

**The Whistle Repertoire and Acoustic Behaviour of Short-Beaked
Common Dolphins, *Delphinus delphis*, around the British Isles,
with Applications for Acoustic Surveying**

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of Science in Marine Mammal Science at the University of Wales, Bangor.**

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Abstract

Cetaceans have adapted to life underwater by developing specialised hearing and echolocation abilities, as well as a communication system that is largely based on acoustic signals. Part of the vocal repertoire of many delphinid odontocetes are narrowband tonal whistles used mainly for communication. The aim of this study was to describe the whistle repertoire of short-beaked common dolphins, *Delphinus delphis*, recorded in the Celtic Sea off South Wales between May and August, 2005. Comparisons between acoustic and visual detection rates during these surveys showed that acoustic surveying can increase the chances of detecting common dolphins compared to visual methods alone, especially if group size was small and animals were far away from the vessel. However, even though group size was correlated to whistle density, the regression was not strong enough to reliably predict the number of animals based on acoustic data alone. The whistles recorded were classified into six broad categories and thirty sub-types, of which simple upsweeps and downsweeps were the most common. Furthermore, the parameters duration, inflections, steps and various frequency variables were measured. Whistle parameters varied with behavioural context, group size and between encounters. The whistle repertoire of Celtic Sea common dolphins was compared to that of *D. delphis* from the western approaches of the English Channel, recorded during a WDCS/Greenpeace survey between January and March, 2004. The relative abundances of the broad whistle categories did not differ between the two locations, but most whistle parameters were significantly different. Almost all frequency parameters measured were higher for English Channel whistles, which supports the possibility that these may be two distinct populations of short-beaked common dolphins. The English Channel dolphins may have shifted the frequencies of their vocalisations up to avoid masking by low-frequency ambient noise produced by high levels of vessel traffic in this area.

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DECLARATION

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STATEMENT 1

This dissertation is being submitted in partial fulfilment of the requirements for the degree of Master of Science (MSc) in Marine Mammal Science.

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This dissertation is the result of my own independent work/investigation, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

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1. Introduction

1.1. Cetacean Vocalisations

The sounds produced by whales and dolphins (Cetacea) are complex and highly variable and the functions of most are not well known. Generally, marine mammals vocalise to explore their environment (in odontocete cetaceans through echolocation) or to communicate with conspecifics or even animals from other species (Richardson et al. 1995). Vision is often limited under water while sound travels much further and 4.5 times faster in water than in air. Thus, it is not surprising that cetaceans have developed not only specialised acoustic tools such as echolocation, but also a communication system that is based largely on acoustic signals (Dudzinski, 2002).

The hearing organ of cetaceans has special adaptations to their life underwater. For example, high frequency sound can be received through the tissue of the mandible rather than an air-filled external auditory meatus as in terrestrial mammals (Thewissen, 2002). This allows cetaceans to dive to great depths without compromising their hearing ability through pressure effects on air-filled spaces (Ridgway et al. 2001). Audiograms of several odontocete species have shown that they can hear a wide range of frequencies spanning over nine octaves and up to 150 kHz, with best hearing sensitivities around 10-100 kHz (fig. 1.1; Au, 1993, 2000). Bottlenose dolphins can discern frequency changes of as little as 0.2-0.4 % (Thompson and Herman, 1975).

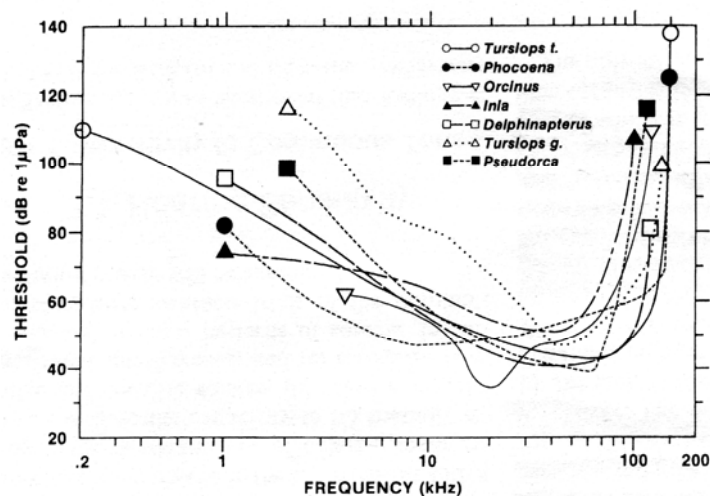


Figure 1.1. Audiograms for different odontocete species (Au, 1993).

1.1.1. Mysticete Vocalisations

Baleen whales (Mysticeti) produce sounds that are mostly below 1 kHz in frequency. Due to the lack of absorption loss at these low frequencies, mysticete sounds can travel over vast distances, possibly thousands of kilometres (Dudzinski, 2002). These signals have been described, for example, as moans, thumps, knocks or pulses (Richardson et al. 1995). Some mysticetes also produce much more complicated vocalisations. The best-known example is the humpback whale (*Megaptera novaeangliae*) song which can range in duration from 5 to 30 minutes and consists of several different units, phrases and themes (Darling, 2002). It is only sung by solitary males and thought to be a reproductive advertisement display signal (Tyack, 2000). While songs differ between geographically separate populations, all males of one population sing the same song, which is gradually modified over time (Darling, 2002). One particular population has been reported to entirely change its song after a small number of individuals from a different population immigrated (Noad et al. 2000). Within only two years the song resembled that of the population that the new immigrants had come from. This observation indicates a certain level of cultural transmission and vocal learning in humpback whales (Noad et al. 2000).

1.1.2. Odontocete Vocalisations

Toothed whale (Odontoceti) sounds are generally grouped into three types: short pulsed sounds that are used in echolocation, less distinct burst pulse calls (sometimes described as cries, barks, grunts or squeals as their high pulse repetition rate makes them audible to humans) and narrowband tonal whistles (Richardson et al. 1995). The latter two seem to be used mainly for communication, but most studies have focused on whistles rather than burst pulse sounds because whistles are largely in the audible or sonic range and easier to record and analyse (Au, 2000).

1.1.3. Echolocation

Odontocetes have developed highly specialised echolocation abilities. Au (2002) defines echolocation as “the process in which an animal obtains an assessment of its environment by emitting sounds and listening to echoes as the sound waves reflect off different objects in the environment”. Bottlenose dolphins (*Tursiops truncatus*), for example, utilise this process by emitting short high-frequency broadband click pulses of tens of kHz bandwidth and 40-70 μ sec duration (Au, 2002). These clicks are projected in a directional beam with a centre frequency that has been measured at 110-120 kHz, and the signal gets distorted and decreases in amplitude with increasing distance from the beam axis. Using echolocation, a bottlenose dolphin can reliably discriminate between very similar targets (for example aluminium plates that varied in as little as 0.23 mm thickness) and detect objects from a distance of over 113 m away (Au, 2002). Cetaceans live in an environment where these kinds of acoustic specialisations are a huge advantage. They frequently have to navigate in murky waters or other situations with limited visibility and their echolocation abilities allow them to detect a potential obstacle or prey item much earlier than they would be able to see it (Tyack, 2000).

1.1.4. Whistles

Odontocetes can be split into whistling and non-whistling species. Generally whistling species are more social, often occurring in groups of several, sometimes even thousands of animals, while non-whistling species tend to be solitary or found in groups of only few individuals (Richardson et al. 1995). Two exceptions to this pattern are the sperm whale (*Physeter macrocephalus*) and the killer whale (*Orcinus orca*) both of which are highly social even though the sperm whale produces mostly clicks and the killer whale mostly burst pulse calls (Richardson et al. 1995). An example of a non-whistling dolphin is the Hector’s dolphin (*Cephalorhynchus hectori*). It produces a few different types of broadband clicks which have a centre frequency of around 125 kHz and are used for

echolocation as well as communication (Dawson and Thorpe, 1990; Dawson, 1991). Most other delphinids do whistle.

Whistles are narrowband tonal calls with durations up to a few seconds and fundamental frequencies that typically fall between 5 and 20 kHz (Dudzinski, 2002). They can also have harmonic components at integer multiples of the fundamental reaching up to 100 kHz (Lammers et al. 2003). It has been shown that the higher frequency components of whistles of spinner dolphins (*Stenella longirostris*) are directional, meaning that harmonics at higher frequencies decrease in amplitude with increasing distance from the projection beam axis (Lammers and Au, 2003). Lammers and Au (2003) suggest that listening dolphins may utilise this characteristic to infer the whistling dolphin's orientation or direction of movement which would facilitate coordinated movements between individuals.

Dolphin whistles are frequency modulated and typically described based on spectrogram views of their time-frequency contours. Contour categories commonly used are unmodulated constant frequency whistles, upsweeps, downsweeps, U-shapes (or concave), inverted U-shapes (or convex), or wavering sinusoidal whistles (Richardson et al. 1995; Dudzinski, 2002). However, repertoires are often more complex and may include intermediate types between those categories, as well as whistles that consist of repeated types or a combination of different types. Also, whistle contours may not be continuous but may contain breaks (Richardson et al. 1995).

The whistle repertoires of odontocetes show great variability between different species, different geographically separate populations, different groups within populations or even between individuals. Rendell et al. (1999) compared the whistle characteristics of five odontocetes, the false killer whale (*Pseudorca crassidens*), short-finned pilot whale (*Globicephala macrorhynchus*) long-finned pilot whale (*G. melas*), white-beaked dolphin (*Lagenorhynchus albirostris*), and Risso's dolphin (*Grampus griseus*). They found significant differences of whistle parameters, especially mean call frequency, between all species except the white beaked dolphin and Risso's dolphin (and this particular case may have been biased by small sample size). Even the two *Globicephala* congeners differed in mean call frequency, frequency range and duration. Based on the whistle parameters, it was possible to classify whistles to the correct species

in more than double the cases than would be expected by chance alone. Classifying whistles to subfamily level (Delphinae versus Globicephalinae) even had a correct classification level of 90% (Rendell et al. 1999). Oswald et al. (2003) also found that whistles could be attributed to the correct one out of nine delphinid species at a rate much higher than expected by chance. However, the rate of correct classification varied greatly between species, from 7 to 66%. The frequency parameters were the most important variables in discrimination between species (Oswald et al. 2003).

1.1.5. Population-Level Variation in Vocalisations

The characteristics of vocal repertoires not only differ between species but also – to varying degrees – within species. Morisaka et al. (2005a) found that three populations of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Japan had different whistle characteristics. Again, frequency parameters were the most important variables to discriminate between populations while within population variability was higher for the parameters duration and number of inflections (Morisaka et al. 2005a). Similarly, the whistles of tucuxi dolphins (*Sotalia fluviatilis*) in Brazil have most variation in duration and number of inflections, but differences between geographically separate populations were mostly caused by frequency parameters (Azevedo and Van Sluys, 2005). Also, this study reported that variation was greater between populations that were geographically further apart than between adjacent populations. The variation in whistle characteristics between different species or populations, which is usually variation in frequency parameters, is likely to be the result of physiological or environmental factors such as body size or ambient background noise (Rendell et al. 1999; Morisaka et al. 2005a, 2005b). Some odontocetes, for example, show variation in frequencies of their echolocation clicks (observed in *Delphinapterus leucas*) or whistles (observed in *Globicephala* spp. and *Tursiops aduncus*) related to varying background noise levels in different locations (Rendell et al. 1999; Tyack, 2000; Morisaka et al. 2005b). Within populations, parameters such as duration or number of inflections or steps are usually

more variable and these variations may carry information about individual identity or behaviour (Rendell et al. 1999; Bazúa-Durán and Au, 2004; Morisaka et al. 2005a).

Bazúa-Durán and Au (2004) compared the whistle characteristics of spinner dolphins (*Stenella longirostris*) recorded at several locations around the Hawai’ian Islands. They did not find any significant differences between locations (or different islands), which may indicate that the spinner dolphins in this area live in fluid, inter-mixing pods (Bazúa-Durán and Au, 2004). However, some clusters of pods with different whistle characteristics, not related to location or time of recording, were found and termed “whistle-specific subgroups”. These may be caused by recording the same individuals, by stronger associations between certain individuals, or by related animals sharing similar whistles (Bazúa-Durán and Au, 2004). The authors suggest that these subgroups may imply different dialects within Hawai’ian spinner dolphins. Generally, dolphins and other species that live in fluid societies of changing groups tend to show much variation in the whistle repertoire at the level of individuals, while those that live in stable groups usually do not have individually distinct whistles but they have group-distinct repertoires often referred to as dialects (Tyack, 1986). The best-known example of dialects in an odontocete species is that of the killer whale. Killer whales spend their lives in stable matrilineal groups which associate on a regular basis with particular other closely related matrilineal groups. These associating matrilines form a pod and have a distinct repertoire of discrete calls that is unique to each pod. Related pods share several calls and form so-called acoustic clans but no calls are shared between different clans (Ford, 1991; Yurk et al. 2002). These pod-specific vocalisations probably facilitate group cohesion, recognition and coordinated behaviour within pods (Ford, 1991).

