (20% randomly selected from original dataset).

Sampling area	**In class**	**Beaufort Estuary**	**Beaufort coast**	**Pamlico Sound**	**Offshore**	**Total (%)**
Beaufort Estuary	82	**14.6%**	65.9%	6.1%	13.4%	100
Beaufort coast	242	5.4%	**84.7%**	1.7%	8.3%	100
Pamlico Sound	114	8.8%	23.7%	**58.8%**	8.8%	100
Offshore	135	2.2%	20.0%	0.0%	**77.8%**	100

4.3.4 Variation in means of whistle variables

Significant variation was found between the sampling areas in all whistle variables included (Kruskal-Wallis: p<0.001, df=3) and pair-wise, post-hoc comparisons (Mann-Whitney U tests) revealed that these differences were significant in 43 out of 54 pair-wise comparisons. Most variables varied significantly between inshore and offshore waters while the least amount of difference was found between Beaufort Estuary and Pamlico Sound and between Beaufort estuarine and coastal waters (Table 6).

Table 6. Results from pair-wise comparisons between all areas using Mann-Whitney U tests (* p < 0.001). Frequency variables are in kHz, duration in seconds, harmonics in percentage of whistles with harmonics and inflection points in means of number of inflections.

	Beaufort Estuary vs. Coastal	**Beaufort Estuary vs. Pamlico**	**Beaufort Coastal vs. Pamlico**	**Beaufort Estuary vs. Offshore**	**Beaufort Coastal vs. Offshore**	**Pamlico Sound vs. Offshore**
MaxF	*	NS	*	*	*	*
MinF	NS	*	*	*	*	*
SF	NS	*	*	*	*	*
EF	*	NS	*	NS	*	NS
FR	*	*	*	*	*	*
CF	*	*	*	*	*	*
D	*	*	NS	*	*	*
H	NS	*	*	NS	NS	*
I	*	NS	*	*	*	*

Variable codes: MaxF=max frequency, MinF=min frequency, SF=start frequency, EF=end frequency, FR=frequency range, CF=carrier frequency, D=duration, H=harmonics, I=inflection points.

4.4 Discussion and conclusions

This study presents clear evidence of vocal variation among bottlenose dolphins in North Atlantic waters. This variation was evident at different spatial scales and particularly prominent between animals using inshore versus offshore waters in the US, reflecting known genetic and social separation between ecotypes inhabiting these different habitats (Hoelzel et al. 1998; Torres et al. 2003). While other studies have shown variation in other characteristics between these ecotypes (Hersh & Duffield 1990; Mead & Potter 1990; Wells & Rhinehart 1999), this is the first study to demonstrate considerable vocal distinctiveness.

More subtle differences were found at a smaller scale, in inshore waters where adjacent and sympatric groups are present. Vocal variation could here be the result of varying levels of social mixing or be due to adaptations to the characteristics of particular locations, habitats, feeding or predator defence strategies. The differences found in this study may thus reflect differences in degrees of social interaction, in habitat use and in ranging behaviour.

Whistles recorded from offshore animals demonstrated overall higher mean frequencies, longer durations and more inflection points compared to coastal and estuarine dolphins. Some of this variation is likely to be of social origin, reflecting the need for identification within and between social units or for distinction between communities, playing a role in the maintenance of social boundaries. Variation may also be a response to differences in environmental conditions between habitats, reflecting disparity in sound transmission properties due to variation in water depth and temperature (Kuperman & Lynch 2004), or reflect a response to masking due to ambient noise levels (Ding *et al.* 1995; Rendell *et al.* 1999; Lesage *et al.* 1999). Such vocal plasticity has been proposed to promote acoustic variation between populations in other areas (May-Collado & Wartzok 2008; Jensen et al. 2010, 2012).

Since some of the morphological differences between the ecotypes are fundamental to structures for sound production (e.g. differences in the basal part of the rostrum) (Kurihara & Oda 2007; Perrin *et al*. 2011), the variation found between inshore and offshore groups could also reflect such morphological differences as well as indicate responses to variation in background noise levels, habitat characteristics and behaviour. However, offshore animals are larger than those in nearshore waters and overall use of higher frequencies were not expected. However, another study found a similar pattern within the *Tursiops* genus with the larger *T. truncatus* using higher frequencies than the smaller *T. aduncus* (Gridley 2010).

In general, since whistles are learned signals, acoustic variation tends to be less pronounced if populations have overlapping home ranges and interact socially (e.g. Wang et al. 1995a). This appears to be true for North Carolina bottlenose dolphin inshore communities between which there are no apparent morphological differences and the vocal variation is less than what was found between inshore and offshore waters. While the results showed high levels of similarity of whistles from Beaufort estuarine and coastal groups, detailed analysis revealed a comparably high level of similarity between Beaufort Estuary and the estuarine waters of Pamlico Sound as well. Insights gained through photo-identification explained some of the observed patterns, revealing a high degree of individual overlap between the two estuarine areas. Greater similarity in whistle characteristics was also found when individuals were shared between groups or when a high level of social interaction and overlapping home ranges were revealed from historical sighting records. It is however possible that some of the patterns found are due to repeated recordings of the same individuals, using their individually distinctive signature whistles and therefore creating some pseudo replication in the data set.

Vocal variation may reflect a need for identification, on an individual, group or species level. Recognition of individuals or groups based on call characteristics alone has been shown for some animal species, generally due to the existence of distinctive dialects. Dialects are common among birds (Nelson & Marler 1994; Wright & Wilkinson 2001; Slabbekoorn & Smith 2002; Ellers & Slabbekoorn 2003; Beecher & Burt 2004; Soha *et al*. 2004; Yoktan *et al*. 2011), and have been found in some mammals, including bats (Boughman 1997), humans (Clopper *et al*. 2006) and non-human primates (Green 1975; Mitani *et al*. 1992), but are uncommon among cetaceans where they have so far only been shown for killer whales (*Orcinus orca*) (Ford 1991; Deecke *et al*. 1999, 2000; Foote & Nystuen 2008; Riesch & Deecke 2011; Filatova *et al*. 2012) and sperm whales (*Physeter macrocephalus*) (Weilgart & Whitehead 1997; Rendell & Whitehead 2001, 2005; Deecke *et al*. 2010; Antunes *et al*. 2011).

Beaufort coastal encounters included a large number of animals, of which very few had previously been recorded in the study area and none had ever been encountered in estuarine waters. Higher prevalence of *Xenobalanus* among these animals indicate that they are likely to range into deeper coastal waters (Toth *et al*. 2012) and they may therefore be part of a more migratory assemblage. This is consistent with other findings in the western North Atlantic where the percentage of groups carrying barnacles was successfully used as one of the variables distinguishing populations (Toth-Brown & Hohn 2007). The prevalence of *Xenobalanus* was significantly higher for groups encountered further from the shore than groups closer to the shoreline in coastal areas (<2 km). The level of barnacle occurrence may be determined by water temperature (Orams & Schuetze 1998) and has been found to decrease when the water temperature increases which could explain the lower relative abundance in warmer estuarine waters. However, no published study was found specifically comparing *Xenobalanus* presence between estuarine and coastal waters to support this suggestion.

Considering the close proximity of Beaufort estuarine and coastal waters and the high level of vocal similarity found between these areas, some evidence of social interaction would have been expected. However, even though this was not evident during this study, historical records confirmed that some estuarine dolphins regularly use nearby coastal areas and overlap with more migratory and transient groups is therefore likely, at least on a seasonal basis (Rosel *et al*. 2009). The apparent lack of association between acoustically similar groups could be further explained if overlap coincides with levels of low scientific survey effort. The lack of variation could therefore reflect complex movement patterns of dolphin groups in North Carolina waters and indicate patterns of seasonal overlap of migratory, coastal and estuarine assemblages.

Our findings showed that vocal variation can be found on a range of scales for the common bottlenose dolphin. Vocal variation between adjacent and sympatric groups can be the result of vocal learning, social isolation or adaptations to particular locations or habitats. Such behavioural plasticity in bottlenose dolphins could lead to community specialization over time and therefore indicate that the differences found are behaviourally maintained and socially functional. While the sources of variation are complex, resulting vocal distinctiveness and potential community specialization could confer an advantage to group members, enabling distinction on an individual as well as on a group level and thus aid in the creation and maintenance of social boundaries.

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Chapter 5

Signature whistle production, use and diversity among sympatric, adjacent and geographically separated bottlenose dolphin communities in the North Atlantic.

Contents

Abstract

Common bottlenose dolphins (*Tursiops truncatus*) use individually distinctive, "signature whistles" as contact calls. Recordings from a number of free-ranging bottlenose dolphin communities in western Irish and eastern US Atlantic waters were analysed to investigate signature whistle use and to examine how frequency and time characteristics and whistle contour shape of signature whistles vary between geographically separated areas and between adjacent communities in different habitat types (estuarine, coastal, continental shelf and offshore waters). A dynamic time warping, neural network and bout analysis approach were employed to identify signature whistles, resulting in 66 identified in Irish waters and 96 in US waters. Repetitions of these made up between 13 and 58% of all whistles recorded from the different communities and this emission rate was correlated to group size and to the number of whistles emitted overall. High levels of acoustic variation were found between US communities, while Irish communities showed less variation. Significant differences in signature whistle characteristics were found between the different ecotypes in inshore and offshore waters in the western Atlantic, and it is possible that these differences are related to social isolation as well as morphological variation between the ecotypes. The highest proportion of signature whistles to total number of whistles was recorded from dolphins in continental shelf waters (Ireland, 58%) and in offshore waters (US, 48%), likely reflecting an increased requirement for more frequent use of contact calls in large, highly mobile communities and the importance of maintenance of group cohesion in a more open water habitat.

5.1 Introduction

While humans and other animals that use sound for individual recognition are dependent on voice characteristics that are morphologically determined (Fitch 2000; Gentner et al. 2000; Soltis et al. 2005; Reby et al. 2006), common bottlenose dolphins (*Tursiops truncatus*) have individually distinctive calls known as “signature whistles” that appear to serve a similar function (e.g. Cook et al. 2004a; Janik et al. 2006a; Sayigh et al. 2007). The development of these highly stereotyped calls is strongly influenced by learning (Tyack & Sayigh 1997; Janik & Slater 2000; Tyack 2008) and they have been shown to encode identity information even when voice features are removed (Janik et al. 2006). Such transmission of identity information that is independent of the caller’s voice or location is otherwise only found in humans (Janik et al. 2006). The ability to learn is maintained through life and bottlenose dolphins can copy or mimic whistles (Tyack 1986; Janik 2000) in order to address another individual and signature whistles thus play a role in the maintenance of social bonds (King et al. 2013).