1.1.6. Individual-Level Variation – Signature Whistles

Rather than this type of group-specific repertoire, many dolphin species have whistles that are unique to individual animals. The concept of “signature whistles” was first introduced by Caldwell and Caldwell (1965) who recorded five captive bottlenose dolphins and found that each animal had a specific whistle which – with slight variations

in intensity or duration but always the same contour – made up over 90% of that individual's vocalisations. The individual signature whistles of bottlenose dolphins remain stable throughout their lives and are developed within the first year after birth (Sayigh, 2002). Calves appear to develop their signature whistles based on the signature whistles of other animals in their community (Fripp et al. 2005). Male calves tend to model their signature whistles after their mother's while female calves develop signature whistles that are highly distinct from their mother's whistle (Sayigh et al. 1990, 1995). This sex difference may well reflect the difference in social group behaviour throughout later life stages. Male bottlenose dolphins disperse from their natal groups, thus a signature whistle that is similar to their mother's may facilitate kin recognition and avoidance of inbreeding. Females often associate with other related females and in this situation it should be advantageous that the females in a group have distinct signature whistles so that their calves can discriminate between them (Sayigh et al. 1990, 1995).

Since cetaceans are highly mobile and live in an environment where visibility is limited, individual-specific calls are useful for maintaining contact between animals which frequently separate over distances that make vision unreliable (Tyack, 2000). Janik and Slater (1998) demonstrated that signature whistles are indeed used to maintain group cohesion, by showing that captive bottlenose dolphins emitted predominantly their signature whistle when they were separated from their group but almost never when they were together with their group. Observations of bottlenose dolphins in the wild have also shown that signature whistles are used during separations of mother-calf pairs (Smolker, et al. 1993) or allied male pairs (in bottlenose dolphins two adult males often form close alliances) (Watwood et al. 2005). Furthermore, wild bottlenose dolphins have been recorded repeating another individual's signature whistle, apparently to address the other (Janik, 2000). Another experiment with wild (temporarily restrained) bottlenose dolphins demonstrated that they do recognise particular signature whistles. Individuals responded more strongly to playbacks of signature whistles of their close relatives (mothers or independent offspring) than other familiar animals (Sayigh et al. 1998).

Although most studies of signature whistles have been undertaken with bottlenose dolphins, several other dolphin species have also been found to produce these highly stereotyped individual whistles (Richardson et al. 1995). For example, a stranded Pacific

humpback dolphin (*Sousa chinensis*) emitted only one type of whistle (with slight variations to the general contour), a type that had not been recorded in a study of the whistle repertoire of humpback dolphins in that area. Thus it is likely that this was a signature whistle (Van Parijs and Corkeron, 2001).

1.1.7. Behavioural Context Variation in Vocalisations

As odontocete whistles and burst pulse calls have primarily a social function, they can be expected to show some variation depending on behavioural context. During feeding, for example, bottlenose dolphins have been observed to increase the rate of whistling (the number of whistles emitted per animal per minute). As a result of this, new conspecifics join the feeding group, but it is not clear whether this is an intentional effect or a by-product (Acevedo-Gutiérrez and Stienessen, 2004). Beluga whales (*Delphinapterus leucas*) in Cunningham Inlet, North-West Territories, have higher vocalisation rates during social interactions than during swimming, resting or alarm contexts (Sjare and Smith, 1986). Furthermore, the types of whistles they produce vary depending on behavioural context, with upsweeps being more frequent during socialising and directive swimming. Pulsed calls were also more common during socialising and swimming than during alarm situations (Sjare and Smith, 1986). Herzing (1996) described the underwater behaviour and vocalisations of Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins in the Bahamas. She found clear associations between certain types of sounds and certain behavioural contexts. For example, signature whistles were produced by spotted dolphins during reunions of mother-calf pairs, during alloparental care and during courtship behaviours. “Excitement vocalisations” occurred during distress or excitement, particularly in calves. “Squawks” were related to aggressive encounters or sexual play, both within or between the two species, and “screams”, “barks” and “synchronised squawks” were all associated with agonistic and aggressive behaviour of males between or within species (Herzing, 1996).

1.2. Studying Acoustic Behaviour in Cetaceans

Even though much research on the acoustic behaviour and repertoires of cetaceans, especially odontocetes, is carried out these days, the specific functions and meanings of particular types of vocalisations are still largely unknown. This is mostly due to the complexity of repertoires and the difficulties of associating a sound with the particular vocalising individual in larger groups of animals in the wild (Dudzinski, 2002; Frankel, 2002). Much of what we know about odontocete hearing abilities and sound production comes from experiments in a captive setting where it is easier to determine which individual is emitting a sound (e.g. Janik and Slater, 1998; Sayigh, 2002). In the wild, recorded vocalisations can often only be related to general behaviour of the whole group. However, to determine the meaning of sounds associated with (often subtle) interactions between individuals, it is necessary to identify the vocalising and the listening/responding animal (Tyack, 2000; Dudzinski, 2002).

One possible way around this problem is the use of passive acoustic localisation techniques, in which the vocalising animal's position is calculated from the offset between the times of arrival of the signal at a number of different hydrophones, spaced a certain distance apart (Janik et al. 2000). Janik et al. (2000) used an array of three hydrophones, positioned in a triangle on the shores of a natural channel in Scotland, with hydrophone distances between 208 and 560m to localise bottlenose dolphins and harbour seals (*Phoca vitulina*) in the area. The error of acoustic localisation ranged from 2.5 to 20.4 m with a maximum of 13 m if the sound source was within the triangle described by the hydrophones. These kinds of error distances imply that this system may not be useful to determine the locations of individuals within a large tightly aggregated group of animals. Generally, increasing the number of hydrophones in the array and/or the spacing distances between the hydrophones will increase the accuracy of localisation (Janik et al. 2000).

Research on communication sounds in odontocetes has mostly focused on whistles, because their fundamental components fall in the human audible range and are easily recorded and analysed with standard equipment such as standard digital audio tape (DAT) recorders (Au, 2000). This is also the reason why the higher frequency harmonics

are often not considered in studies of whistle characteristics, even though they seem to have an important function (Lammers and Au, 2003; Lammers et al. 2003).

There are two commonly used approaches to describing whistle characteristics. The first one is the quantitative method of measuring a range of parameters of each whistle. Typically measured variables include duration, start frequency, end frequency, minimum frequency, maximum frequency, number of inflection points (defined as points at which the slope of the whistle changes direction, from rising to falling or falling to rising slope), breaks in contour, and presence of harmonics (Au, 2000; e.g. Oswald et al. 2003). These variables can then easily be analysed using statistical tests such as discriminant function analysis to determine inter-specific differences (Au, 2000; e.g. Oswald et al. 2003).

The second traditional approach to studying whistle repertoires is to classify whistles into several types based on the shape of their frequency versus time contour (Au, 2000). Six broad whistle type categories have been used in many studies: constant frequency, upsweep, downsweep, concave (or u-shaped), convex (or inversely u-shaped), and sinusoidal (or wavering) contours (e.g. Bazúa-Durán and Au, 2002). However, whistle contour repertoires are usually more variable and can consist of up to 40 different types. It is also possible that they may not actually have distinguishable types at all but rather should be considered graded systems where whistle contours transition from one general shape to the next through several intermediate forms (Dudzinski, 2002). The main problem with this methodology is that contour classification is based on human judgement and thus highly subjective (Au, 2000). This leads to much variation and little comparability between different studies and there is an obvious need of standardised methodology and nomenclature (Au, 2000; Bazúa-Durán and Au, 2002).

In an attempt to overcome this problem, computer algorithms and software have been developed that objectively measure the similarity between whistle contours. For example, Datta and Sturtivant (2002) used a computer algorithm that automatically extracted a whistle contour, split it into segments, and determined whether the contour in each segment was rising, falling or constant in frequency or whether there was a break in the contour. These data were then combined into a quadratic equation for each segment which allowed comparisons between segments. Whistles were classified based on the

overall and detailed contour shape as described by the sequence of segments (Datta and Sturtivant, 2002). Janik (1999) compared the performance of subjective human classification of bottlenose dolphin whistles to three different quantitative computer methods which used frequency measurements data and statistical principal component, cluster or cross-correlation analyses. He found that all three computer analyses were not as reliable as human subjects in identifying signature whistles and they also did not agree amongst each other. Janik (1999) suggests that humans were better able to determine classes that are also significant for the dolphins, but that generally the disagreement between all methods showed that external validation is needed in any case. To solve the problem of whistle classifications it is necessary to determine how the animals themselves perceive whistles and what variables they use to categorise them (Tyack, 2000).

1.2.1. Acoustic Surveying

Another application of acoustic recording is as a survey method to determine the presence, abundance and distribution of cetacean species. Traditionally abundance and distribution estimates of cetaceans are made using visual techniques such as line-transect surveys and mark-recapture methods based on photo identification (Evans and Hammond, 2004). Acoustic surveying – detecting animals by listening for their sounds in continuous recordings – is a valuable alternative in some situations. There are certain disadvantages of visual surveys. One is that the ability to see cetaceans is highly influenced by weather and sea state, so much so that surveys should not be carried out in sea states above Beaufort 2. This often limits the ability to survey evenly across seasons, as weather is generally worse in winter (Evans and Hammond, 2004). Another limitation is that visual surveys cannot be carried out at night. Acoustic surveys can cover the full 24 hours of a day and can also be used across all seasons as weather has a much smaller effect on it than on visual techniques (Goold, 1996; Evans and Hammond, 2004). Also, animals can usually be detected from a greater distance using acoustics than by eye-sight, especially in higher sea states (Goold, 1996).

The usefulness of acoustic survey techniques depends on a number of factors, such as the behavioural characteristics of the target species. If animals tend to be silent for a long time, then acoustics may fail to detect them (Goold, 1996; Evans and Hammond, 2004). However, species that are highly vocal but have relatively inconspicuous surface behaviour such as the harbour porpoise (*Phocoena phocoena*) are more likely to be missed by visual surveys but acoustics should be successful in detecting them (Evans and Hammond, 2004).

Another factor is the ability to identify different species based on their vocalisations. The sounds of many delphinid species are not necessarily easily distinguishable (Evans and Hammond, 2004). Analyses trying to determine the correct species from recorded whistles gave correct classification rates that were much higher than by chance alone but still lower than the standard levels of near certainty in visual identification (Oswald et al. 2003). On the other hand, some species may actually be more easily distinguished acoustically than visually, which seems to be the case for the long-finned and short-finned pilot whales (*Globicephala* spp.) (Rendell et al. 1999).

Furthermore, the aims of the study need to be considered. To establish the distribution or simple presence of a species in an area, acoustic surveying is useful. However, if precise abundance estimates are needed, the use of acoustic techniques may be limited (Evans and Hammond, 2004). Estimating group sizes based on the rates of vocalisations is generally difficult, especially for species that occur in large groups (Goold, 1996). However, some studies have been able to determine a regression relationship between dolphin whistle rate and group size, and succeeded in relatively accurately predicting group size from the number of whistles recorded (e.g. Van Parijs et al. 2002).

1.3. The Short-Beaked Common Dolphin, *Delphinus delphis*, Linnaeus (1758)

Common dolphins (*Delphinus* spp., family Delphinidae) are considered to be of high abundance with a worldwide distribution. Many different populations seem to exist which often show varying morphological characteristics. This has caused some confusion over their taxonomy and more than 20 different species have been suggested over time (Carwardine, 1995). Two distinct species are now widely recognised: the short-beaked common dolphin (*Delphinus delphis*) and the long-beaked common dolphin (*D. capensis*). A third form exists, the very-long-beaked common dolphin, *D. tropicalis* or *D. capensis tropicalis*, if viewed as a subspecies of *D. capensis* (Stockin and Vella, 2005), which is endemic to the Indian Ocean. However, little is known about this last form and its taxonomic status is still regarded as uncertain (Perrin, 2002).

1.3.1. Morphology

Common dolphins are slender and their body length has been measured to range from 1.6 to 2.4 m in Californian waters where both *D. delphis* and *D. capensis* occur (Perrin, 2002). Males are slightly larger than females (in the short-beaked form: 1.7-2.0m for males versus 1.6-1.9 m for females) and the long-beaked form is larger and heavier than the short-beaked form (1.9-2.4 m and up to 235 kg versus 1.6-2.0 m and 200 kg respectively). However, there is much variation to body sizes between different populations within the two species (Perrin, 2002). For example, the common dolphins in the North-east Atlantic, which are classified as short-beaked common dolphins based on beak length and colouration, can reach a total body length of 2.5 m in males or 2.3 m in females (Murphy, 2005).

Common dolphins are easily distinguished at sea by their elaborate hourglass colour pattern (fig. 1.2; Carwardine, 1995; Perrin, 2002). They have a dark grey to black uppermost portion or cape which dips to form a V-shape directly below the dorsal fin. Anterior from this V-shape the side (thoracic patch) has a tan to yellow colouration and the posterior portion of the body (flank patch) is light to medium grey in colour. The

abdominal field is white with varying grey stripes. These stripes differ between short-beaked and long-beaked forms and between populations. They may run from the flipper to the anus, from the lower beak to the flipper and sometimes extend into the yellow or grey side patches. Another common variation even between individuals within a population is the colouration of the dorsal fin which can range from all black to black with a grey patch to white with a dark border. Calves have a paler colour pattern than adults (Carwardine, 1995).

The colour pattern is more muted in the long-beaked form than in the more brightly coloured short-beaked form, but the two species are more obviously distinguished by the beak, which – as the name suggests – is much longer and more slender in the long-beaked common dolphin and shorter and stubbier in the short-beaked form (Carwardine, 1995; Perrin, 2002).



Figure 1.2. Short-beaked common dolphins in the Celtic Sea, showing the typical hourglass pattern with yellow and light grey side patches.