The existence of signature whistles in bottlenose dolphins was first proposed by Caldwell and Caldwell (1965) who demonstrated that when an individual dolphin was kept isolated, the majority of the whistles emitted were of an individually distinct type that could easily be distinguished from any other dolphins’ predominant whistle in the group. Signature whistles can remain stable for decades, although some features like duration or frequency may vary (Caldwell et al. 1990) and some males (*T. aduncus*) may alter their signature whistle later in life to resemble that of an alliance partner (Watwood et al. 2004). Variation in signature whistle development has been found between the sexes, where female calves more commonly produce signature whistles that are distinctly different from those of their mothers, likely reflecting higher levels of association between females creating selective pressures for vocal distinctiveness (Sayigh et al. 1995).

Signature whistles are thought to aid in the maintenance of group cohesion, have a function as contact calls (Janik and Slater 1998) and comprise over 90% of dolphin whistle repertoires in captive conditions when kept separate from other dolphins (Caldwell and Caldwell 1965) and around 40-70% in the wild (Cook et al. 2004;

Watwood et al. 2005). Non signature whistles are often referred to as ‘variant whistles’ (Tyack & Sayigh 1997). These are non-stereotypic, individually non-specific, produced in a variety of situations (Tyack & Sayigh 1997) and have a function that is largely unknown.

Common bottlenose dolphin whistles range in mean minimum frequencies from 5.3 kHz (May-Collado & Wartzok 2008) to 7.9 kHz (Oswald et al. 2007) and in mean maximum frequencies between 11.3 (Wang et al. 1995a) and 17.6 kHz (May-Collado & Wartzok 2008). Acoustic variation in bottlenose dolphin communities occurs on different spatial scales and variation in communication calls have been established between geographically separated areas where direct mixing is unlikely (Wang et al. 1995a; Camargo et al. 2006; Baron et al. 2008), between adjacent populations where there is potential for intermixing (Wang et al. 1995a; Bazúa-Durán 2004; Azevedo & Van Sluys 2005; Morisaka et al. 2005; Rossi-Santos & Podos 2006; Ansmann et al. 2007; Baron et al. 2008) and between social units within populations (Deecke et al. 2000). Call repertoires may be shared by genetically related or socially affiliated groups and could result in convergence on calls with similar acoustic properties or similar call types (contour shapes) leading to reduction in individual variability within groups or populations and a heightening of group distinctiveness (Boughman 1997; Crockford et al. 2004; Rendell & Whitehead 2004; Cortopassi & Bradbury 2006).

Dolphin whistle variation is often quantified using frequency and duration values, including minimum, maximum, start, end, mean frequency and frequency range as well as duration and measures of modulation (e.g. Wang et al. 1995b; Matthews et al. 1999; Oswald et al. 2003; Morisaka et al. 2005a). Alternatively, the perceived similarity of contour shapes can be compared using human observers or computers. One approach for contour comparison is based on manual classification (by human observers) of whistles into predefined categories or contour types. Whistle classes commonly used for this are constant frequency, upsweep, downsweep, concave, convex, or wavering sinusoidal whistles (Richardson et al. 1995). One problem with this approach is the risk of observer bias (Milinski 1997) and reproducibility since threshold values are often poorly defined. Also, whistle repertoires are generally more complex than a system of broad contour types can incorporate even if intermediate types are included (Richardson et al. 1995) and small but important variations may therefore be missed by the observer. More importantly, this method is unlikely to classify whistles into categories that are meaningful to the animals studied.

To categorise whistles into biologically meaningful categories (here known signature whistles) a number of studies have successfully matched known signature whistles with the correct individual by using human observers and their natural pattern recognition skills to sort contours into categories of perceived similarity (Janik 1999). Early computerised approaches to classify and compare whistle contours include similarity measures (e.g. cross-correlation coefficients), principal component and cluster analysis. In general, the computerised methods do not perform as well as human observer based classification, likely due to failure to consider important factors in acoustic perception, such as flexibility in the time domain and the exponential perception of sound frequency (Janik 1999; Deecke & Janik 2006).

A new method has recently been developed that identify signature whistles from recordings of bottlenose dolphins as reliably as human observers (Janik et al. 2013) This method is based on a neural network approach, time warping and findings that signature whistles tend to be emitted in bouts with whistles of the same distinct type occurring within 1-10 seconds of each other. This bout distinction has been used to reliably identify signature whistles from recordings of wild bottlenose dolphins (Janik et al. 2013).

5.1.1 Bottlenose dolphin distribution and ranging patterns

In Ireland, bottlenose dolphins (*T. truncatus*) occupy coastal and estuarine waters, primarily along the West and South coasts. The species is considered resident in the Shannon Estuary in the summer months during which calving also takes place. Dolphin encounters decrease in the Shannon during the winter months (Rogan et al. 2000; Ingram & Rogan 2002). This is likely to represent an expansion of the population's geographic range during winter months but their movements outside of the estuary are largely unknown. The Shannon Estuary is a critical habitat for bottlenose dolphins (Ingram & Rogan 2002) and currently the only candidate Special Area of Conservation under the European Habitats Directive for this species in Irish waters. Bottlenose dolphins are also regularly encountered in coastal areas where they show varying degrees of site fidelity at a number of coastal sites (Ingram et al. 2003). Cork Harbour in the South West has been regularly used by a small group of dolphins (n=6-8) since 2007 (Ryan et al. 2010). Cork Harbour is the second largest estuary in Ireland, and also a busy and heavily industrialised port (Minchin et al. 1996; Ryan et al. 2010).

Irish continental shelf waters are used by bottlenose dolphins that are assumed to belong to a third genetically distinct group, indicated from stranding data. While the origin of stranded animals remains uncertain, high levels of genetic diversity suggest that they may belong to a larger continental shelf assembly (Mirimin et al. 2011). The Shannon Estuary population of bottlenose dolphins is genetically distinct from other coastal as well as from putative continental shelf groups, except for the small group in Cork harbour which is likely to represent a recent dispersal (Mirimin et al. 2011). While estimates for coastal regions are low and measure in the hundreds, offshore surveys have estimated around 7,500 bottlenose dolphins (95% CI: 2,900 - 11,100) in Irish waters north of 53 degrees latitude at depths greater than 200 meters (CODA 2009).

Along the Atlantic coast of the US, bottlenose dolphins also occur commonly in estuaries and coastal areas. One such area is Beaufort Estuary and Pamlico Sound in North Carolina, where Beaufort Inlet links coastal waters to a complex estuarine system. Beaufort Estuary and Pamlico Sound are both estuarine areas that are connected through river systems and separated from the Atlantic Ocean by barrier islands (Figure 1). While animal movements have been reported between estuaries and adjacent coastal waters (Urian et al. 1999), estuarine animals are genetically distinct from migratory animals found in nearby coastal waters (Rosel et al. 2009; Caldwell 2001). Offshore bottlenose dolphins are primarily distributed along the outer continental shelf and continental slope with a separation of the inshore and offshore ecotypes across the bathymetry during summer months (NMFS 2008).

During winter months, the range of inshore and offshore groups overlap spatially (Torres et al. 2003) south of Cape Hatteras.

The aims of this study were to investigate if frequency and time variables or alternatively, the level of similarity in whistle contour shapes could be used to discriminate between dolphins found in different areas. I also wanted to investigate how any such variation relates to levels of social interaction between adjacent and sympatric communities. This was investigated for a number of sympatric and adjacent communities as well as for geographically separated areas where range overlap is highly unlikely (North East vs. North West Atlantic).

The objectives were to: (1) identify signature whistles in recordings from western Irish and eastern US waters using a neural network, time warping and bout analysis approach, (2) summarise and describe the structural characteristics of identified signature whistles and compare these between the communities, (3) measure the similarity in contour shape and investigate how contour similarity compares within and between areas, and finally, (4) to relate any variation found to levels of genetic similarity and social overlap.

5.2 Methods

The whistles used in this study were recorded while in the presence of bottlenose dolphin groups in western Irish and eastern US waters (Figure 1 and 2). Locations sampled covered a variety of habitats, including estuarine and coastal as well as continental shelf (Ireland) and offshore waters (US).

In Ireland, dedicated vessel based surveys were carried out in the Shannon Estuary, three coastal sites on the Irish west coast and in continental shelf waters between June 2008 and June 2011. North Mayo and the Connemara survey region covered both County Galway and Mayo waters and the Northern part will therefore be referred to as North Mayo to avoid confusion. Cork Harbour surveys were limited to the harbour area and around the mouth of the estuary.

In the US, recordings of bottlenose dolphins were collected from Beaufort estuarine and coastal waters in May 2010, while recordings from the southern part of Pamlico Sound were collected in June – July 2007 and in September and October 2008

(Laura 2009). Offshore recordings were collected in July 2008 and in August and September 2009 between 50 and 150 km from the coast.

5.2.1 *Photo identification*

Photographs of dolphin dorsal fins were taken during acoustic sampling sessions using a Canon EOS D1 SLR, to investigate ranging patterns and levels of social interaction between sampling areas. The photographs were compared between encounters, sampling areas and with id-catalogues maintained by University College Cork (Ireland) the Duke Marine Lab, Beaufort (US) and the University of North Carolina, Wilmington (US). To minimise the risk of misidentification, all included photographs were required to be in focus, well exposed and with the dorsal fin fully visible and oriented in parallel view. Also, only dorsal fins with clear and permanent or semi-permanent markings were used.