1.3.2. Distribution and Abundance

Common dolphins have a worldwide distribution from warm-temperate to tropical waters between latitudes of about 40-60°N and about 50°S. The short-beaked common dolphin is abundant in all oceans except the South Atlantic and Indian Ocean. In the North

Atlantic it is found from Newfoundland to Florida in the west and from southern Norway to West Africa in the east. In the Pacific it occurs from southern Canada to Chile, in pelagic waters of the eastern and central North Pacific, from Japan to Taiwan and around the islands of New Caledonia, New Zealand and Tasmania (fig. 1.3; Perrin, 2002).

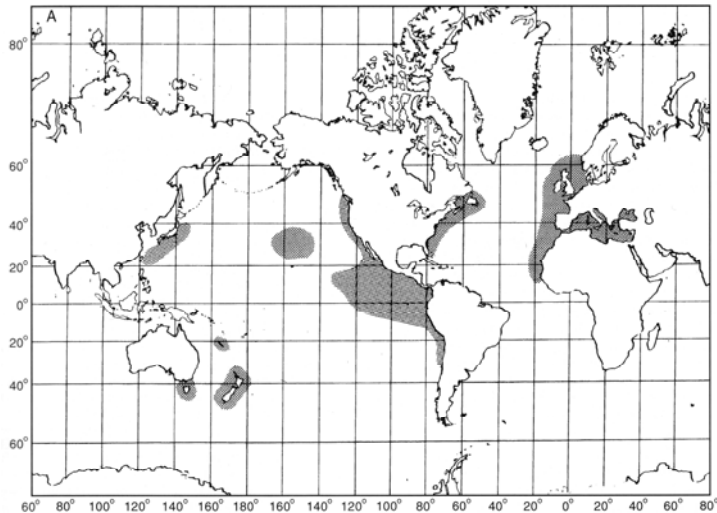


Figure 1.3. Shaded areas indicate the worldwide distribution of short-beaked common dolphins (*D. delphis*) (Perrin, 2002).

D. delphis is also found in enclosed waters such as the Mediterranean and Black Seas (Carwardine, 1995; Perrin, 2002) however, in these areas as well as in the eastern tropical Pacific declines in abundance have been noticed (Carwardine, 1995). Bearzi et al. (2005) recorded a significant decline in numbers of short-beaked common dolphin groups encountered in the eastern Ionian Sea of the Mediterranean from 1997-2003, as well as a decrease in group sizes. These population declines were attributed mostly to anthropogenic impacts such as habitat degradation caused by overfishing and pollution, as well as incidental by-catch in fishing gear (Bearzi et al. 2003; Bearzi et al. 2005). The subpopulation of common dolphins in the Mediterranean Sea was listed as endangered on the IUCN Red List of Threatened Species in 2003 (Bearzi, 2003). Even though some populations are threatened, short-beaked common dolphins worldwide are thought to have an abundance of millions of animals and are thus one of the most numerous cetacean species (Carwardine, 1995).

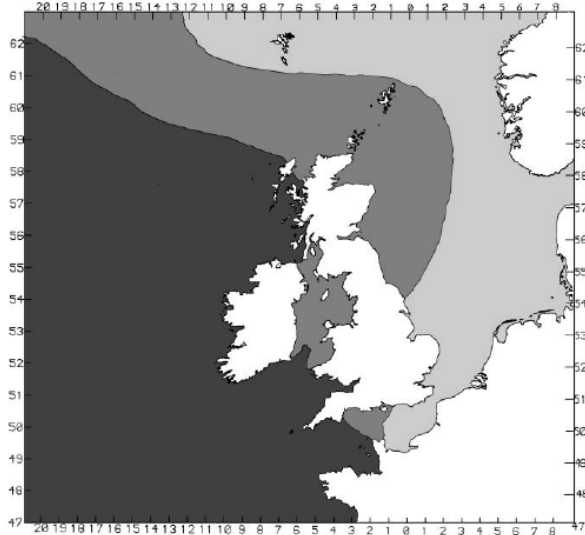


Figure 1.4. Distribution of short-beaked common dolphins around the British Isles. Dark grey: regular occurrence; medium grey: occasional occurrence; light grey: absent/casual (Evans, 1998).

Around the British Isles, the short-beaked common dolphin is regularly found in the southern Irish Sea and the Celtic Deep area, in the western approaches to the English Channel, around the Inner Hebrides and west of Ireland (fig. 1.4; Evans, 1998). In the Celtic Sea, which is the focus area of the present study, *D. delphis* abundance has been estimated at 75,450 animals (with a confidence interval of 23,000 – 249,000) (Hammond et al. 2002).

1.3.3. Habitat and Migration

While the long-beaked form is generally found in shallower water close to shore (Perrin, 2002), the short-beaked common dolphin usually occurs in deeper offshore waters over the continental shelf (Carwardine, 1995). *D. delphis* is often found associating with upwelling areas and many populations show seasonal migration patterns that may be related to oceanographic features such as warm water currents (Carwardine, 1995; Perrin, 2002). To the north of the study area of the present study, the Celtic Sea Front marks the boundary between the Irish Sea and the Celtic Sea (Goold, 1998). This front, caused by different sea surface temperatures of the two water masses, develops during spring and summer and causes high primary productivity and thus more prey for top level predators such as the common dolphin (Savidge and Foster, 1978; Goold, 1998). As the front breaks down in autumn, common dolphins are sighted less frequently in the region and it has been suggested that they migrate offshore during this season (Goold, 1998).

Around the Maltese Islands in the Mediterranean, short-beaked common dolphins have been shown to prefer deep offshore waters, but during summer and autumn they also move further inshore (Vella, 2005). Similarly, in New Zealand, *D. delphis* are found at a mean distance of 20.2km from shore during autumn but they move inshore to a mean distance of 9.2km from shore in spring/summer. These seasonal migrations seem to be related to changes in sea surface temperature which are likely to influence prey distribution (Neumann, 2001). Off the northeastern United States, common dolphins were found mainly in waters between 100 and 200m depth paralleling the continental slope. A seasonal north-south migration was observed in this area (Selzer and Payne, 1988). Not much is known about the home ranges of short-beaked common dolphins due to their offshore habitat preference which makes research such as long-term photo-identification studies of this species difficult (Neumann et al. 2002; Bearzi et al. 2003). A three-year photo-identification study in north-east New Zealand showed that *D. delphis* in this area are highly mobile and some individuals moved between areas up to 200km apart (Neumann et al. 2002).

1.3.4. Ecology and Behaviour

Common dolphins feed on a range of different prey items, varying between seasons and different geographic areas. Their prey includes epipelagic shoaling fishes as well as smaller mesopelagic fishes and squids (Perrin, 2002). Shoaling fishes such as mackerel (Scombridae), sardines (Clupeidae) or anchovies (Engraulidae), and to a lesser extent cephalopods made up the majority of the stomach contents of stranded or incidentally caught *D. delphis* in several areas of the world (eastern United States: Overholtz and Waring, 1991; Portugal: Silva, 1999; Mediterranean Sea: Bearzi et al. 2003; New Zealand: Neumann and Orams, 2003). In general, common dolphins seem to be flexible opportunistic feeders that can adjust their diet according to local and seasonal prey availability as well as individual abilities related to sex and age of the animal, such as diving capacity (Silva, 1999; Bearzi et al. 2003; Neumann and Orams, 2003).

To be able to feed on such a large variety of prey, common dolphins also exhibit a range of different feeding behaviours. These include different individual strategies, where one dolphin captures prey on its own, as well as various coordinated strategies, in which a group of dolphins works together to herd and capture fish (Neumann and Orams, 2003). The short-beaked common dolphin is a very gregarious species that is usually encountered in large schools which can reach sizes of thousands of animals (Carwardine, 1995; Perrin, 2002). These large schools are often structured, with several subgroups of around 20-30 animals (Perrin, 2002). In the Mediterranean, they are more commonly found in groups of 50-70 individuals, occasionally in groups of a few hundred (Bearzi et al. 2003). In some coastal waters of the Mediterranean group sizes are much smaller, with on average less than 15 animals (Bearzi et al. 2005). A small mean school size of 11 individuals was also measured in the Celtic Sea (Hammond et al. 2002). In the English Channel and Bay of Biscay, group sizes of common dolphins averaged at 32 with a maximum group size of around 2,000 animals (Brereton et al. 2005).

Common dolphins are often observed in association with other cetacean species (Perrin, 2002). In the Mediterranean Sea, for example, they have been recorded in mixed groups with striped dolphins (*Stenella coeruleoalba*) and/or Risso's dolphins (*Grampus griseus*), showing behaviours such as synchronized swimming and aggressive or playful interactions (Frantzis and Herzing, 2002). During feeding, short-beaked common dolphins in New Zealand have also been observed in association with mysticetes such as sei whales (*Balaenoptera borealis*), Bryde's whales (*Balaenoptera edeni*) or minke whales (*Balaenoptera acutorostrata*), as well as seabirds including gannets (*Morus serrator*) and shearwaters (*Puffinus griseus*) (Neumann and Orams, 2003). In the present study in the Celtic Sea, common dolphins were often seen feeding together with fin whales (*Balaenoptera physalus*), minke whales and seabirds such as gannets (fig. 1.5; *personal observation*).

The short-beaked common dolphin is known as a very active, acrobatic dolphin. Large groups can often be spotted and even heard from some distance due to their porpoising, breaching, tail/flipper-slapping and splashing behaviour (Carwardine, 1995). Common dolphins are also famous for approaching vessels to bow-ride (fig. 1.6) and they have even been observed "bow-riding" on mysticete whales (Perrin, 2002).



Figure 1.5. Short-beaked common dolphins (right) associating with fin whales (left) and sea birds in the Celtic Sea.



Figure 1.6. Short-beaked common dolphin porpoising alongside the survey vessel.

1.3.5. Vocal Behaviour

Common dolphins are highly vocal animals, whose sounds may even be heard from above the surface (Carwardine, 1995). Like most delphinids they produce echolocation click trains, burst pulse sounds and whistles. Their calls have been described as “chirps” with dominant frequencies between 8 and 14 kHz, “barks” with low dominant frequencies below 3 kHz and whistles that cover a dominant frequency range from 2 to 18 kHz (based on recordings of captive *D. delphis* made by Caldwell and Caldwell (1968) as quoted in Richardson et al. 1995). Oswald et al. (2003) described the whistle characteristics of short- and long-beaked common dolphins in the eastern tropical Pacific Ocean. Short-beaked common dolphin whistles had a mean beginning frequency of 9.8 kHz, mean end frequency of 11.4 kHz, mean minimum and maximum frequencies of 7.4 and 13.6 kHz respectively, a mean frequency range of 6.3 kHz, and a mean duration of 0.8 seconds. Their average number of inflection points was 1.2 and they had on average 1 step within their contours. The frequency parameters of long-beaked common dolphin whistles were consistently slightly higher with mean beginning and end frequencies of 10.1 and 14.1 kHz respectively, mean minimum and maximum frequencies of 7.7 and 15.5 kHz respectively and a mean frequency range of 7.9 kHz. Mean duration was minimally shorter than in short-beaked common dolphins, at 0.7 seconds and the degree of complexity or frequency modulation was slightly higher, described by means of 1.3 inflection points and 1.5 steps per whistle (Oswald et al. 2003).

Goold (2000) found that the whistle density of *D. delphis* off the Welsh coast, UK, increased significantly at night and he suggests that this may be related to higher communication rates between individuals during cooperative feeding on nocturnally surface-migrating prey. Possible signature whistles have been recorded in common dolphins (Richardson et al. 1995), however, in his review on sound production in marine mammals, Frankel (2002) states that “in common dolphins (*Delphinus* spp.), there appears to be a lack of sound “signature” per individual, and it has been guessed, but with little data support, that there may well be regional dialects per population or subpopulation, as in killer whales”. However, the present author was not able to locate a source for Frankel’s statement on lack of signature whistles and presence of dialects in

common dolphins. As described above in chapter 1.1.5 on population variation in vocalisations, Bazúa-Durán and Au (2004) reported the presence of whistle-specific subgroups in Hawai'ian spinner dolphins that may represent a form of dialects. However these were not as distinct as dialects in killer whales (Bazúa-Durán and Au, 2004). It has been suggested that dolphin species with similar ecological and behavioural characteristics may have similar whistle systems (Au, 2000). In this case the whistle characteristics and function of the common dolphin may resemble that of the spinner dolphin as both are highly gregarious species that are found in large fluid groups and generally in pelagic habitats (Bazúa-Durán, 2004).

Wakefield (2001) identified 18 different types of whistles with varying degrees of frequency modulation in the repertoire of short-beaked common dolphins in the Celtic and Irish Seas, including the six broad types generally used in studies of whistle repertoires (constant, upsweep, downsweep, convex, concave and sinusoidal). Simple upsweeps, downsweeps and constant frequency whistles were the three most common types (in that order) and whistles ranged in frequency from 4.7 to 20.3 kHz. Wakefield (2001) also found that during periods of intense background noise from seismic surveying, whistle frequencies of common dolphins were significantly higher and vocalization rate increased. Scullion (2004) also recorded short-beaked common dolphins in the Celtic Sea and found a slightly wider whistle frequency range from 3.4 to 21.0 kHz. Whistles had durations between 0.017 and 2.148 seconds and 20 different whistle types were determined, with upsweeps again being the most often recorded type (Scullion, 2004).

1.4. Objectives and Aims of this Study

The purpose of this study was to describe the whistle repertoire of short-beaked common dolphins (hereafter common dolphins), *Delphinus delphis*, in the Celtic Sea and compare this repertoire to that of common dolphins in the English Channel. It is not clear whether the dolphins in these two areas inter-mix because not much is known about the home ranges of common dolphins. Differences in the vocalisations between them might be an indication of geographical separation and would present a clue as to whether these animals could be distinct populations. The question of whether sub-groups within a species can be considered different populations has important implications in conservation biology as a population that is geographically separated from and does not interbreed with other conspecifics will be more vulnerable to population decreases caused by anthropogenic impacts. Also it is necessary to determine biologically significant units to assess changes in population size and the scale of potential impacts, as well as to implement regionally effective management laws (Baker and Palumbi, 1996). In the case of the common dolphins around the British Isles this is an important consideration as there appears to be a serious problem of incidental catch of common dolphins in fisheries in the western English Channel area. The magnitude of the effect this impact has on the population is unclear (De Boer et al. 2005).

A further aspect of this study was to examine the methodology used in acoustic surveying and whether this is a valid alternative to conventional visual surveying techniques. In particular, it was examined whether whistle densities can be used as a reliable indicator of the group size of dolphins recorded.

The following specific questions are asked:

Part A: Acoustic Survey Methodology

- How do acoustic contact data compare to sightings data? In what cases were dolphins heard but not seen or vice versa?
- Is there a relationship between whistle density and group size of common dolphins?
- Is there a diel pattern of acoustic records and/or sightings of common dolphins?

Part B: Whistle Repertoire of Celtic Sea Common Dolphins

- What are the characteristics of the whistle repertoire of common dolphins in the Celtic Sea (average duration, frequencies, whistle types)?
- Are whistle characteristics related to behaviour and/or group size, and are there significant differences between encounters?

Part C: Comparison between Whistles from the Celtic Sea and the English Channel

- Are the whistle repertoires of common dolphins in these two regions significantly different in parameters such as average duration and frequencies?
- Are the whistle types and their relative frequencies different between the two areas?

2. Materials and Methods

2.1. Celtic Sea Recordings

2.1.1. Field Work

A total of four surveys were conducted, one in each month from May to August 2005. Three of these were two-day surveys (May 16-17, July 13-14 and August 16-17) and one was carried out in one day (June 22) due to limited availability of a vessel and bad weather conditions. The survey area was situated in the Celtic Sea, over the Celtic Deep, southwest of Wales and southeast of Ireland, between 51°30'N and 52°00'N latitude and 005°30'W and 006°20'W longitude. The line transect surveys were carried out along pre-determined track lines (picked in random order; see appendix 7.1 for transect waypoints), each of which ran in a zigzag pattern across the entire study area (fig. 2.1).

Two different platforms were used. The May survey was undertaken aboard the vessel *Llanstadwell* (fig. 2.2), run out of Milford Haven marina. For the other three surveys *Predator* was used, a 12m long dive charter boat fitted with a Caterpillar 420hp engine, out of Neyland marina (fig. 2.3).

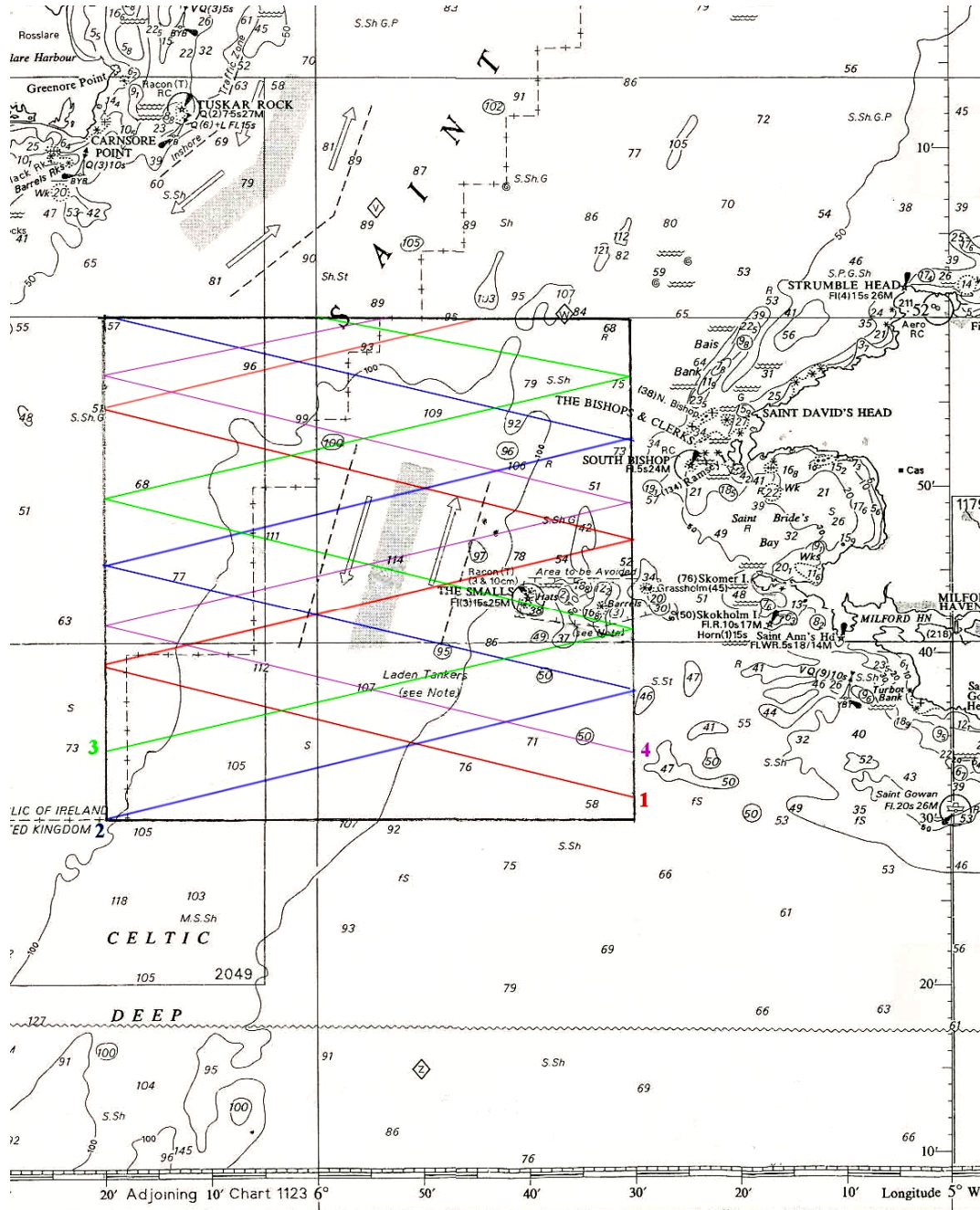


Figure 2.1. Nautical map of the survey area in the Celtic Sea with transect lines. Different colours indicate the different surveys: (1) 16-17 May 2005 (red), (2) 22 June 2005 (blue), (3) 13-14 July 2005 (green), (4) 16-17 August 2005 (purple) (Admiralty Chart, Hydrographic Office).



Figure 2.2. *Llanstadwell*, the vessel used for the first survey.
Photograph by Hanna Nuuttila, Sea Watch Foundation.



Figure 2.3. *Predator*, the dive charter vessel used for surveys 2-4
(<http://www.divepembrokeshire.com>).

Throughout these surveys, observers of the Sea Watch Foundation team rotated positions so that there was always three visual observers (two primary observers on the flying bridge and one independent observer on the deck) keeping watch. The purpose of the independent observer was as a control to check whether the primary observers missed any cetaceans. Observers were in place throughout the entire transect, as well as on the way out and back in from the harbour to the start/end of the transect line. Visual observers recorded details such as date, time, GPS (Global Positioning System) position, species, number of animals, life stages of animals, behaviour, distance and direction from the boat and boat course for all cetacean sightings. Furthermore, a continuous record of effort, boat position and course, travel speed and environmental conditions was kept approximately every 15 minutes (for sightings and effort forms see appendix 7.2). The author acted as an “acoustic observer” and continuously monitored recordings using Sennheiser HD 202 headphones connected to the DAT recorder. During sightings she noted DAT recorder settings as well as her own visual observations of the animals including start and end time of sightings, depth, start and end distance of the animals from the vessel, species, group size, life stages and behaviour (for acoustic observer form see appendix 7.2). These observations were later compared to those made by the Sea Watch team and where they differed, Sea Watch observations were used as their primary observers had more experience in recording cetacean sightings, especially of large groups of animals, and their position on the flying bridge of the vessel gave them a better view. Behavioural observations were recorded based on the prominent behaviour of the whole group, categorised as (1) travelling (fast directed swimming), (2) foraging (rapid movements, changing directions, diving behaviour, sometimes fish chasing was observed), (3) socialising (group staying in one general area without obvious travelling or foraging, breaching/leaping and other aerial behaviour) and/or (4) bow-riding (animals approaching the vessel to ride the bow wave or stern wake).

Recordings were made continuously throughout the transect as well as opportunistically on the way between harbour and transect start/end points, as soon as the boat had left the harbour area and was far enough from the shore to ensure that the hydrophone would not be damaged by hitting the sea floor in too shallow water. Due to

equipment problems, three different hydrophones had to be used. All were custom built out of Benthos AQ4 transducers with built-in preamplifiers which were housed in a 34cm plastic tube filled with oil as a damper liquid and attached to screen cable. For the first survey a stereo hydrophone of 88m length was used, for the second and third survey a 230m long stereo hydrophone was used and on the fourth survey a mono hydrophone (with only one channel) of 130m length was used (fig. 2.4). The array was towed behind the vessel at a speed of around 10 knots (fig. 2.5). The hydrophones were connected to a 3 kHz high pass filter to reduce low frequency engine noise and then to a Sony TCD-D8 digital audio tape (DAT) recorder with a sensitivity of 20 Hz to 22 kHz (fig. 2.6). The DAT recorder's internal clock, which was synchronised with that of the observers' portable GPS, recorded time and date throughout all recordings so that they could later on be linked to visual data records.

The times of “sightings” recorded during surveys were defined as the times at which an individual group of dolphins was seen. However, often these sightings overlapped, i.e. several groups which were noted as distinct sightings, came together in the same area around the survey vessel. It is likely that during recordings from these times, all of the groups in the area can be heard. Therefore it seemed unreasonable to analyse recordings grouped into “sightings”. Instead, different sightings were grouped together into “encounters” if they overlapped or if less than 5 minutes lay between the end time of one and the start time of the next sighting. This is based on the assumption that throughout one encounter, the animals from all the different groups (sightings) were still in the range within which their vocalisations are picked up by the hydrophone.

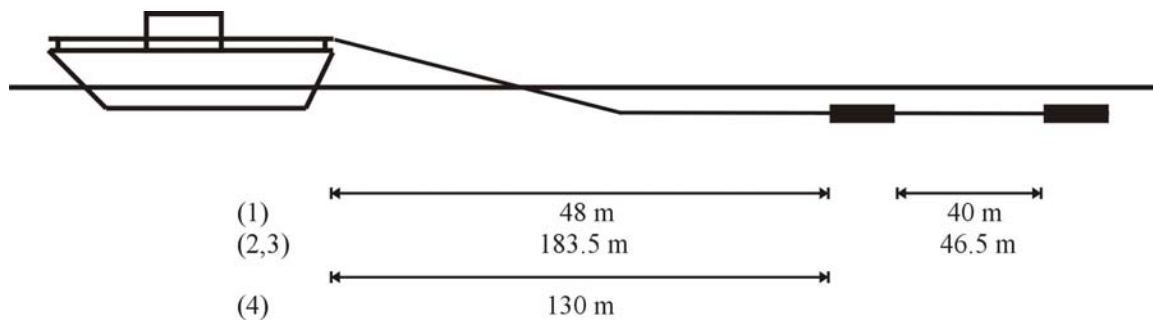


Figure 2.4. Setup of the towed hydrophone array and cable lengths for the four different surveys.



Figure 2.5. Hydrophone towed behind the stern of *Predator*.



Figure 2.6. Hydrophone cables, high pass filter (on the right) and DAT recorder (top left).

2.1.2. Computer Transformation of Recordings into Data Files for Analysis

The recordings made in the field were digitally downloaded onto a Dell Inspiron 8200 laptop computer by connecting the DAT recorder to a Creative Sound Blaster Extigy (24 bit, 96 kHz, 100 dB SNR) external Dolby Digital sound card, using a Sony optical fibre cable. The tapes were then played back and recorded as windows PCM wave files (.wav), at a sample rate of 48 kHz and 16 bit resolution, using the program Adobe Audition version 1.5 (Adobe Systems Incorporated). The continuous recordings of each survey day were first broken down into 10-minute-intervals. The number of whistles in each of these 10-minute-files was counted visually using the spectral view function in Adobe Audition (spectrogram settings: Hanning window, 512 band resolution) (fig. 2.7). Whistle intensity was noted as clear (if at least 50% of whistles stood out clearly from background noise) or faint (if at least 50 % of whistles could only be seen faintly, their entire contours could not be made out clearly). Correlating the recordings to visual data, it was noted for each 10-minute-file whether there was a sighting during this period. Furthermore the type of hydrophone used during the recording and any possible errors or tape changes that occurred were noted for each 10-minute-period. Whistle density was then calculated by dividing the counted number of whistles by the duration of the file. In most cases this was 10 minutes, except where, for example, a tape change or recording error caused a short pause within a 10-minute-period. In these cases the duration was adjusted accordingly.