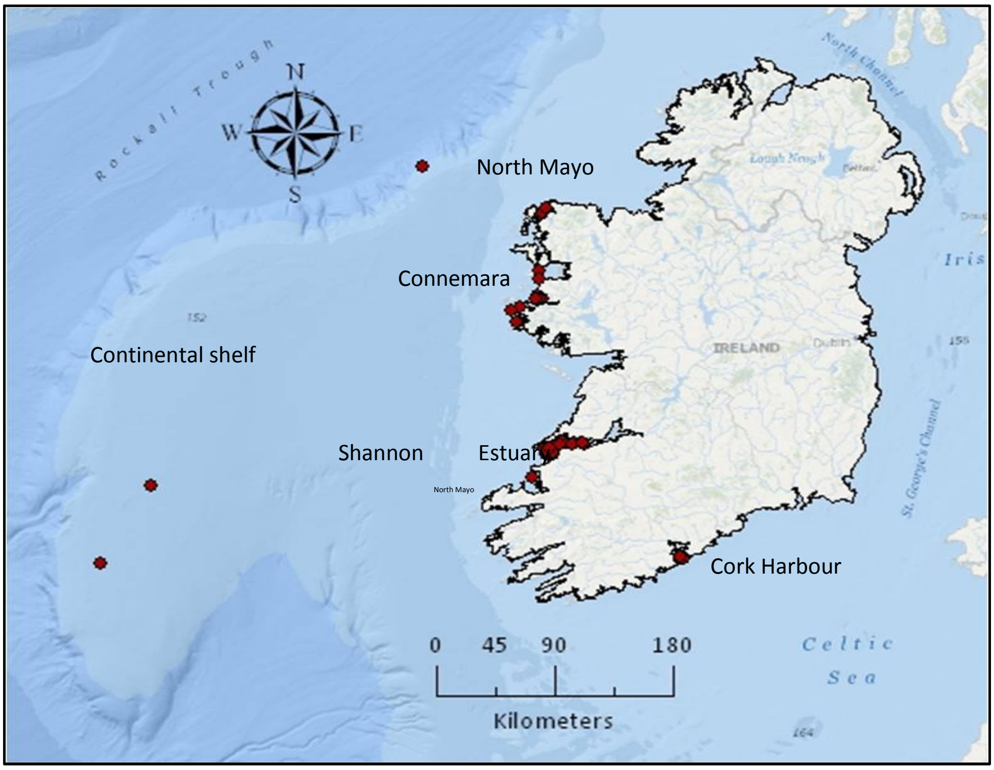

Figure 1. Map showing sampling locations in Irish waters.

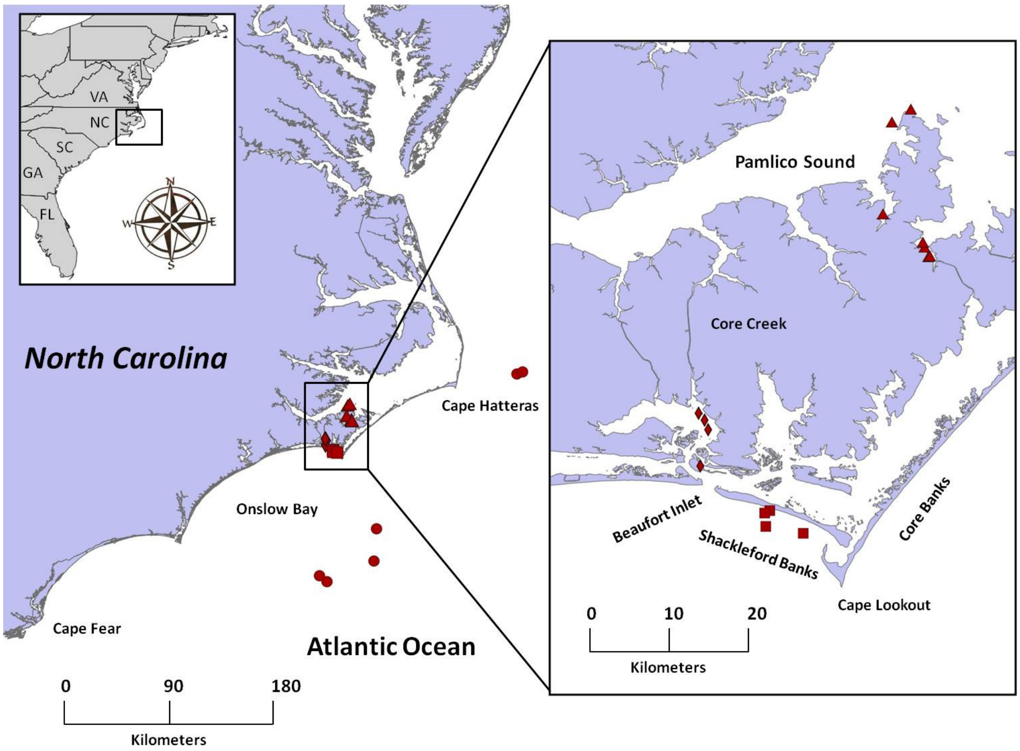

Figure 2. Map showing sampling locations in US waters.

5.2.2 *Recording whistles*

Sampling in inshore waters were made using a 6m RIB (Ireland and US coastal waters) or a flat bottomed fibreglass boat in (US estuarine waters). Sampling in US offshore waters took place on larger ship surveys as part of a larger monitoring project (Hodge 2011) between 50 and 150 km from the coast (Figure 2). Recordings in Irish continental shelf waters were made on larger ship surveys on the R/V Celtic Explorer (Cetaceans on the Frontier Survey II, 18th – 31st August, 2009) and on the R/V Song Of The Whale (Acoustic survey for beaked whales, 15th September – 12th October, 2010), a research sailing vessel.

To standardise field techniques, acoustic data were, when possible, collected using the same recording system, deployed in the same manner. However, the suitability of recording systems depended on vessel type employed for the survey in question (Table 1). For analysis purposes, 96 kHz sampling rate was used for most recordings providing an effective band width of 48 kHz with the exception for recordings in Pamlico Sound where the sampling rate was 88 kHz resulting in an effective band width of 44 kHz. Recordings made with a higher sampling rate were down-sampled using Adobe Audition 3.0$^{©}$ (1992-2007 Adobe Systems Incorporated) to ensure comparability between sampling occasions. While the upper frequency limit of the recorder was 48 kHz (96 kHz sampling rate) the limit of the system was determined by the 30 kHz upper limit of the hydrophone.

Table 1. Summary of recording equipment used, including type of hydrophone, recording device and sampling rate for each setup.

Survey	Hydrophone type	Recording device	Sampling rate
All inshore surveys (US & IRE)	Single channel hydrophone, model HTI-96-MIN. High Tech Inc., MS, US	Edirol R-09-HR or R-44 digital solid state recorder, Roland Systems Group, UK	96 or 192 kHz 24 bit
Continental shelf (IRE) 2009	Four element 200m towed hydrophone array. Seiche Ltd., UK	Magrec HP-27 buffer box through laptop and DAQ-6255 USB NI sound card	192 kHz 16 bit
Continental shelf (IRE) 2010	Four element 400m towed hydrophone array. Seiche Ltd., UK	Bespoke buffer box through laptop and, RME Fireface 800 sound card	192 kHz 16 bit
Pamlico Sound (US)	Single channel hydrophone, model HTI-94-SSQ. High Tech Inc., MS, US	Fostex FR-2 field memory recorder, Foster Electric Co., Ltd	88 kHz 24-bit
Offshore (US)	Four element towed hydrophone array. Seiche Instruments, UK	Laptop with MOTU traveller interface Mark of the Unicorn, Cambridge, MA, US	192 kHz 16-bit

5.2.3 Whistle contour extraction

Whistle contours (defined as uninterrupted tonal sounds with a narrow-band fundamental frequency and a duration of more than 100ms), were identified in the recordings by visually inspecting spectrograms (Hanning window, FFT resolution 256) in Raven Pro v 1.4 (Cornell Lab of Ornithology). An identification number was assigned to each contour and logged together with the start and end time, information about the quality of the whistle (based on signal to noise ratio and level of overlap with other whistles) and presence of harmonics. Single whistle files were created from the recordings and whistle contour details extracted using a custom made script (Beluga: Deecke unpublished) in MATLAB, where whistle contours were traced using a semi automatic process within which a peak-finding algorithm selects the fundamental frequency contour (supervised by the user who can employ filtering and make corrections if necessary). The resulting file comprises a list of frequencies for each contour, with known time and frequency resolution (0.667ms, 23.438Hz respectively) and provided the means to calculate whistle frequency, complexity (i.e. inflection points) and time variables.

5.2.4 Identification of signature whistles

To identify potential signature whistles (see example in Figure 3), contour files were processed using a classification procedure that include a time warping and neural network approach (ARTwarp: Deecke & Janik 2006) in MATLAB in which whistle contours are individually compared based on the actual shapes of the contours. The application of ARTwarp is fully explained by Deecke and Janik (2006), but the main features are summarised here, along with any modifications.

The numbers of distinct whistle types (ARTwarp categories) were considered representative of the diversity of whistles in the signature whistle repertoire recorded from each community. In ARTwarp, contours are sorted into categories of similarity (based on a critical similarity level set by the user) and the resulting categories represent groups of similar frequency modulation patterns. If a contour is matched to an existing category it is added to this category and its reference contour is modified to represent an average of all contours contained within. If a contour does not match any existing category, a new category is created and the contour becomes this new category’s reference. The program iterates through the data set in a random sequence until no contour is re-classified, resulting in a set of distinct whistle types for each sampling area. A critical similarity level of 91% was considered appropriate for the current data set since it has been found suitable for bottlenose dolphin signature whistles from captive and temporarily restrained bottlenose dolphins (Deecke & Janik 2006) as well as for wild, unrestrained dolphins (Quick & Janik 2006, 2012). Information about the resulting distinct whistle types were stored in an MS Access database and analysed further in MS Excel.

In order for a distinct whistle type to be considered a signature whistle the category had to contain at least four whistles occurring in a bout sequence recognised using the signature identification (SIGID) method, which was developed to reliably identify signature whistles from recordings of unrestrained bottlenose dolphins (Quick & Janik 2012; Janik et al. 2013). Likely signature whistles were identified as those with at least one sequence where 75% or more of the whistles had an inter whistle interval of 1-10 seconds to the preceding or following whistle within the same category.

The total number of signature whistles identified (Figure 3) were summarised per encounter and sampling area. Any signature whistles occurring in more than one encounter were noted and used to investigate individual overlap between encounters. Nine standard whistle variables were calculated, including: start frequency (SF), end frequency (EF), max frequency (MaxF), min frequency (MinF), frequency range (FR), carrier frequency (CF, median of max and min frequency), duration (D), number of inflections (IF, changes between positive and negative slope), presence of harmonics (H) and duration (D) (following Oswald et al. 2003; Morisaka et al. 2005). Four repetitions of each signature whistle type were included and the mean of each such subsample used to represent each signature whistle in order to cover minor variations in individual characteristics which can occur due to differences in number of loops, whistle duration or smaller frequency shifts. If a signature whistle type included more than four repeated whistles, a subsample was chosen from the whistles that had the required inter-whistle interval of 1-10 seconds and the highest quality (highest signal to noise ration without overlapping whistles) based on database inputs.

5.2.5 Variation in signature whistle characteristics

To visualise clustering within the datasets based on frequency and time characteristics of signature whistles, I used discriminant function analysis (DFA) on whistle variables averaged per signature whistle type and encounter. DFA was also used to identify which of the variables provided the most discrimination between any groupings. Non-normality for all whistle variables was found and inequality of error variances (Laverne test for homogeneity of variances ($p < 0.05$)). All whistle variables were therefore Box-Cox transformed and successfully transformed values used in the DFA. To test for differences between encounter and study areas any variables that could not be transformed to normality were instead compared using Kruskal Wallis test and Mann-Whitney U-test.

5.2.6 Variability of signature whistle contour shapes

The level of similarity in contour shapes was quantified to provide a measure of diversity in signature whistle types within and between communities. A similarity matrix was created based on the output from ARTwarp analysis providing all possible pair wise comparisons (n samples generating 0.5 * n (n-1) comparisons). In this analysis, contours that are very different return a value of zero and identical contours return a value of 100. Mann-Whitney U-tests were used to compare variation in levels of contour similarity between areas. This was done separately for US and Irish waters.

5.3 Results

Surveys in Irish waters resulted in 55 encounters with bottlenose dolphin groups over the study period (2008 –2011). From a total of 8 252 whistles logged, 1 754 high quality frequency contours were extracted and 1 694 were over 0.1 s duration and included in the analysis. Data from US waters included recordings from 35 encounters and resulted in 10 216 whistles logged. The frequency contours of 2 829 good quality whistles were extracted and the characteristics of 1 981 (over 0.1 s duration) used in the analysis (Figure 3).

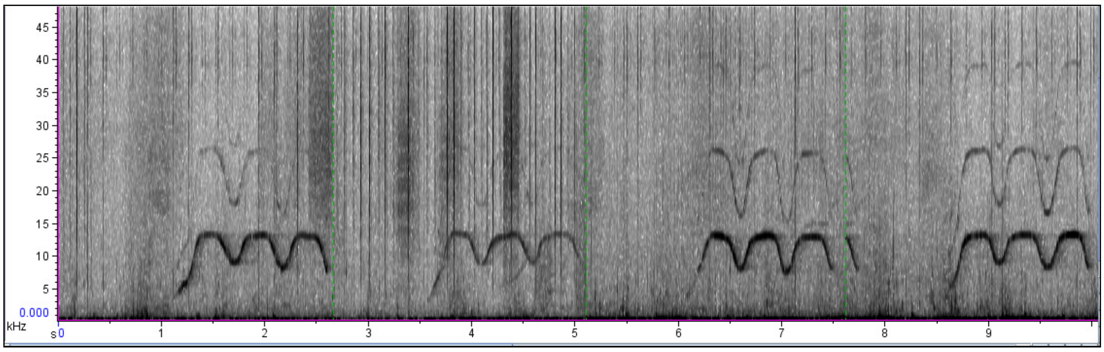

Figure 3. Example of a spectrogram of a highly stereotyped and complex (6 inflection points) signature whistle identified using ARTwarp and the SIGID analysis. Time is displayed on the x-axis (s) and frequency (kHz) on the y-axis.

5.3.1 Repertoire diversity

The total number of whistle types generated through the neural network analysis, the number of signature whistles identified through SIGID analysis and the repetitions of those signature whistles varied between the communities (Table 1) and were correlated with the total number of whistles available for analysis from each sampling area (Pearson correlation, p<0.01). The total number of signature whistles identified overall was 162 (IRE: n=66, US: n=96) and the repetitions of these corresponded to 37% (IRE) and 33% (US) of all available whistles, with the largest number of signature whistles found in relation to individuals present (signature whistles per dolphin) were found in Cork Harbour (0.38), US offshore waters (0.36), North Mayo (0.36), and Beaufort Esgtuary (0.32) and the lowest numbers in Pamlico Sound (0.09) and in Irish continental shelf waters (0.08) (Table 2, Figure 4).

Table 2. Summary of survey effort including: number of dolphins (field and photo-ID), number of encounters in each area, number of whistles logged as well as whistle types, signature whistles (SWT) identified and number of repetitions of SWTs. Numbers in brackets represent the percentage of total number of whistles included in the analysis.

Habitat type Survey area	**No. of dolphins**	**No. of enc.**	**Total whistles**	**Whistle types**	**No. of SWT**	**Rep. SWT**
Estuarine						
Shannon Estuary (IRE)	75	27	479	41 (9)	16 (3)	96 (20)
Cork Harbour (IRE)	8	11	130	27 (21)	3 (2)	17 (13)
Beaufort Estuary (US)	63	14	344	76 (22)	20 (6)	150 (44)
Pamlico Sound (US)	90	7	457	64 (14)	8 (2)	68 (15)
Coastal						
Connemara (IRE)	91	10	229	36 (16)	10 (4)	90 (39)
North Mayo (IRE)	39	3	365	51 (14)	14 (4)	146 (40)
Beaufort coast (US)	171	6	1103	117 (11)	31 (3)	318 (29)
Shelf and offshore						
Continental shelf (IRE)	(280)	5	491	52 (11)	23 (5)	283 (58)
Offshore waters (US)	(102)	8	668	74 (11)	37 (6)	318 (48)
Total (IRE)	491	55	1694	207 (12)	66 (4)	632 (37)
Total (US**)**	426	35	2572	327 (13)	96 (4)	854 (33)

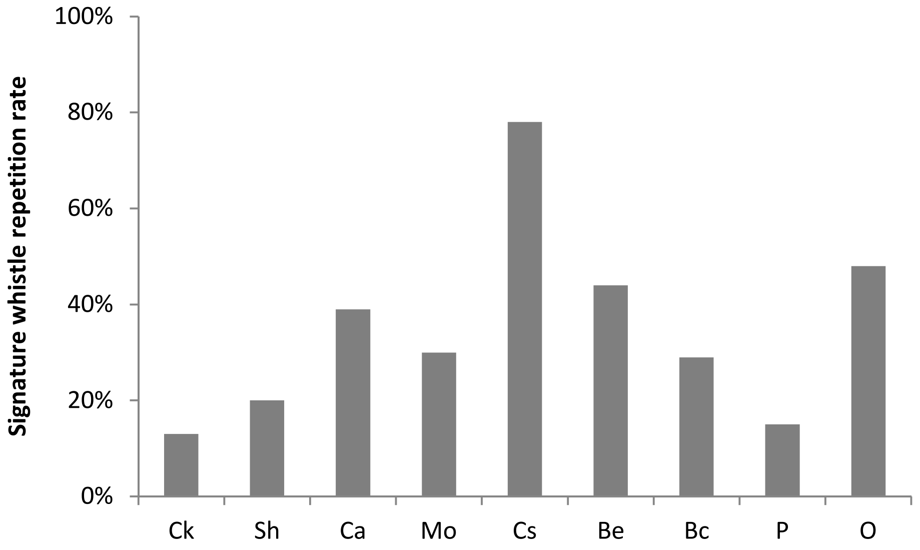

Figure 4. Repetition rates (%) of signature whistles in relation to total number of whistles included in the analysis (high quality, >0.1 s) from Irish (Ck = Cork harbour, Sh = Shannon Estuary, Ca = Connemara, Mo = North Mayo and Cs = continental shelf) and US waters (Be = Beaufort estuary, Bc = Beaufort coast, P = Pamlico Sound and O = Offshore).

5.3.2 Photo identification

Over 16 000 photographs were taken during the surveys, with 459 individuals matched with existing catalogues in Irish (n=222) and US waters (n=230). Average group size varied between sampling areas with the smallest in Cork Harbour (6.0 ± SD 1.4), followed by the Shannon Estuary (14.9 ± SD 9.4), Connemara (25.3 ± SD 3.8), North Mayo (50.5 ± SD 4.9) and continental shelf waters (90.7 ± SD 138.3). Average group size for US waters was lowest for Pamlico Sound (16.0 ± SD 4.2) followed by offshore waters (16.85 ± SD 9.4), Beaufort Estuary (25.0 ± SD 7.1) and Beaufort coast (62.5 ± SD 31.8). No photographs were available from US offshore waters. There was a positive correlation between the mean number of individuals and the mean number of signature whistles identified per encounter and sampling area (Pearson correlation coefficient, r = 0.544, p<0.01, Figure 5).

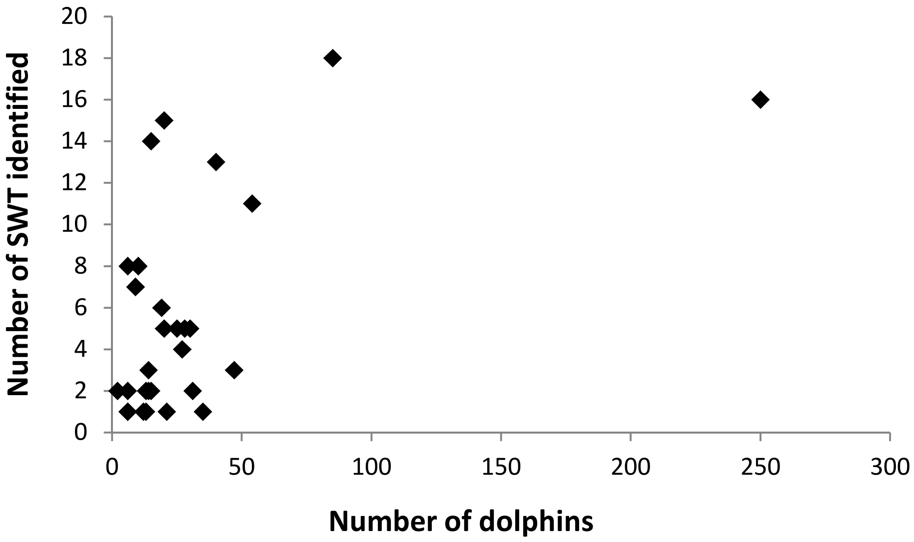

Figure 5. Relationship between number of dolphins encountered and signature whistle identifications per encounter and sampling area.

5.3.3 Social overlap between sampling areas

In Irish waters, photo-identification supported previous findings of individual overlap between Connemara and North Mayo waters (Ingram et al. 2009), while no matches were made between these areas and the Shannon Estuary, Cork Harbour or continental shelf waters. A total of 91 individuals were matched with UCC catalogues for Connemara waters, 39 in North Mayo waters (of which a total of 20 individuals were also matched between Connemara and North Mayo waters), 8 in Cork Harbour and 86 in the Shannon Estuary during the study period. None of the animals encountered in continental shelf waters were matched with the catalogue.