Separate sound files were created for the times where common dolphin sightings were recorded. Thus, there was generally only one continuous sound file that covered the entire duration of each sighting (except where tape changes caused a necessary break in the recording during a sighting) from first visual contact to the time the group was last seen where this data was available, or alternatively to the start of the next sighting if they overlapped. The number of whistles within each of these sighting files was also counted and divided by the duration of the recording (duration of the sighting minus possible recording errors/tape changes where present) to get whistle density. Details of each sighting were noted from the visual sightings data, such as number of animals, behaviour, start and end distance of the animals to the boat and depth at the time of sighting.

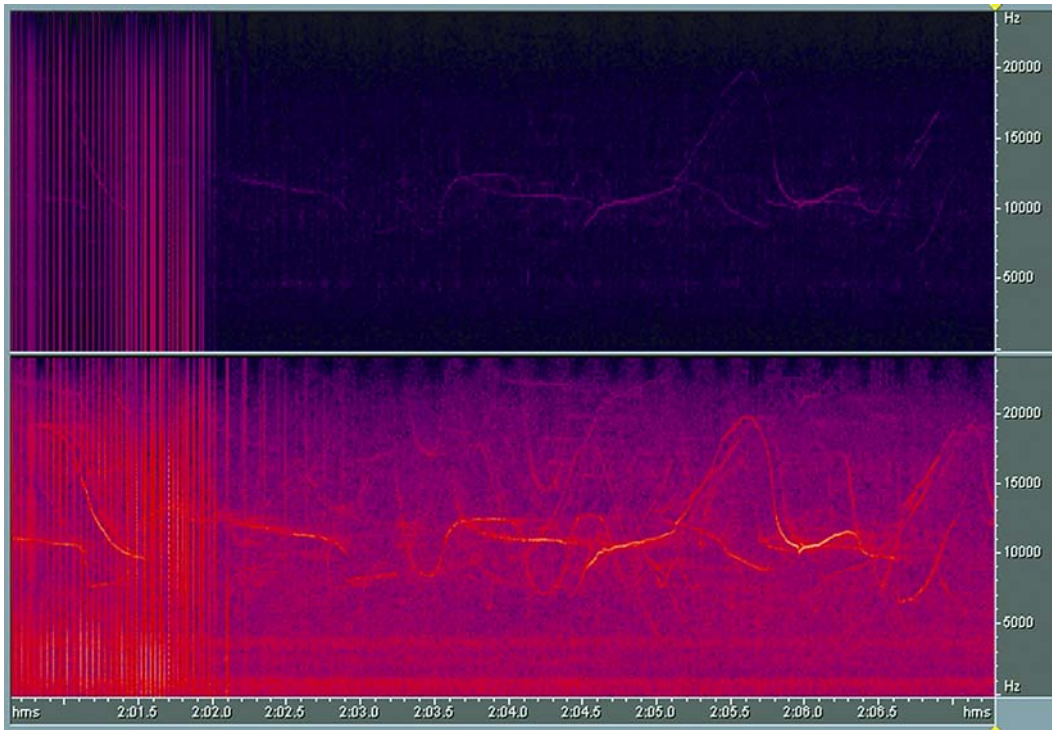


Figure 2.7. Adobe Audition 1.5 spectrogram window produced by Fast Fourier Transform, using a Hanning window with a 512 band resolution. The two spectrograms show the recordings from the two elements of the stereo hydrophone, the top spectrogram is from the front element, the bottom from the rear element. Time is shown on the x-axis and frequency on the y-axis. The amplitude is indicated by colouration, from black to orange with rising amplitude. Several common dolphin whistles can be seen, as well as broadband clicks (on the left edge).

The recordings during sightings were then broken down into 1-minute-sound files. If a stereo hydrophone had been used, channel 1 which was recorded on the front element of the hydrophone was discarded since the rear element generally produced better quality recordings with less background noise due to its larger distance from the engine. These mono 1-minute-files could then be imported into the program MATLAB, version 5.2 (The MathWorks, Inc.) by running a script called “wav2raw” (© 1984-1994 by The MathWorks, Inc.). This script allows you to open .wav sound files, returning the sampled data points as the variable “sig”, the sample rate as “Fs” and the format of the .wav file as “Format”. Then a second script, called “delphi” (written by Dr. John C. Goold, 2001), was run. This produces a rolling spectrogram of the sound file, with a Fast Fourier Transform (fft) resolution of 512 bands, and a sampling frequency (Fs) of 48000Hz. This spectrogram window shows 1.25 seconds of recording and can be

advanced by the user. Dolphin whistles can then be marked using cross-hairs that can be moved along the whistle contour with the mouse. Clicking on the left mouse button saves the coordinates (time and frequency) at the current point marked by the cross-hairs (fig. 2.8). In this way, up to 50 points can be marked, tracing along a whistle contour. Whistles were marked by clicking at intervals of roughly 0.02 to 0.04 seconds but these intervals varied slightly depending on the length and the degree of frequency modulation of the whistle. Most whistles fitted into one screen of the spectrogram, however, occasionally a whistle's duration was longer than the 1.25 seconds of the window. In these cases the whistle was broken up into two pieces and marked as two whistles (so that the spectrogram could be advanced in between) and a note of this was taken. The two strings of numbers were later reattached to show the whole whistle as one. Only whistles that could be clearly distinguished from background noise and other overlapping whistles were marked, taking care not to include harmonics or "ghost whistles". A "ghost whistle" is a repetition of a whistle after a short time lag. This occurs when the sound wave of the whistle is reflected from the water surface and this reflection reaches the hydrophone shortly after the original sound wave of the same whistle.

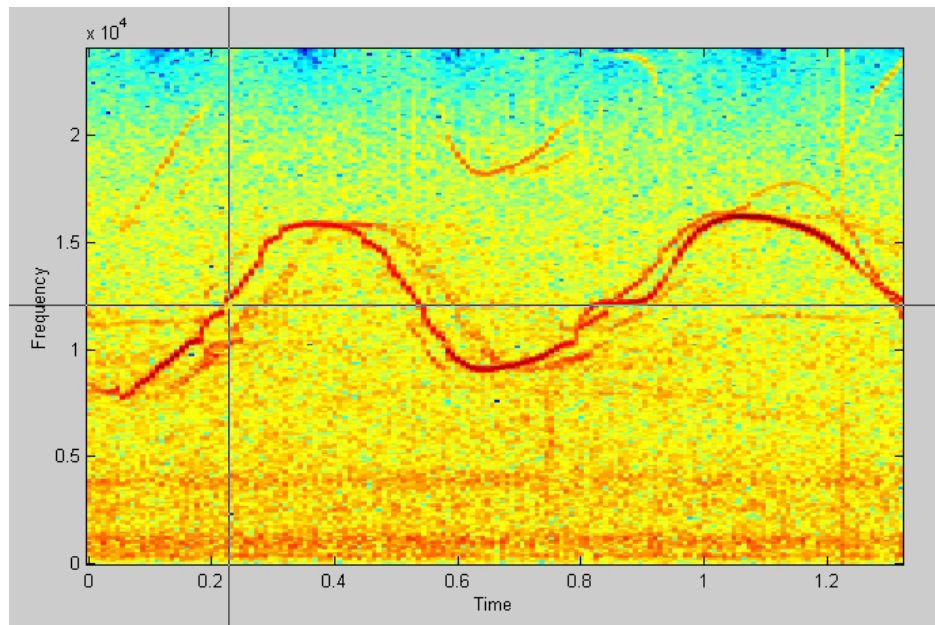


Figure 2.8. MATLAB 5.2 spectrogram in which whistles were marked using cross-hairs as shown. The whistle in this example has a high-frequency harmonic (partially cut off) and a ghost whistle.

After all clear whistles in a file had been marked, the time and frequency data strings for all whistles were saved as .txt files which were then imported into Microsoft Excel where time and frequency data columns were combined into one sheet so that each whistle was described by two adjacent columns. To avoid oversampling particular groups or individuals, a maximum number of 100 whistles from each encounter (randomly selected if more than 100 had been marked from one encounter) were used in the analysis.

Some whistles (especially signature whistles) may consist of two or more subunits, which may be repetitions of one contour type or combinations of different contours. If these segments are consistently produced together as a unit, the whole unit is often analysed as one whistle and each continuous segment is called a “loop” (Tyack, 2000). It should be noted that for the purpose of this study, the author disregarded such multi-loop whistles. During many of the recordings analysed in this study, whistle density was high with overlapping contours that made it generally impossible to decide whether two contours were part of a multi-loop whistle or two whistles produced by different individuals. Thus, for consistency and to avoid making highly subjective decisions, the author analysed each continuous contour as one whistle, even in cases where a certain combination of contours appeared to be repeated several times as a unit.

2.1.3. Analysis

All statistical tests were carried out using SPSS statistical software, version 12.0 for Windows (SPSS Inc.).

Part A: Acoustic Survey Methodology

This part of the analysis was based on the continuous record of recordings and sightings data broken down into 10-minute-intervals. For each of these 10-minute-periods it was noted whether there was acoustic contact (as a binary variable: yes/no), that is whether any whistles had been counted, and whether there was a sighting during that period

(yes/no). The data were then broken down into cases where there was (1) no acoustic contact and no sighting, (2) acoustic contact and sighting, (3) acoustic contact but no sighting or (4) a sighting but no acoustic contact. Possible reasons for (3) and (4) were examined using statistical correlation, regression and homogeneity tests as appropriate.

The relationship between group size (# of animals) and whistle density (# of whistles/minute) was examined using correlation and regression analyses to develop an equation from which group size can be predicted based on whistle density. Other possible factors that could influence whistle density such as the mean distance of the animals from the vessel and the behaviour of the animals were analysed by looking for significant correlations/regressions. Multiple regression analysis was carried out to determine which of the possible factors had the most important influence on whistle density.

The continuous acoustic and visual data throughout the survey days was used to look for diel patterns in acoustic contact and/or common dolphin sightings. Continuous recordings were broken down into 10-minute-intervals and the whistle density (# of whistles/min) and number of sightings was averaged for each particular 10-minute-time frame across all survey days. Statistical analysis was then used to determine whether there was a significant relationship between time of day and whistle density recorded or number of sightings.

Part B: Whistle Repertoire of Celtic Sea Common Dolphins

For each whistle, eleven parameters were calculated or entered in the Excel spreadsheet. These were:

1. Duration:
The time duration (sec) of the whistle, (end time minus start time).
2. Start Frequency (SF):
Frequency (Hz) at the start point of the whistle.
3. End Frequency (EF):
Frequency (Hz) at the end point of the whistle.
4. Minimum Frequency (MinF):

Frequency (Hz) at the lowest point of the whistle.

5. Maximum Frequency (MaxF):

Frequency (Hz) at the highest point of the whistle.

6. Mean Frequency (MeanF):

Average/mean frequency (Hz) of all points marked along the whistle. This variable is sensitive to the distribution of marking points along the whistle, for example if more points were marked along the first half of a simple whistle of falling frequency than along the second half, the resulting MeanF would be higher than if distribution of points was even along the whistle. Thus, the author tried to keep marking intervals consistent within in a whistle.

7. Frequency Gradient (FG):

The overall gradient/steepness (Hz/s) of the rise or fall of the whistle, calculated as:

$$FG = (EF - SF) / \text{Duration}$$

8. Absolute Frequency Gradient (AFG):

The absolute value of FG (Hz/s), removing positive or negative sign.

9. Frequency Range (FR):

The range of frequencies (Hz) spanned by the whistle, calculated as:

$$FR = \text{MaxF} - \text{MinF}$$

10. Inflections:

The number of inflections in a whistle, where “inflections” are defined as turning points where the frequency modulation or slope of the whistle changes from falling to rising or rising to falling frequency.

11. Steps:

The number of steps in a whistle, where “steps” are defined as periods of constant frequency between two periods of the same frequency modulation, ie. two periods of rising or two periods of falling frequency.

Figure 2.9 illustrates these parameters.

Based on the overall shape of the whistle contour (which was plotted in Excel) rather than specific frequencies and durations, the author subjectively grouped the whistles into separate schematic whistle types.

Statistical tests were then carried out to analyse whether these whistle parameters, as well as the relative proportions of the whistle types showed correlations with group size (# of dolphins) and/or behaviour, and whether they differed significantly between the individual encounters.