For US waters, investigations into individual movement patterns and associations between individuals and between the sampling areas using the local photo-identification catalogues showed that no individuals used both estuarine and coastal waters around Beaufort in 2010 while historical records showed some use by estuarine animals of coastal waters none of the coastal animals encountered in 2010 had ever been observed in estuarine waters. Also, one encounter in Beaufort estuary and another in Pamlico Sound had a minimum of two individuals in common and a number of the individuals recorded in Pamlico Sound had a history of using Beaufort Estuarine waters in the past. Some of the animals matched with previous records were well known from the area, with 10 animals previously sighted between eight and 51 times and four individuals initially recorded as early as 1995. For animals encountered in Pamlico Sound in 2007/08, the majority (65%) had previously been recorded around Pamlico or Beaufort, in estuarine as well as in coastal waters and some additionally in estuaries around Wilmington close to Cape Fear in the South (Figure 1), suggesting large home ranges and the use of estuarine as well as coastal waters.

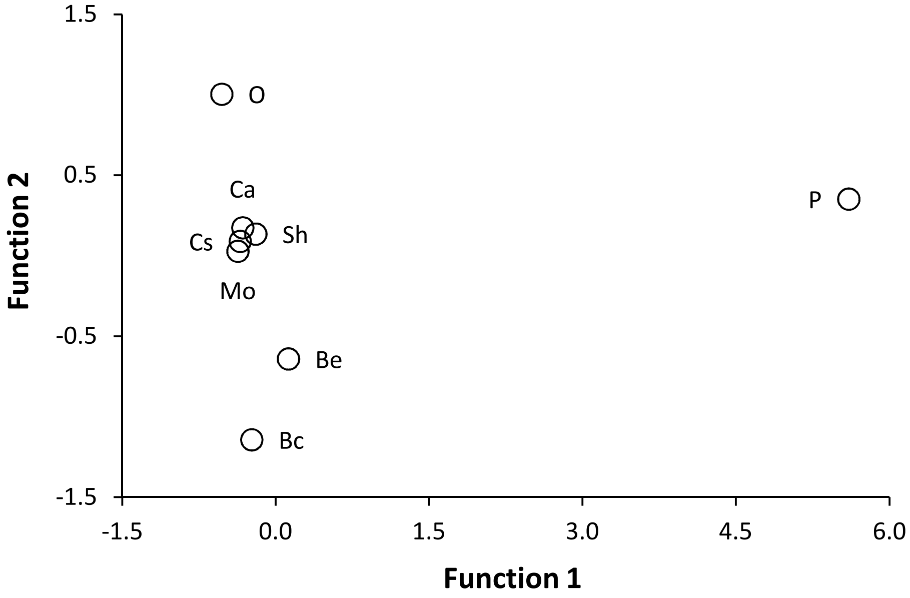

Figure 6. Canonical discriminant function scatter plots of the first two functions, with group centroids displaying clustering based on whistle characteristics averaged by encounter in Irish and US waters (Sh = Shannon estuary, Ca = Connemara, Mo = North Mayo and Cs = Continental shelf waters, Be = Beaufort estuary, Bc = Beaufort coast, P = Pamlico Sound and O = offshore waters).

5.3.4 Variation in signature whistle variable characteristics

Overall, mean frequencies ranged between a 7.0 kHz (SD=1.6) for minimum frequency and a mean of 13.8 kHz (SD=2.7) for maximum frequency with a mean carrier frequency of 10.1 kHz (SD=1.9). The means for start and end frequency was 8.7 kHz (SD=2.7) and 9.9 kHz (SD=3.5) respectively and the mean frequency range 7.12 kHz (SD=2.6). The mean duration was 0.6 s (SD=0.3) with a median of 0.7 s. The mean number of inflection points were 1.1 (SD=1.1) with a maximum of 7 (for both Ireland and the US). The presence of harmonics ranged between 53% (US) and 56% (Ireland) of the whistles.

Within- and between-area variation was found among signature whistle variables (Figure 7). In general, US offshore groups produced higher frequency whistles. Six whistle variables varied significantly (Kruskal-Wallis test: $p<0.05$, df=8) and pair-wise Mann-Whitney U tests revealed that differences were significant in 32% of all pair-wise comparisons (Table 2). Whistle duration was the variable that was most often (n=10) significantly different between communities (Figure 8). Overall, frequency variables had the lowest CV, while duration and number of inflection points in general had higher CV values (Appendix 1). Connemara waters provided the highest mean number of inflection points followed by North Mayo and US offshore waters while presence of harmonics was highest in Pamlico Sound (Figure 8).

Variation in the largest number of variables was found between Ireland and US offshore waters, followed by Pamlico Sound, Beaufort coast and Beaufort Estuary. Significant variation between communities was found for eight (MaxF, MinF, SF, CF, FR, D, I and H) of the variables (Kruskal Wallis test, df=7, $p<0.05$). For Irish waters, significant differences were only found between inshore and continental shelf waters and only in inflection points and presence of harmonics (Table 3). Variation was found between US communities in four out of six (14 variable comparisons) community pair comparisons. For comparisons between US and Irish waters, 13 out of 20 possible pair wise comparisons were significantly different (30 variable comparisons) with most of the variation found between Irish communities and US offshore waters. The variables that varied most overall were; duration (Figure 8), carrier frequency, frequency range, inflection points (Figure 9) and presence of harmonics (Table 3). Harmonics were most commonly present in Pamlico Sound where 69% (range 63-71%) of all signature whistles had at least one harmonic, followed by offshore waters (57%, range 47-68%), Beaufort Estuary (50%, range 45-65%), while least common among Beaufort coast (47%, 46-47%) signature whistles.

Table 3. Pair wise comparisons between communities in Irish and US waters. Numbers in the bottom half of the matrix represent number of variables that differed significantly in pair wise comparisons using Mann-Whitney U-test (p<0.005). The variables that varied significantly are shown in the top part of the matrix.

Ireland						US			
	Ck	**Sh**	**Ca**	**Mo**	**Cs**	**Be**	**Bc**	**P**	**O**
Ck		-	-	-	I	-	-	-	-
Sh	0		-	-	I	-	D	D	MaxF, SF, CF
Ca	0	0		-	I, H	H	D, H	FR, D, I	MaxF, CF, H
Mo	0	0	0		I	-	-	FR, D	MaxF, CF, FR, I, H
Cs	1	1	2	1		H	D, H	FR, D, H	MaxF, Cf, FR, D, H
Be	0	0	1	0	1		-	-	MinF, SF, CF, D
Bc	0	1	2	0	2	0		FR	MaxF, MinF, SF, CF, FR, D, I
P	0	1	3	2	3	0	1		CF, D
O	0	3	3	5	5	4	7	2	

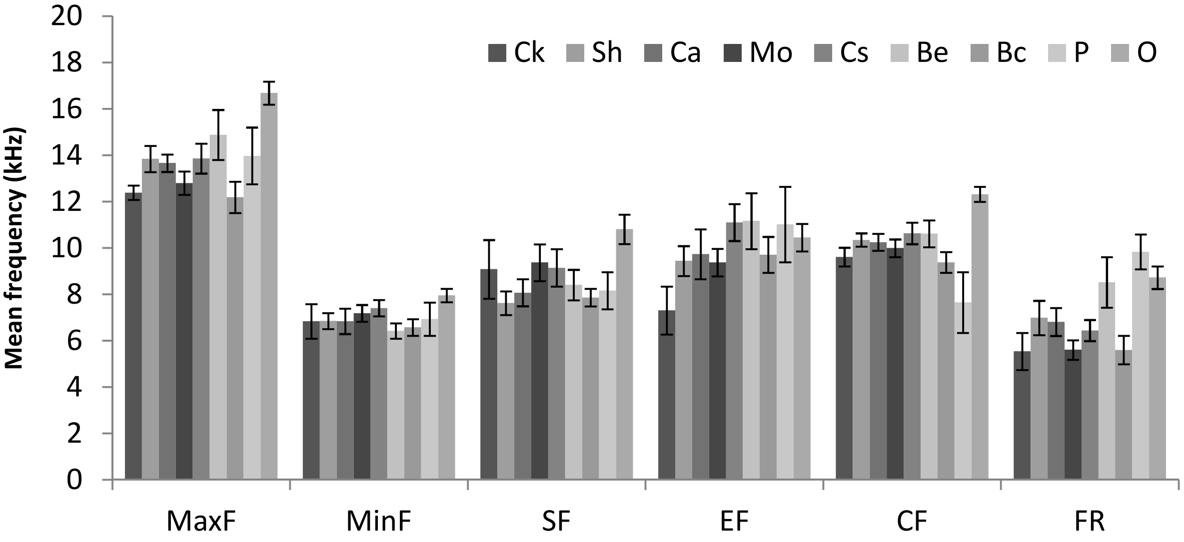

Figure 7. Mean frequency parameters (± standard error) for signature whistles identified.