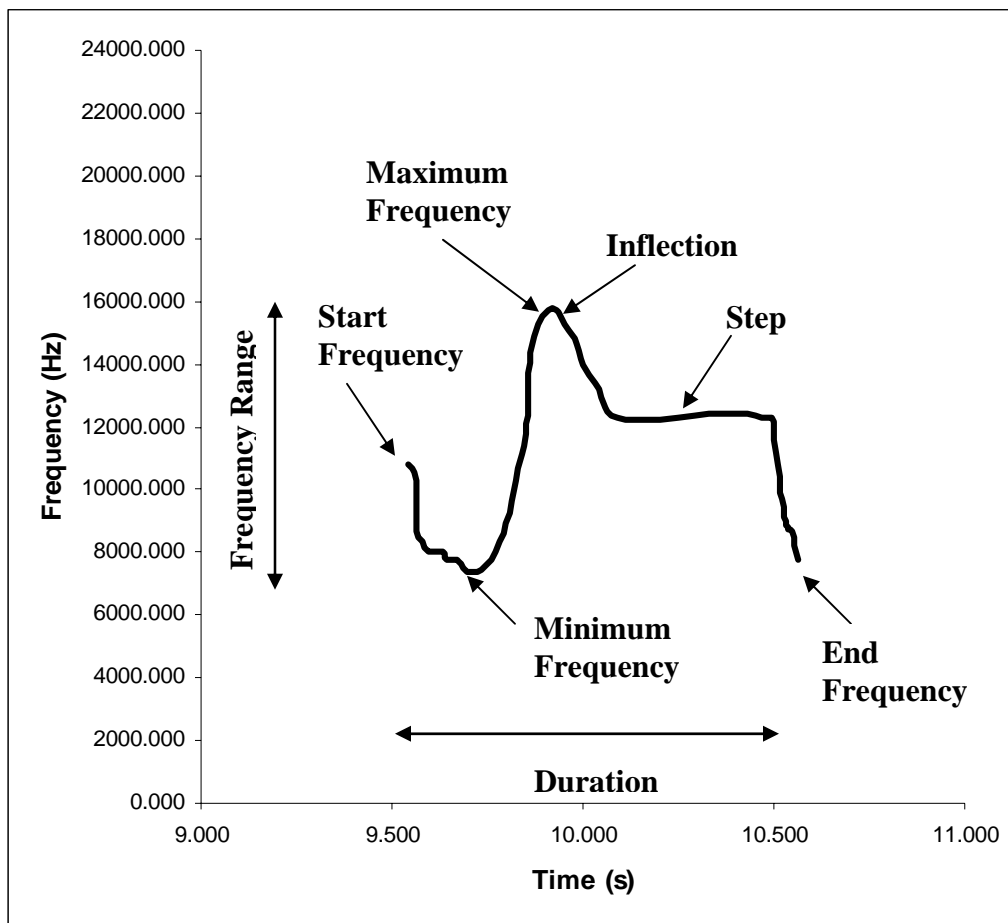


Figure 2.9. Whistle contour illustrating parameters measured.

2.2. English Channel Recordings

2.2.1. Field Work

For a detailed description of field work methodology see De Boer et al. (2004). The following brief summary of aspects of their methods relevant to this study is based on the information given in De Boer et al.'s report.

Recordings of common dolphins in the English Channel were made during line-transect surveys conducted by the Whale and Dolphin Conservation Society (WDCS) and Greenpeace between January 21st and March 8th, 2004. As a platform the *MV Esperanza*, a 72.3m Expedition/Research vessel travelling at average speeds of 5.3-8.6 knots, was used. The survey area was situated in the western approaches of the English Channel, between 49°20'N to 50°20'N and 003°26'W to 006°10'W (fig. 2.10). Visual observations of cetacean sightings as well as environmental information were recorded by two observers.

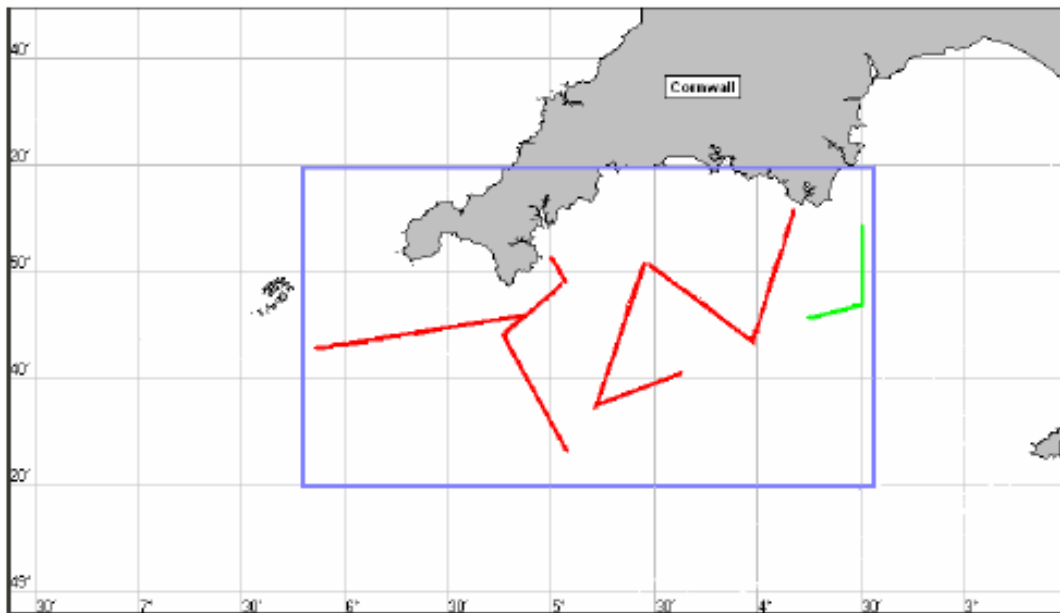


Figure 2.10. Survey area (blue box) and transect lines of surveys at fast speed of 8.6 knots (red) and slow speed of 5.3 knots (green) in the western approaches of the English Channel, south of Cornwall (De Boer et al. 2004).

Recordings were made between February 13th and March 4th, using a towed hydrophone array with two elements that were 7.5m apart, contained within an oil-filled PVC pipe of 13m length. The array was towed at a cable length of 300m behind the vessel and occasionally pulled in to 200m or 100m. Data was recorded directly onto a laptop computer onboard, using a Roland UA5 analogue to digital converter (ADC) which was connected to the computer using a FireWire connector. The software SeaPro version 1.2 (Nauta rcs – Ricerca e Consulenza Scientifica) was used to create a spectrographic display and record data on the computer. The sampling rate of the system was 96 kHz. Data was monitored by listening and watching the spectral display and interesting acoustic activity was recorded as sound files on the computer.

2.2.2. Computer Transformation of Sound Files into Data Files for Analysis

The sound files received from WDCS by the author were compared to their sightings records and only recordings made during times of common dolphin sightings were used for analysis. These were broken up into mono 1-minute-sound files using the channel that had the better quality recording. The sound files were then imported into MATLAB and whistles were marked as described above for Celtic Sea data. However, since sampling rate of the English Channel recordings was 96 kHz, the MATLAB delphi script was modified to have a sampling frequency (Fs) setting of 96000 Hz instead of 48000 Hz. The upper bandwidth limit of the English Channel recordings was 48 kHz compared to only 24 kHz for the Celtic Sea recordings. English Channel whistles of frequencies above 24 kHz were still included in the analysis and how this may have influenced results is discussed later on.

2.2.3. Analysis

Part C: Comparison Between Whistles from the Celtic Sea versus the English Channel

The same 11 whistle parameters as for the Celtic Sea recordings were determined for the English Channel whistles using Microsoft Excel. Then whistles were subjectively categorised using the same category system as for the Celtic Sea whistles.

English Channel whistles were then statistically compared to a random subsample of Celtic Sea whistles of the same sample size. Using the appropriate statistical tests, it was determined whether whistle characteristics (duration, SF, EF, MinF, MaxF, MeanF, FG, AFG, FR, inflections and steps) were significantly different between the two sampling locations and whether the proportions of whistle types were correlated to location.

3. Results

During the four surveys in the Celtic Sea, a total of 57.5 hours of recordings were made. Of those, 16 hours were recorded during Survey 1 (May 16-17), 13 hours during Survey 2 (June 22), 17 hours during Survey 3 (July 13-14) and 11.5 hours during Survey 4 (only on Aug 17 due to hydrophone failure on Aug 16). A total of 31,888 whistles were counted (table 3.1). Inaccuracies in these counts are likely especially during times of high vocal activity (a maximum of 2,309 whistles were counted in one 10-minute-file) as whistles often overlapped each other and could not always be clearly distinguished. Counts should thus be seen as best estimates of whistle numbers.

A total of 101 common dolphin sightings were recorded, of which 6 were disregarded in the further analysis because (a) a second dolphin species (*Tursiops truncatus*) was present in the area, thus whistles could not safely be attributed to common dolphins (one sighting); (b) the DAT recorder was accidentally set to LP, reducing the sampling rate and thus probably cutting off some higher frequency whistles (3 sightings); (c) the species was not definitely identified as common dolphins (1 sighting); or (d) the animals were seen at a distance of 2 km away, thus highly unlikely to be picked up by the hydrophone and whistles during this period were assumed to be from the previous sighting (1 sighting). The remaining sightings were grouped into 43 encounters.

Table 3.1. Summary of the recording duration and number of whistles counted during each survey.

Survey #	Date	Duration (hrs)	Whistles Counted
1	16-17 May 2005	16.0	4832
2	22 June 2005	13.0	9019
3	13-14 July 2005	17.0	4401
4	(16-)17 Aug 2005	11.5	13636

In total, 4,218 Celtic Sea whistles were marked. Out of those, 1,835 were used in the subsequent analysis (after a maximum of 100 whistles from each encounter were randomly selected). The maximum whistle density within an encounter was 160.25 whistles/min. The highest group size observed was 128+ for an encounter or 50-60 for an individual sighting (minimum group size was 1 for both) with an average group size of 23 animals for encounters and 11 for sightings.

3.1. Acoustic Survey Methodology (Part A)

3.1.1. Acoustic and Visual Detection Rates

The continuous recordings were broken down into 366 10-minute-pieces. Out of those, 163 (44.5%) had no acoustic contact and no sighting associated, 86 (23.5%) had both acoustic contact and one or more sightings, 110 (30.1%) had acoustic contact but no sighting and only 7 (1.9%) had a sighting but no acoustic contact (fig. 3.1).

In 30% of all 10-minute-files, whistles were recorded even though no dolphins were seen during that time. Out of those 110 cases, 47 (42.7%) were within 10 minutes of a sighting, implying that those sightings were not missed completely but rather that the dolphins were heard before they were seen or still heard some time after they were last seen. Out of the remaining cases, where sightings were missed, 6 were recorded during sea states greater than 2 (5.5% of the total 110 cases), in 28 (25.5% of the total 110) the majority of whistles were faint, and in 14 (12.7%) both of these criteria were met (sea states were greater than 2 and whistles were faint). In the remaining 15 cases (13.6%), none of the above criteria were met (fig. 3.1).

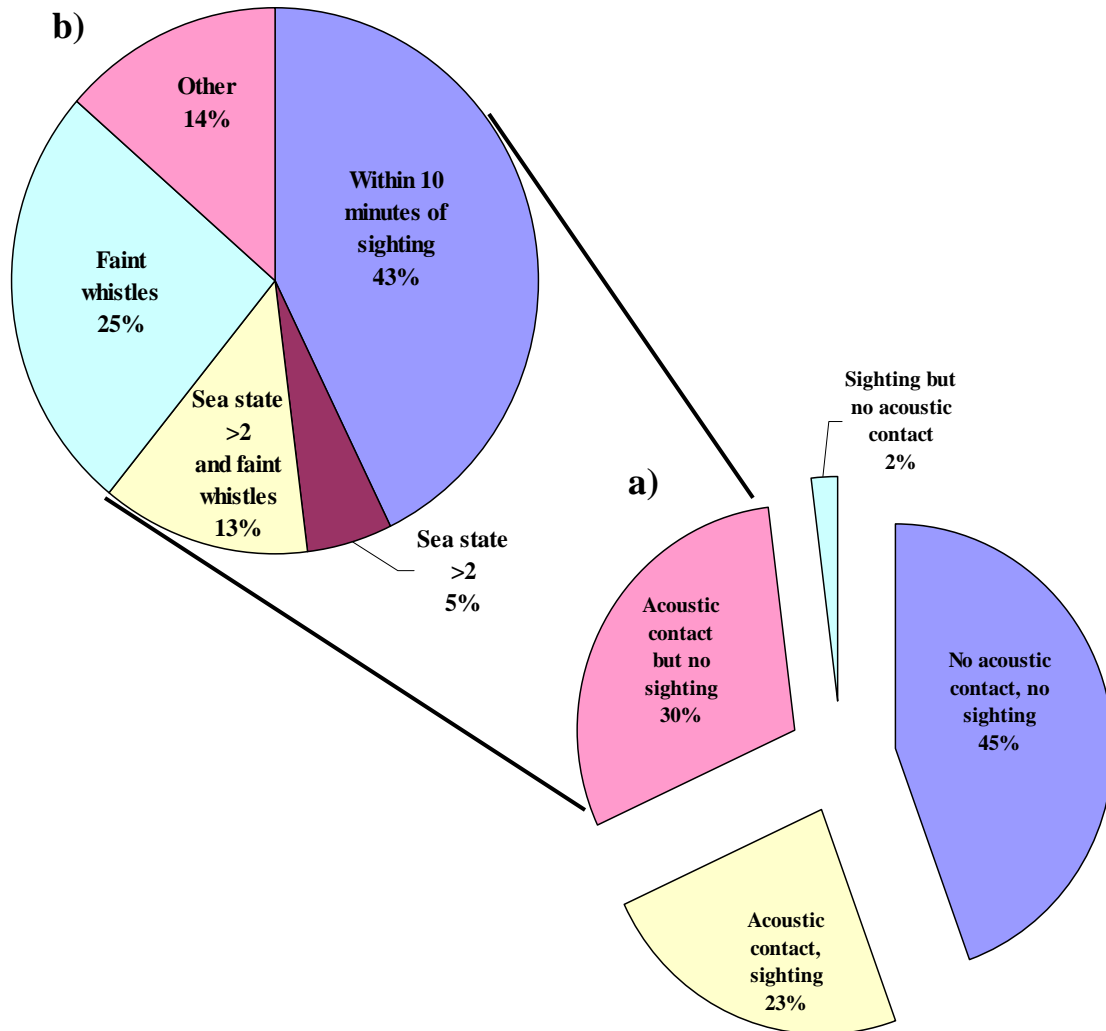


Figure 3.1. Pie charts showing a) all 10-minute-recordings broken down into 4 groups depending on whether acoustic contact and/or sightings were recorded during that period and b) the group in which there was acoustic contact but no sighting, broken down into cases in which certain factors were present that could explain why no sighting was recorded.

These situations, in which acoustic contact confirmed the presence of dolphins but sightings were missed (i.e. disregarding the cases of acoustic contact within 10 minutes of a sighting), were further analysed statistically by looking at all 10-minute-intervals during which there was an acoustic contact, both with or without a sighting. Cases with a sighting were compared to those where the sighting was missed even though acoustic contact showed that animals were in the area. Three factors were identified as possible reasons why a sighting could have been missed. These were sea state, group size of the dolphins and distance of the animals from the vessel. Since no sightings were recorded for the cases in question, obviously no observational data about the group size and distance of the dolphins was available. Thus, whistle density was taken as an expression of the group size (assuming that more whistles per unit time are recorded from a larger group of dolphins) and whistle intensity was used as an expression of the distance (assuming that whistles are clearer if the animals are closer to the vessel and hydrophone). Spearman rank and Kendall's tau non-parametric methods were used to test for significant correlations between each of these three factors (sea state, whistle density, whistle intensity) and whether there was a sighting recorded. Neither of the two tests showed a significant correlation between sea state and whether or not a sighting was recorded (Spearman's $\rho = -0.089$; Kendall's $\tau = -0.082$; $N = 189$; $p > 0.05$). However, both whistle intensity as well as whistle density were significantly correlated with whether there was a sighting (whistle density: Spearman's $\rho = 0.379$; Kendall's $\tau = 0.312$; $N = 189$; $p < 0.001$; whistle intensity: Spearman's $\rho = 0.341$; Kendall's $\tau = 0.341$; $N = 189$; $p < 0.001$).

Cross tabulation showed that the sighting was missed in 75% of cases where whistles were faint but only in 41% of the periods with clear whistles (see fig. 3.2). A Pearson Chi-Square test of homogeneity (with correction for a 2x2 table) found a significant relationship between whistle intensity and sighting record ($X^2 = 21.964$; $df = 1$; $p < 0.001$) and Cramer's V (a measure of effect size ranging from 0 – no relationship, to 1 – perfect relationship) was 0.341, indicating that although significant, whistle intensity had a relatively weak effect on sighting record.

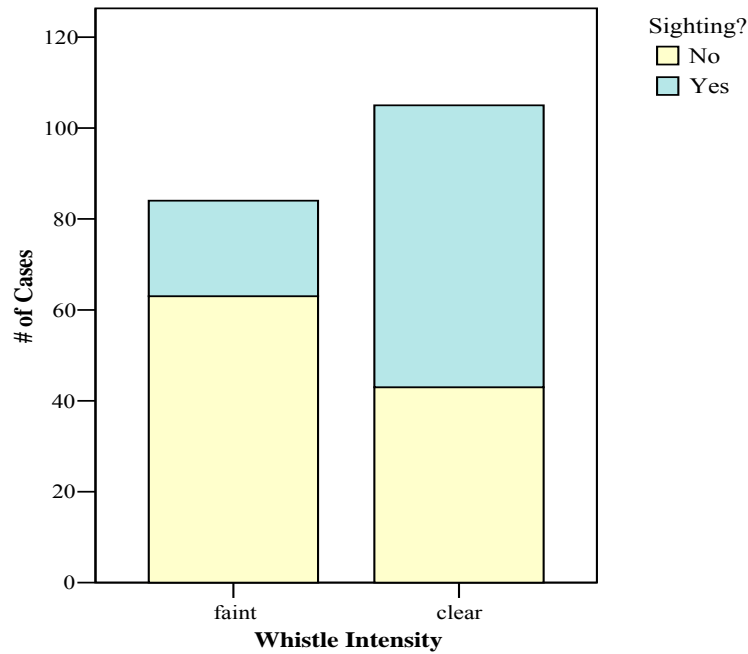


Figure 3.2. Bar graph showing the effect of whistle intensity on whether a sighting was recorded or not.

Whistle density had a mean value of 7.99 whistles/minute (Standard Deviation (SD)=18.39; 95% Confidence Interval (CI)=4.45-11.54) when no sighting was recorded compared to a mean of 30.39 whistles/minute (SD=48.58; 95% CI=19.78-41.00) when there was a sighting. Whistle density data for both categories (sighting yes/no) was not normally distributed (sighting no: Kolmogorov-Smirnov coefficient =0.337; df=106; $p < 0.001$; sighting yes: Kolmogorov-Smirnov coefficient =0.267; df=83; $p < 0.001$), and variances were not equal (Levene's Test: $F=37.354$, $p < 0.001$). However, if the group sizes between categories are approximately equal, an independent samples t-test is robust to violations of these two assumptions (Francis, 2001). Group sizes in this case were 106 (no sighting) and 83 (sighting) and thus considered "approximately equal". The t-test, not assuming equal variances, found a significant mean difference of 22.39 whistles/minute (95% CI=11.24-33.55) between mean whistle densities for the two categories (sighting: yes/no) ($t=-3.982$; $df=100.442$; $p < 0.001$) (fig.3.3). The significant result was also confirmed by a non-parametric Mann-Whitney test ($U=2460.5$; $N=189$; $p < 0.001$).

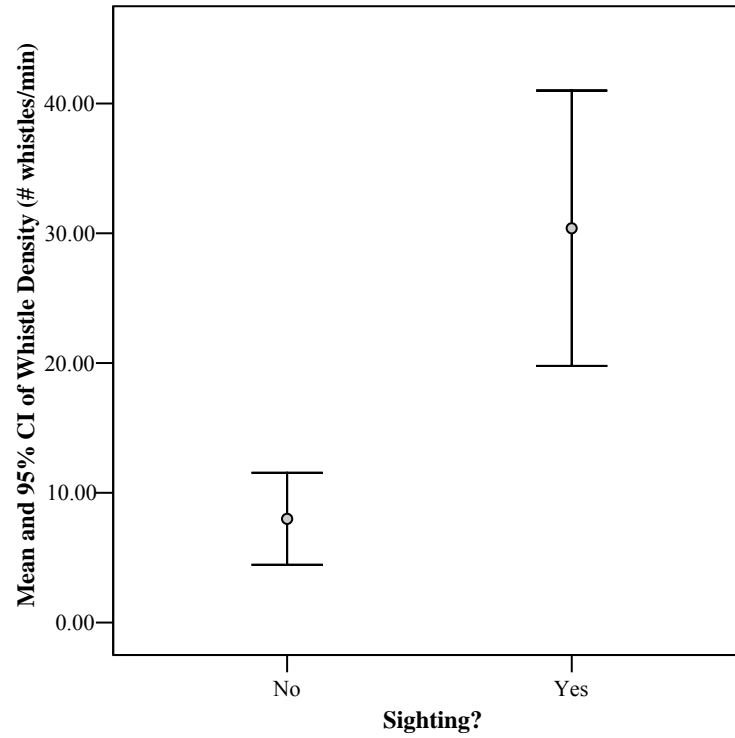


Figure 3.3. Error bar graph showing means and 95% confidence intervals of whistle densities (whistles/min) when a sighting was or was not recorded.

3.1.2. Relationship between Whistle Density and Group Size

Using the cases where acoustic contact as well as a sighting was recorded, the relationship between whistle density and group size was analysed by first creating a scatterplot of the two variables and fitting a line to them (fig. 3.4). This indicated a moderately strong positive relationship although a large spread of the data around the line was observed. Group size explained 22.6% of the variation in whistle density ($r^2=0.226$). A Pearson Correlation test found a significant correlation of moderate strength between whistle density and group size ($r=0.475$; $N=43$; $p=0.001$). A regression analysis was then carried out to examine the form of the correlation. This yielded a significant regression ($b=0.634$; $t=3.456$; $n=43$; $p=0.001$) and the equation for the regression line (line of best fit):

$$\text{Predicted whistle density (\#/min)} = 18.501 + 0.634 \times \text{group size} \quad \text{[Eqn. 3.1]}$$

This says that for every unit increase in group size (i.e. for every 1 extra animal), there is a predicted increase in whistle density of 0.634 whistle per minute.

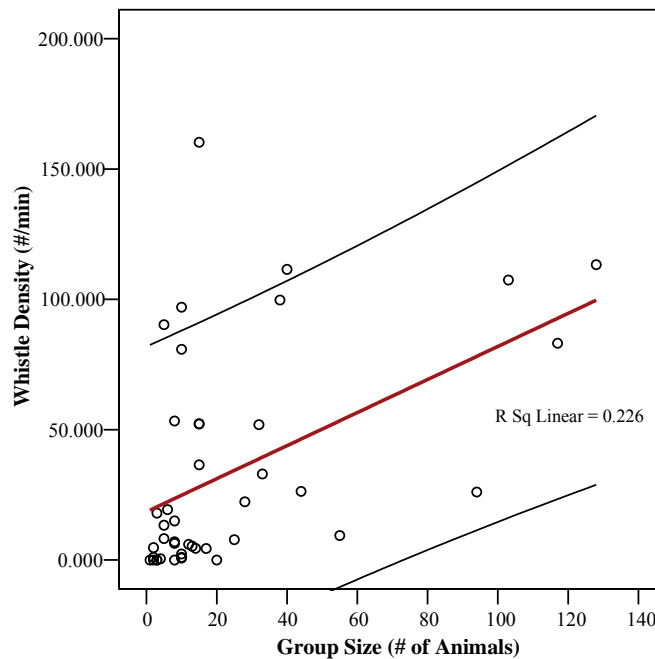


Figure 3.4. Scatterplot of whistle density versus group size showing the best fit regression line (thick, red) and individual 95% confidence intervals (thin, black lines).

Rearranging this equation allows a prediction of group size based on whistle density:

$$\text{Predicted group size} = 1.577 \times \text{whistle density (\#/min)} - 29.181 \quad \text{[Eqn. 3.2]}$$

However, testing the assumption of normality showed that the residuals of the whistle density data were slightly skewed and not normally distributed. Thus whistle density was transformed using the natural logarithm ($\text{LN}(\text{whistle density} + 1)$, because whistle density was = 0 in some cases) which yielded an approximately normal distribution. Repeating the correlation test with the LN transformed whistle density data gave similar results as before (Pearson Correlation: $r=0.479$; $N=43$; $p=0.001$). Repeating the regression analysis resulted in a new equation:

$$\text{Predicted LN transformed whistle density (\#/min)} = 1.955 + 0.025 \times \text{group size} \quad \text{[Eqn. 3.3]}$$

Thus, using these data, for every increase in group size by 1, an increase in $\text{LN}(\text{whistle density} + 1)$ of 0.025 is predicted.

Since a significant regression between whistle density and group size had been found, it was then analysed whether any other factors also influence whistle density, such as the mean distance of the animals to the vessel (determined as the mean between recorded minimum and maximum distances) and/or the behaviour of the dolphins. The mean distance showed no significant correlation with the untransformed whistle density (Pearson Correlation: $r=-0.153$; $N=43$; $p>0.05$) (fig. 3.5) but a weak significant negative correlation with LN transformed whistle density (Pearson Correlation: $r=-0.315$; $N=43$; $p<0.05$) (fig. 3.6). Regression analysis of mean distance and LN transformed whistle density ($b=-0.001$; $t=-2.125$; $n=43$; $p<0.05$) yielded the following regression equation:

$$\text{Predicted LN transformed whistle density (\#/min)} = 3.207 - 0.001 \times \text{mean distance (m)} \quad \text{[Eqn. 3.4]}$$

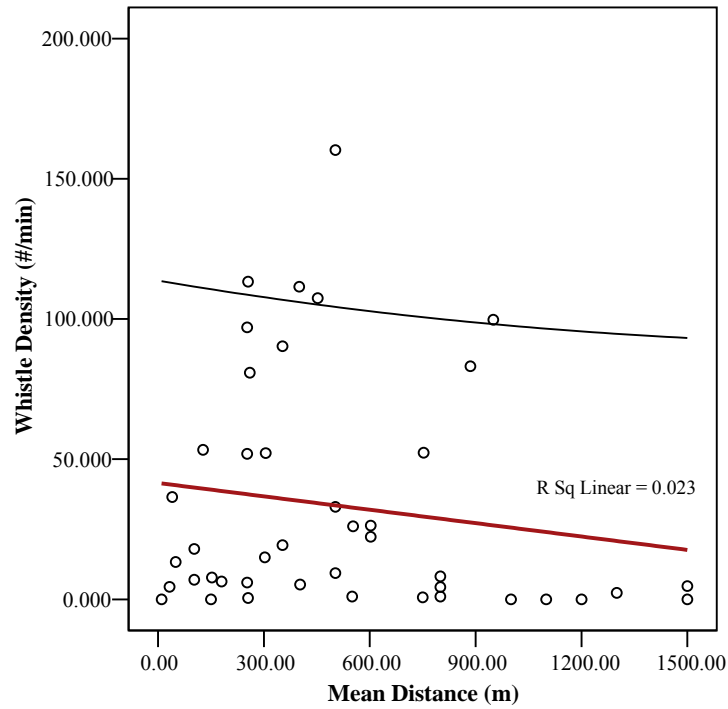


Figure 3.5. Scatterplot of whistle density vs. mean distance showing best fit regression line (thick, red) and individual 95% confidence intervals (thin, black lines).