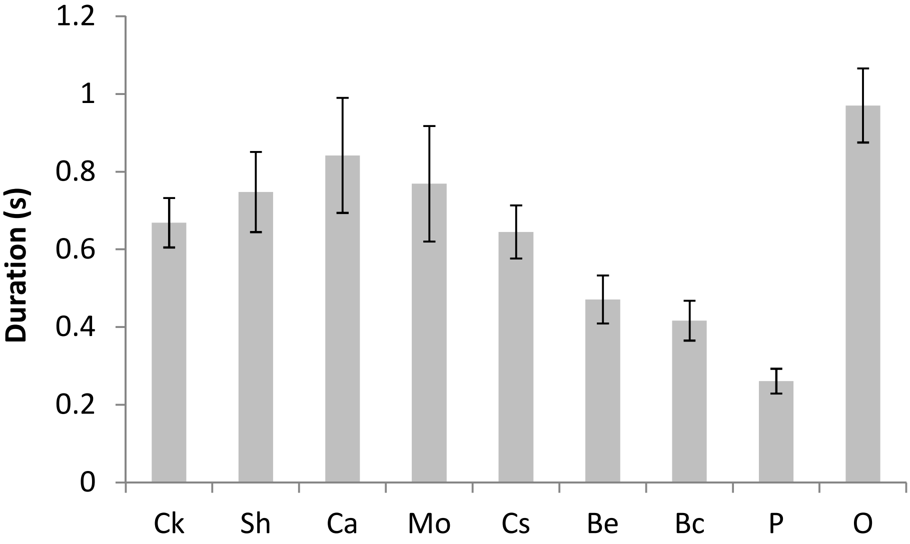

Figure 8. Mean duration (± SE) of signature whistles

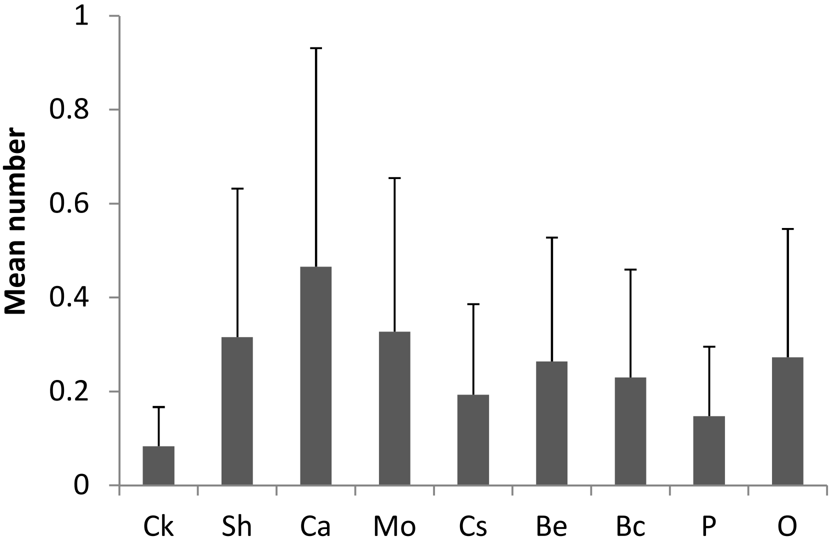

Figure 9. Mean number of inflection points (±SE) per signature whistle averaged for each location.

5.3.5 Variability of signature whistle contour shapes

Whistle contour shape was examined between communities on an encounter by encounter basis. Within-area similarity in contour shapes was highest (92%) for Cork harbour whistles (n=3, 17 repetitions), while other communities were all on similar, lower levels, ranging between 56 and 66% (Figure 10). For US waters the highest within-area similarity was found for Pamlico Sound (74%), while the other communities ranged between 57 and 63% (Figure 10).

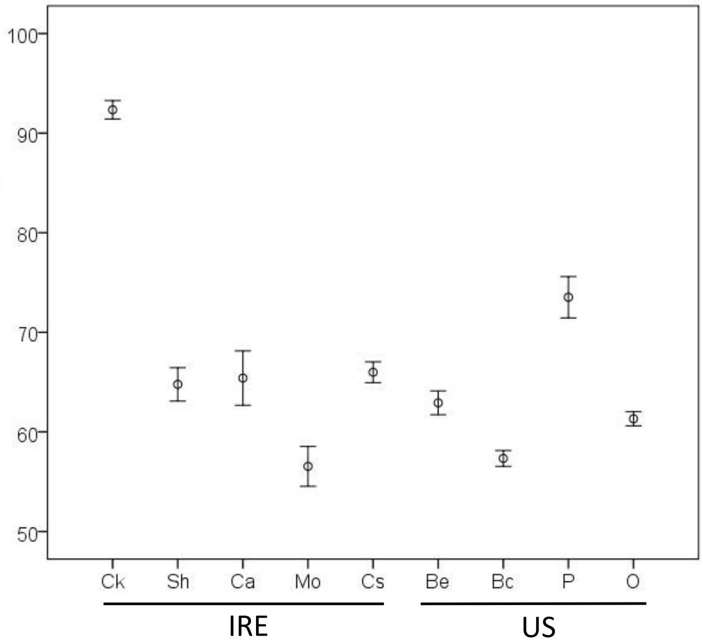

Figure 10. Mean within-area similarity (x-axis) in whistle contour shape for the nine areas in Irish and US waters. Error bars symbolise 2 x standard error of the mean (Ck=Cork harbour, Sh=Shannon estuary, Ca=Connemara, Mo=North Mayo, Cs=continental shelf waters, Be=Beaufort estuary, Bc=Beaufort coast, P=Pamlico Sound and O=Offshore waters).

The majority of between-area comparisons of similarity in whistle contour shape were significant ($p<0.001$) when compared to the level of similarity within each area (Table 4). Seven between-area comparisons returned non-significant results in Irish waters, these included Shannon/Cork, Shannon/Connemara, Connemara/Cork and continental shelf compared with all inshore areas (Table 3). For US waters, the only between-area comparison that was not significant was Beaufort estuary compared with Pamlico Sound (Table 4).

Table 4. Pair-wise between-area similarity compared with each area's within-area similarity in whistle contour shapes for Irish waters (*=significant differences).

	Average similarity within		**Average similarity between**	**MW-U test p-value**
Cork Harbour (Ck)	92.3	**Ck-Sh**	75.4	<0.001*
		Ck-Ca	76.1	<0.001*
		Ck-Mo	71.4	<0.001*
		Ck-Cs	75.9	<0.001*
Shannon Estuary (Sh)	64.8	**Sh-Ck**	75.4	0.449
		Sh-Ca	64.0	0.214
		Sh-Mo	60.3	<0.001*
		Sh-Cs	64.8	<0.001*
Connemara (Ca)	65.4	**Ca-Ck**	76.1	0.022
		Ca-Sh	64.0	<0.001*
		Ca-Mo	59.4	<0.001*
		Ca-Cs	63.2	<0.001*
North Mayo (Mo)	56.5	**Mo-Ck**	71.4	<0.001*
		Mo-Sh	60.3	<0.001*
		Mo-Ca	59.4	<0.001*
		Mo-Cs	60.7	0.059
Continental shelf (Cs)	66.0	**Cs-Ck**	75.9	<0.001*
		Cs-Sh	64.8	0.012
		Cs-Ca	63.2	0.614
		Cs-Mo	60.7	0.202

5.4 Discussion

In this study, I provide evidence that signature whistles vary on a range of geographic scales and that this variation is particularly prominent between the two ecological types of bottlenose dolphins present in US waters. Variation was also evident among inshore communities in the US while variation between Irish inshore communities was comparably low. Populations that are known to be genetically distinct (e.g. Shannon Estuary vs. Irish coastal groups) were relatively similar to adjacent and potentially sympatric communities in Connemara and North Mayo waters which may indicate social contact between these areas. While no evidence has been found for interaction between Shannon animals and any from coastal areas, such interaction may occur at times or locations were sampling effort is low or absent (e.g. in offshore waters or during the winter period) Variation was found when comparing frequency variables, modulation and time characteristics as well as in the level of similarity in whistle contour shapes between areas.

The shape and detailed characteristics of signature whistles is influenced by learning and social interaction (Miksis et al. 2002; Fripp et al. 2005) A higher level of variation was therefore expected between genetically distinct communities that interact socially but not between groups that are separated socially or geographically. Areas for which known overlap in home range and a level of social interaction exist (Beaufort Estuary vs. Beaufort Coast and Pamlico Sound) did not vary significantly in any of frequency or time variables tested reflecting high levels of interaction. While genetic samples were not acquired, previous research has shown that at least some migratory coastal dolphins are genetically divergent from more resident estuarine animals (Caldwell 2001; Rosel et al. 2009).

Variation was also found in the rate of signature whistle emissions, with the highest repetition rate recorded in Irish continental shelf waters followed by US offshore waters suggesting an increased requirement for the use of individually distinct calls in large, highly mobile communities and the importance of maintenance of group cohesion in open water habitats.

A positive correlation was also found between group size and number of identified signature whistles. However, without the ability to localise the source of whistle emissions it is not possible to determine the exact number of individuals that were actively vocalising, particularly for some of the larger encounters. It is likely that only a small proportion of the animals were detected and their signature whistles repeated regularly enough to comply with the stringent method used for signature whistle identification in this study. Through localisation techniques, Quick and Janik (2008) found that many whistles assumed to be produced by a focal group were emitted by groups nearby, suggesting that overestimation of whistle rates may occur when such techniques are not applied. They also found that whistle rates were affected both by behaviour and by group size but that individual whistle rates decrease in larger groups (>15 individuals) suggesting an upper limit of the number of whistles that can successfully transmit information due to signal masking by other whistles (Quick & Janik 2008).

For one of the Irish sampling areas (Cork Harbour) very few signature whistles (n=3) were identified through the automated categorisation and SIGID methods used. It was expected that this group, considering the relatively large number of recording opportunities and small number of individuals involved (n=8), would be likely to provide an equal number of signature whistles to the number of individuals available. However, this group was markedly quiet, providing a lower whistle rate in general than any other sampling area (Table 1) and the high level of within area similarity of signature whistles in Cork Harbour (Figure 10) likely reflects the low number of whistles available. This small group was also generally encountered in tight formation which generates lower whistle rates in general (Chapter 2). Signature whistles are most commonly emitted when an individual is separated from its conspecifics and it is probable that the dolphins in Cork Harbour are able to keep in contact by visual means through staying within close range. Also, with such a limited number of individuals present there may be less need to use contact calls or such may be emitted less frequently than in larger groupings. Visual inspection of the distinct whistle type categories created by ARTwarp from the Cork harbour dataset revealed another 4-5 stereotyped whistles that did not qualify for signature whistle designation using the SIGID method, suggesting that for small and less vocal groups a less strict or alternative method of signature whistle identification might be required.

The importance for social animals to remain in contact over large distances makes contact calls such as signature whistles an important component in animal communication systems (Poole et al. 1988; Wanker et al. 1998; Wright & Wilkinson 2001; Cortopassi & Bradbury 2006; Miksis-Olds & Tyack 2009). However, for contact calls to be effective, adaptations may be needed to ensure reliable communication and in the marine environment, features that further enhance long range signal transmission for which degradation is minimised may be selected for. Signal transmission properties can vary between habitat types and may be dependent on factors such as depth, temperature and background noise levels. The longer durations found for groups in a more open habitat (US offshore) might be an example of adaptations that could facilitate long range communication as suggested by May-Collado et al. (2007a). The ability to localise a whistling animal is increased by the production of longer duration whistles and Caldwell et al (1990) showed that a dolphin could localise a 5 second pure tone more accurately than one that was 1 second long. However, the lengthening of a signal may also be a method used to promote transmission in the presence of noise such as boat engines or other anthropogenic sound sources, although this was not investigated in this study.

Additionally, higher frequencies may also reflect differences in body size between ecotypes. While the trend for marine mammals in general is a correlation between lower frequencies and larger body size (Matthews et al. 1999; May-Collado et al. 2007b), bottlenose dolphins are unusual in that larger types, for example *T. truncatus* compared with *T. aduncus* tend to emit higher frequencies (Gridley 2010). With the offshore ecotype being the larger type (Perrin et al. 2011) this would fit in with this pattern.

In conclusion, the results demonstrate a high level of variation in signature whistles of the common bottlenose dolphin, in particular between geographically separated areas. While this variation was evident to a lesser extent between adjacent areas, variation was also found on a local level for some of the adjacent areas included. Vocal learning and/or cultural drift may explain some of the variation observed in both variable measures and in the similarity of contour shapes. Finally, high repetition rate of signature whistles found in continental shelf and offshore waters suggest an increased requirement for individually distinct calls in large, highly mobile communities and the importance of maintenance of group cohesion in a more open habitat.

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Chapter 6

General discussion

Contents

6.1 Summary of findings

This study provides evidence that vocal variation can be found at a range of social and geographic scales for the common bottlenose dolphin. The key findings indicate considerable variation between bottlenose dolphin ecotypes in the western North Atlantic, but also smaller scale variation between adjacent and sympatric communities in both western and eastern North Atlantic coastal, estuarine and continental shelf waters.

A high degree of variability in whistle characteristics was found within a genetically distinct population in Ireland (Chapter 2). Factors such as long term site fidelity, high levels of relatedness and social interaction within the area have likely influenced the vocal repertoire of this population. Similarly, the relatively low levels of vocal variation found between inshore communities in Irish waters overall (Chapter 3 and 5) may reflect that genetically distinct populations do not interact, at least not during the breeding season.

Whistles from inshore communities in US waters, in particular Beaufort Estuary compared with Beaufort coastal waters (Chapter 4) were relatively similar and some indication of contact would have been expected between individuals using these areas. However, no evidence was found of social interaction between any of the individuals encountered, currently or in long term photo-identification records (covering a large area of coastal and estuarine waters) and the similarities found may thus be at least partly explained by seasonal overlap in the ranges of resident estuarine groups and more migrant coastal assemblages that is yet not recorded by researchers.

Finally, high rates of signature whistles found for dolphins in continental shelf (Ireland) and offshore waters (US) may reflect an increased need for communication, highlighting the importance of group cohesion in highly mobile communities that use more open habitats (Chapter 5) Vocal variation and ecotypes

The highest level of variation noted was found between offshore and inshore dolphin ecotypes in the western North Atlantic (Chapter 4). The two ecotypes vary in body size with the offshore being the larger type, but also in morphological features of the skull, some of which are related to sound production (Kurihara & Oda 2007; Perrin *et al*. 2011). However, the larger offshore dolphins were here found to be using higher frequencies overall and morphology is therefore not the most likely factor behind this variation. Social isolation would be a more plausible explanation. Another study investigating vocal variation within the *Tursiops* genus found a similar trend, with the larger *T. truncatus* using higher frequency sounds than the smaller *T. aduncus* (Gridley 2010).

6.2 Effects on vocalisation behaviour

Factors that can cause geographic variation in vocal behaviour include environmental conditions such as ambient noise or the likelihood of interactions with predators or prey. For instance, the use of whistles with higher frequencies, longer durations and greater complexity tend to be associated with higher levels of background noise experienced in inshore habitats (Wang *et al*. 1995; Rendell *et al*. 1999). For example Dahlheim *et al.* (1984) measured ambient noise levels while recording the calls of gray whales (*Eschrichtius robustus*) and bottlenose dolphins (*T. truncatus*) in a Baja California lagoon system. Their data showed that vocalizations produced by these two species generally occurred at frequencies above or below the main concentration of energy of background noise in the area. These authors proposed that cetaceans utilize different acoustic niches, determined partly by the frequency range of high intensity ambient noise at a particular location (Dahlheim *et al.* 1984). In the current study however, lower frequencies were found in areas where ambient noise tend to be higher (generally more boat traffic in inshore waters).

6.3 Individual and group specific vocalisations

Variation in signature whistle development has been found between the sexes for the bottlenose dolphin, with female calves more commonly producing signature whistles that are distinct from those of their mothers. This is likely a consequence of selective pressures for vocal distinctiveness arising from the higher levels of association between females (Sayigh *et al.* 1995). Sex ratio and age structure could therefore have an effect on vocal variation between and within groups.

Group specific calls used by Canadian killer whales can be used to identify social groups within populations (Deecke *et al*. 2010), due to the highly stable social structure of these communities. The lack of group specific calls in bottlenose dolphins and their fluid social structure render acoustics an ineffective alternative to photo-identification techniques for monitoring bottlenose dolphins. However, with a comprehensive reference collection of signature whistles it may be feasible to use individually distinctive calls to distinguish between individual dolphins from adjacent and sympatric communities (Chapter 5).

6.4 Variation between Irish and US waters

The whistles from communities recorded in similar neritic habitats from different sides of the Atlantic showed some interesting similarities. For example, the whistles of inshore (especially estuarine) dolphins in the US are more similar to dolphins from Irish coastal communities than to dolphins recorded on the Irish continental shelf. Some of the comparisons also indicated vocal similarities between the whistles of continental shelf dolphins and those from US offshore waters (Figure 6, Chapter 3).

Since there are no likely opportunities for social contact or reproductive exchange between dolphin communities on different sides of the Atlantic it is unlikely to be a socially mediated driver responsible for vocalisation similarities at these scales. Instead, other causes for the lower levels of acoustic variation found between the communities are more likely. The most probable drivers would be similarities in habitat characteristics and in foraging strategies when comparing communities in inshore habitats and when comparing groups living in Irish continental shelf with US offshore waters.

6.5 Variation in whistle rate

The rate of whistle production in bottlenose dolphins is likely to be influenced by environmental factors as well as by group size and behaviour (Jacobs *et al*. 1993; Cook *et al*. 2004; Nowacek 2005). In this study, the use of whistles in relation to group size, behaviour, group dispersion and presence of calves was investigated for the resident population in the Shannon Estuary (Chapter 2). Rates of whistle emissions varied greatly between encounters and the underlying factors controlling this are likely to be numerous and complex. However, the very low rate of whistles found in the inner parts of the Shannon was notable, and paralleled the low numbers of whistles (in particular signature whistles) recorded from the small group of dolphins residing in Cork Harbour (Chapter 3 and 5). The relatively low number of animals encountered both in Cork Harbour and in the inner parts of the Shannon may reduce the need for frequent vocal communication. Correlation of higher whistle rates with increasing group size has been found in other studies (Jones & Sayigh 2002; Parijs et al. 2002; Cook et al. 2004). It has been suggested that individual whistle rates may decrease when groups are large (>15 individuals) due to responses to masking (Quick & Janik 2008). While only two encounters in the Shannon included a large number of dolphins the largest did provide a much lower whistle rate than the overall trend for smaller groups.

6.6 Methods of classification

All classification methods require researchers to decide which parameters to include and how the importance of these parameters should be weighted. Whistle contour classification has most commonly been based on the recognition and matching of similar contour shapes by human observers. This method has, in most cases, allowed more sophisticated and consistent classification of whistles than has been possible using most computer-based methods (Janik 1999).

The neural network approach used in this study is an objective method that enables classification of whistle contours into biologically meaningful categories (known signature whistles). Additionally, it facilitates calculation of similarity indices which makes community comparisons of the actual shapes of whistle contours possible (Chapter 3), an important aspect of whistles (Janik et al. 2006). For identification of signature whistles (Chapter 5) this method is comparable in accuracy to human classification methods (Janik 1999) but is more objective and can be automated. However, there may still be difficulties in comparing between studies if different algorithms have been used and the level of similarity used may also vary between studies, making comparisons difficult.

6.7 Conclusions

The results from this study add to our understanding of bottlenose dolphin vocal variation and its relationship with social, habitat and behavioural variation within the species. This type of information contributes to our understanding of a species' ecology and the intricacies of its social system. The likely drivers of vocal variation for the bottlenose dolphin include habitat use, individual ranging patterns and levels of social interaction between individuals, suggesting that vocal distinction is socially mediated and behaviourally maintained.

Continuing extensive genetic work will increase our comprehension of community structure and findings from this work will further help our understanding of vocal variation in bottlenose dolphins at a range of geographic scales. The genetic distinctiveness of offshore dolphins in Ireland has been inferred from the results of genetic studies of stranded and by-caught animals. Genetic sampling in combination with photo identification and acoustic recordings across the geographic range of sampling sites reported here (especially in offshore waters) would help to confirm these insights.

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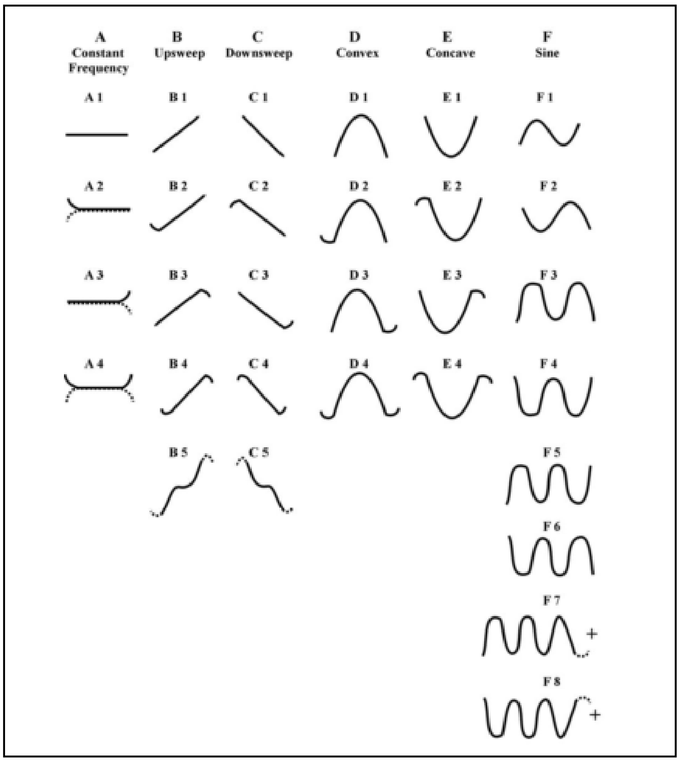
Appendix 1 – Whistle characteristics reported for *T. truncatus*

Descriptive statistics (mean (n), standard deviation/standard error and coefficient of variation) of whistle parameters reported for *T. truncatus* in other studies around the world. Values that are missing were not reported in the literature.

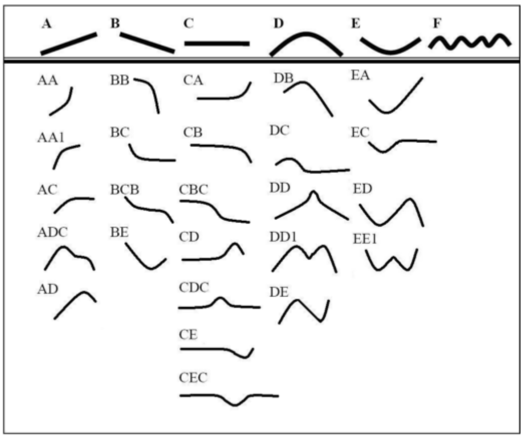
		SF	EF	Min	Max	FR	D	Inf
Shannon estuary, Ireland	Mean	8.94	10.3	7.54	14.2	6.72	0.62	1.06
This study	±SD	3.94	4.11	2.52	3.39	3.20	0.42	1.51
	CV	44.0	39.8	33.5	23.7	47.6	67.6	141.4
Patos Lagoon estuary, Brazil	Mean	8.28	8.37	5.96	12.2	6.25	0.55	1.42
Azevedo *et al.,* 2007	±SD	3.11	3.70	2.15	3.20	3.34	0.39	1.85
	CV	37.6	44.2	36.1	26.2	53.4	70.2	92.5
Argentina	Mean	9.24	6.63	5.91	13.6	-	1.14	1.58
Wang *et al.,* 1995	±SD	2.74	2.29	1.50	1.54	-	0.49	1.24
	CV	29.7	34.6	25.7	11.3	-	42.7	78.7
Galveston, Texas	Mean	7.95	9.02	5.98	11.9	-	0.75	2.57
Wang *et al.,* 1995	±SD	2.88	3.96	2.3	3.08	-	0.46	2.62
	CV	36.6	44.0	38.5	25.8	-	61.9	101.8
Corpus Cristi, Texas	Mean	7.43	8.71	5.88	11.4	-	0.69	2.14
Wang *et al.,* 1995	±SD	2.44	4.04	2.65	3.80	-	0.41	2.97
	CV	32.8	46.3	27.7	33.2	-	60.5	138.5
South Padre Isl, Texas	Mean	8.70	6.40	5.37	10.3	-	0.60	1.37
Wang *et al.,* 1995	±SD	2.95	2.44	1.12	2.80	-	0.26	1.65
	CV	33.9	31.1	20.8	21.1	-	43.7	119.8
Western North Atlantic	Mean	11.2	10.2	7.33	16.2	-	1.30	2.86
Steiner 2011	±SD	3.99	3.65	1.66	2.69	-	0.63	2.45
	CV	35	36	23	17	-	48	86
Sado estuary, Portugal	Mean	5.8	12.1	5.4	15.0	-	0.86	-
dos Santos *et al.,* 2005	±SD	1.8	4.4	1.2	2.7	-	0.40	-
	CV	-	-	-	-	-	-	-
Gulf of California	Mean	12.1	9.19	6.91	13.6	-	0.66	1.15
Wang *et al.,* 1995	±SD	2.89	3.44	2.11	1.72	-	0.35	1.32
	CV	23.9	37.5	30.5	12.6	-	53.1	115.2
Eastern Tropical Pacific	Mean	11.6	10.2	7.92	17.0	9.15	1.11	2.85
Oswald *et al.,* 2007	±SD	5.11	4.78	2.49	4.55	-	0.70	2.67
	CV	-	-	-	-	-	-	-
Pacific Ocean	Mean (?)	11.2	9.0	7.4	17.2	-	1.4	3.7
Oswald *et al.,* 2003	±SD	4.6	3.7	2.2	3.1	-	0.7	3.0
	CV	33	32	23	14	-	44	65
Muroto, Kochi, Japan	Mean	12.1	12.5	10.8	16.4	5.56	1.40	-
Akiyama and Ohta 2007	±SD	2.77	3.66	2.38	3.62	2.82	2.82	1.21
	CV	-	-	-	-	-	-	-
Western North Atlantic	Mean	10.6	12.4	8.24	15.0	-	0.62	1.43
Baron *et al.,* 2008	±SD	0.55	0.61	0.24	0.61	-	0.06	0.21
	CV	-	-	-	-	-	-	-
Gandoca-Manzanillo, Costa	Mean (77)	8.43	13.1	5.68	17.6	11.9	0.89	2.64
May-Collado and Wartzok	±SD	3.66	5.57	2.24	4.93	4.32	0.69	3.41

	CV	43.5	42.4	39.3	28.0	36.2	77.1	129.5
Gulf of Mexico	Mean	10.8	11.1	7.87	16.1	-	0.88	3.02
Baron *et al.,* 2008	±SE	0.35	0.53	0.20	0.40	-	0.05	0.27
	CV	-	-	-	-	-	-	-
Beaufort estuary, NC	Mean	8.29	11.3	6.57	14.8	8.26	0.48	1.30
Englund *et al.,* in prep	±SD	3.66	5.78	2.85	5.07	4.97	0.38	1.60
	CV	44.2	51.0	43.4	34.2	60.2	79.0	123.1
Beaufort coast, NC	Mean	8.36	9.69	6.51	12.8	6.29	0.39	0.84
Englund *et al.,* in prep	±SD	3.79	5.42	2.81	4.90	4.32	0.31	1.27
	CV	45.3	55.9	43.2	38.3	68.6	78.6	150.6
Pamlico Sound, NC	Mean	9.68	11.3	7.30	14.8	10.4	0.43	1.21
Englund *et al.,* in prep	±SD	3.98	5.46	3.30	4.75	3.96	0.39	1.52
	CV	41.1	48.3	45.1	32.0	38.0	89.5	126.0
North Carolina offshore	Mean	10.6	11.4	7.96	17.4	9.48	0.97	1.95
Englund *et al.,* in prep	±SD	3.95	5.26	2.32	4.23	4.47	0.64	1.90
	CV	37.3	45.9	29.2	24.3	47.2	66.0	97.5
Mediterranean Sea	Mean	8.32	9.34	6.13	14.1	8.05	1.03	2.93
Papale 2012	±SD	3.58	4.51	2.08	3.67	3.43	0.58	2.42
	CV	43.0	48.2	33.9	25.9	42.5	55.7	82.69
Canary Islands	Mean (94)	11.1	11.9	7.2	16.2	9.07	0.77	1.18
Papale 2012	±SD	4.42	4.63	1.83	5.01	5.01	0.52	1.77
	CV	39.7	38.8	25.3	30.7	56.2	66.9	150.0
Azores Islands	Mean	10.0	8.66	6.36	15.2	8.9	0.97	2.12
Papale 2012	±SD	4.08	4.09	2	3.9	3.49	0.49	2.55
	CV	40.4	47.2	31.4	25.5	39.2	50.1	120.1
Bay of Biscay	Mean (94)	9.41	11.3	7.19	16.9	9.78	1.1	2.9
Papale 2012	±SD	3.59	4.56	1.61	2.42	2.54	0.43	2.4
	CV	38.1	40.3	22.4	14.2	26.0	39.0	82.52
Texas	Mean	8.01	8.16	5.77	11.3	-	0.68	2.09
Wang et al 1995	±SD	2.81	3.78	1.84	3.31	-	0.4	2.54
	CV	35.0	46.3	31.8	29.2	-	58.8	121.8
Harderwijk	Mean (14)	5.2	12.2	4.3	15.1	10.8	0.7	2
Gridley 2010	±SD	2.7	4.4	1.9	4.5	4.3	0.4	1.8
	CV	-	-	-	-	-	-	-
Florida	Mean (4)	5.8	15.4	5.4	17	11.6	1	4.6
Gridley 2010	±SD	2.0	5.8	1.8	4.7	4.7	0.4	3.8
	CV	-	-	-	-	-	-	-
Scotland W	Mean (5)	5.8	14.9	5.0	15.9	10.9	0.9	0.8
Gridley 2010	±SD	1.0	4.3	0.9	4.8	4.3	0.4	1.2
	CV	-	-	-	-	-	-	-
Scotland E	Mean (18)	7.0	11.5	6.2	15.1	8.9	0.8	1.3
Gridley 2010	±SD	2.9	5.5	2	4.9	5	0.4	1.5

Appendix II – Examples of classification and whistle contour types



(Ansmann *et al*. 2007)



(Hickey *et al*. 2009)

Figure 1. Two examples of category schemes used in studies of dolphin whistle contour shapes, illustrating the variation in classification that may exist between studies of dolphin whistles.

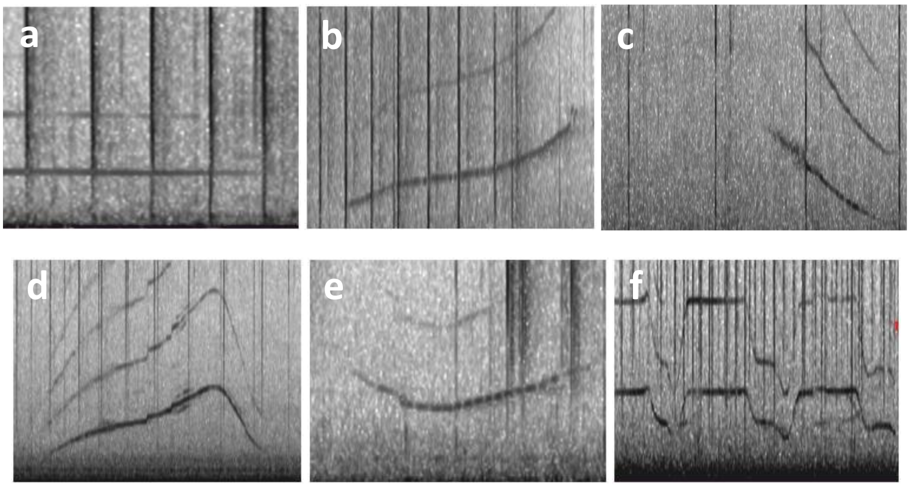


Figure 2. Examples of whistle contour shapes used in this study. constant frequency (a), upsweep (b), down-sweep (c), convex (d), concave (e) and modulated (f).

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