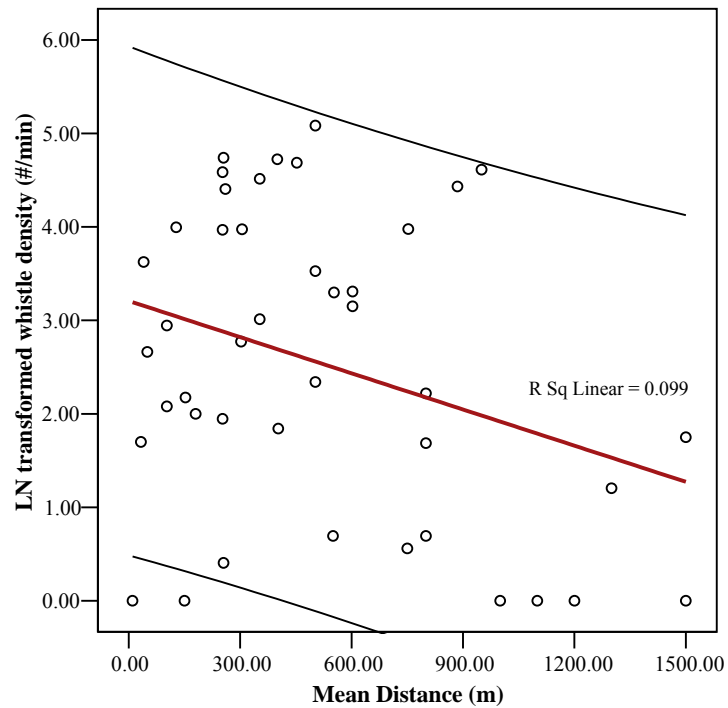


Figure 3.6. Scatterplot of LN transformed whistle density vs. mean distance showing best fit regression line (thick, red) and individual 95% confidence intervals (thin, black lines).

To analyse the relationship between whistle density and behaviour, the observed behaviours were first categorised into (1) Travel, (2) Forage, (3) Socialise, (4) Bow-ride, (5) Two different behaviours, (6) Three different behaviours and (7) Four different behaviours. Levene's test of homogeneity of variances showed that the variances of LN transformed whistle density were significantly different between these seven categories ($F=4.223$; $df_1=5$, $df_2=35$; $p<0.05$), violating the assumption of homogeneity of variances. Thus, a nonparametric Kruskal-Wallis test was used, which did not find a significant relationship between whistle density and behaviour ($X^2=12.209$; $df=6$; $p>0.05$).

Next, only the first four behaviour categories were used, that is only the cases where just one type of behaviour was recorded. In this scenario, Levene's test found no significant difference in variances of LN transformed whistle density between these four behaviour categories ($F=1.644$; $df_1=3$, $df_2=16$; $p>0.05$). Thus, the assumption of homogeneity of variance was met and a One-Way Analysis of Variance (ANOVA) was carried out which showed that there was no significant relationship between LN transformed whistle density and behaviour type (Travel, Forage, Social or Bow-ride) ($F=0.811$; $df(\text{between groups})=3$, $df(\text{within groups})=16$, $df(\text{total})=19$; $p>0.05$). It should be noted that the sample sizes of these behavioural categories were very small.

Since significant correlations were found between LN transformed whistle density and group size as well as mean distance but not behaviour, a multiple regression analysis was carried out for the two significantly correlated predictors (group size and mean distance). Looking at the raw correlations, both predictors were significantly correlated with LN transformed whistle density, as shown before, but not significantly correlated to each other. The multiple regression analysis yielded the following regression equation:

$$\text{Predicted LN transformed whistle density} = 2.624 + 0.025 \times \text{group size} - 0.001 \times \text{mean distance} \quad [\text{Eqn. 3.5}]$$

The standardised regression coefficients showed that group size was the more important predictor of whistle density (Beta = 0.480 versus 0.317 for mean distance). R^2 for this regression equation was 0.330, saying that 33% of the variation in LN transformed

whistle density could be explained by this model. This sample R was found to be significant using an ANOVA ($F(2,40)=9.843$; $p<0.001$), indicating that the relationship found in the sample was strong enough to also imply a relationship in the whole population.

In summary:

- A significant, moderately strong regression between whistle density and group size was found, with the regression equation:

$$\text{Predicted whistle density (\#/min)} = 18.501 + 0.634 \times \text{group size} \quad \text{[Eqn. 3.1]}$$

- Rearranging this equation gave the following model to predict group size:

$$\text{Predicted group size} = 1.577 \times \text{whistle density (\#/min)} - 29.181 \quad \text{[Eqn. 3.2]}$$

- A significant but weak regression between mean distance and whistle density was found, but only for LN transformed data, not for un-transformed whistle density.
- No significant correlations between whistle density and behaviour type were determined.
- A multiple regression analysis gave the following equation:

$$\begin{aligned} \text{Predicted LN transformed whistle density} = & 2.624 + 0.025 \times \text{group size} - \\ & 0.001 \times \text{mean distance} \quad \text{[Eqn. 3.5]} \end{aligned}$$

Group size was the more important predictor of whistle density.

3.1.3. Diel Pattern of Acoustic Contact and Sightings

For the analysis of a diel pattern in acoustic contact and/or sightings, the continuous recordings throughout the survey days, broken down into 10-minute-intervals, were used. The May 16th recordings were disregarded since they only covered the afternoon (starting at 1542 hrs due to hydrophone problems before then). Thus, data from five days was used (May 17th, June 22nd, July 13th, July 14th and August 17th), with a time frame from 0910 hrs through 1700 hrs (as this time frame was covered by each of the five days). One exception was a 20-minute-period during which no recordings were made on June 22nd but this missing data was adjusted for as described in the following paragraph.

For each of the 10-minute-intervals from 0910 to 1700 hrs, the numbers of sightings made and the whistle densities (# of whistles per minute) recorded during this particular interval was averaged for the five survey days. Then the times were pooled into 1-hour-periods from 0900 to 1600 hrs inclusive (the category label marks the start time of the period, eg. the 1600 hrs period includes 10-minute-files from 1600 to 1650 hrs (also labelled by start times, so the recording actually runs until 1700 hrs). Pooling data for each hour made the graph less cluttered and furthermore it allowed adjusting data for the times where recordings were missing (the 20-minute-period from 1450-1510 hrs on June 22nd mentioned above), by taking the average of only the remaining five 10-minute-blocks of that hour and disregarding the 10-minute-blocks with missing data. Similarly for the 0900-hour-period only five 10-minute-blocks were used since recording started at 0910 hrs on one of the five days.

Figure 3.7 shows the histogram of mean whistle density and the mean number of sightings for each one-hour-period from 9am to 5pm. Both whistle density and sightings show peaks in the morning (0900-1000 hrs) and in the afternoon (1300-1600 hrs) with a low point around noon (1100-1200 hrs).

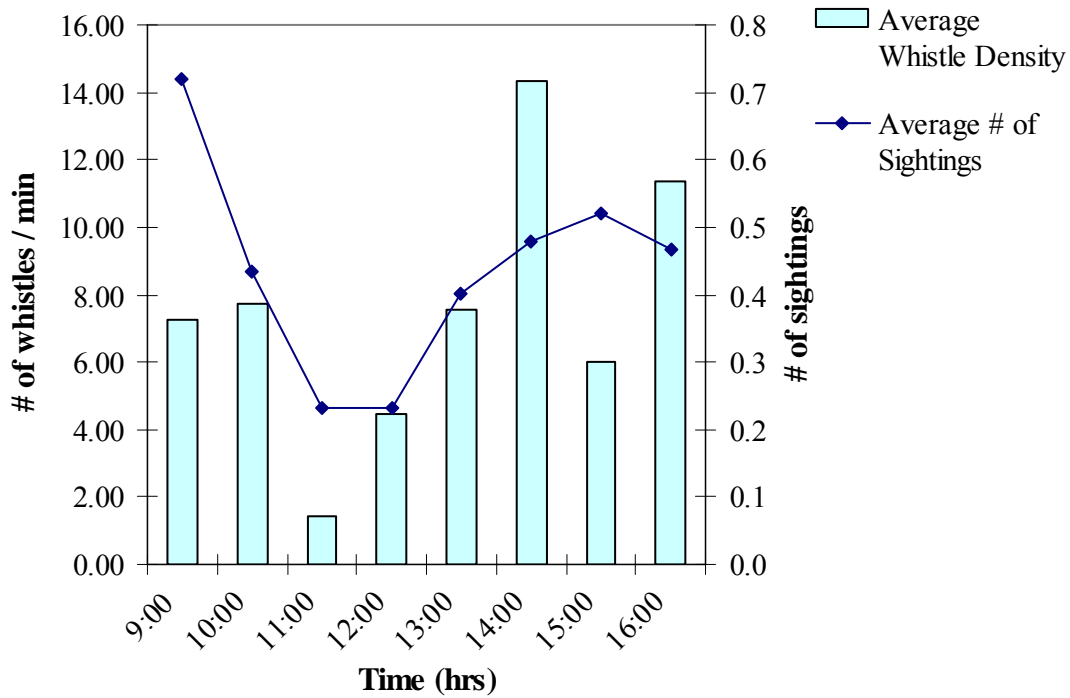


Figure 3.7. Histogram of average whistle density, and line graph of average number of sightings for each one-hour-period from 0900-1700hrs.

Since neither average whistle density nor average number of sightings were normally distributed, and no linear relationship between either of these two variables and time was apparent, the non-parametric Spearman's Rank test was used to determine whether a significant correlation was present. However, neither whistle density nor sightings correlated significantly with the time of day (whistle density: $\rho=0.067$; $N=47$; $p>0.05$; sightings: $\rho=-0.073$; $N=47$; $p>0.05$). As could be expected, there was a significant positive correlation between whistle density and number of sightings ($\rho=0.643$; $N=47$; $p<0.001$). Non-parametric Kruskal-Wallis Tests also did not find any significant differences between the mean whistle densities of the different one-hour-periods nor the mean number of sightings in each one-hour-period (whistle density: $X^2=7.362$; $df=7$; $p>0.05$; sightings: $X^2=9.258$; $df=7$; $p>0.05$).

3.2. Whistle Repertoire of Celtic Sea Common Dolphins (Part B)

3.2.1. Whistle Characteristics and Types

Table 3.2 shows the minimum, maximum and mean values as well as the standard deviations for each of the eleven whistle variables, measured for a total of 1,835 whistles. It should be noted that the value of the mean frequency gradient should not be regarded as a true mean value describing the whistles' average slope since negative and positive values tend to cancel each other out. This is why the absolute frequency gradient was calculated. Disregarding positive or negative signs, it does give a value that describes how steep on average the whistles are. At the same time, the positive mean value for the original frequency gradient shows that there are more whistles with a positive overall gradient in the sample than with a negative gradient.

Table 3.2. Range, Mean and Standard Deviations for the different parameters measured of Celtic Sea common dolphin whistles.

	Minimum	Maximum	Mean	Standard Deviation
Duration (s)	0.048	2.017	0.646	0.327
Start Frequency (Hz)	3555	23514	12025	3474
End Frequency (Hz)	4071	22271	11971	3254
Minimum Frequency (Hz)	3555	19492	9447	2056
Maximum Frequency (Hz)	5740	23514	14685	3134
Mean Frequency (Hz)	4763	20377	11889	2049
Frequency Gradient (Hz/s)	-52544	72372	376	9727
Absolute Frequency Gradient (Hz/s)	0	72372	6971	6792
Frequency Range (Hz)	117	17227	5238	3249
Inflections	0	10	0.64	0.984
Steps	0	3	0.13	0.385

To create whistle type categories, the author considered what subjectively seemed reasonable conceptual categories to her, as well as what systems have been used by other authors to achieve some degree of comparability to other studies. Based on this, a system was created that consists of six major whistle types that describe the overall general appearance of the whistle. (A – Constant Frequency, B – Upsweep, C – Downsweep, D – Convex, E – Concave and F – Sine). These six types were further sub-categorised, depending on the degree of modulation of this general type. Sub-types were coded by numbers, where 1 was no further modulation (eg. B1 would be a perfect straight-line upsweep with no other modulation), 2 was a modulation at the start of the general type (eg. a B2 whistle might have a short constant or falling frequency section just before the start of the upsweep, which characterises the overall shape of the whistle), 3 was a modulation at the end of the general type (eg. B3 might have a short constant or falling frequency section following the upsweep) and 4 indicated a further modulation at both sides of the main type section of the whistle. As a rule of thumb, these features were regarded as further modulations rather than part of the main whistle characteristic, if they had less than half the frequency span of the main part. For example, whistles were considered an upsweep with further downswEEPing modulation at the end rather than a convex whistle if the downswEEPing part covered less than half the frequency span of the main upsweep. For upsweeps and downsweeps a further sub-group 5 was added which indicated a step within the general whistle type (eg. B5 would be an upsweep where the rising frequency section is interrupted by a constant frequency period). For sine types (F) the sub-type numbering follows a different system. Rather than describing the further modulation around the main section, it indicates the degree of sinusoidal modulation, that is the number of inflections, as well as whether the sine contour starts with a rising or a falling frequency section: F1 is a sine contour starting with a rising section and consisting of two inflections, F2 is a similar contour with two inflections but starting with a falling section. F3 and F4 both have three inflections and start with a rising or a falling frequency section respectively. F5 and F6 follow the same system, with four inflections and F7 and F8 combine all sine contour whistles with five or more inflections, also with rising or falling start frequency respectively. Figure 3.8 shows schematic illustrations of

the different whistle types. For spectrogram examples and parameters of each whistle type see appendix 7.3.

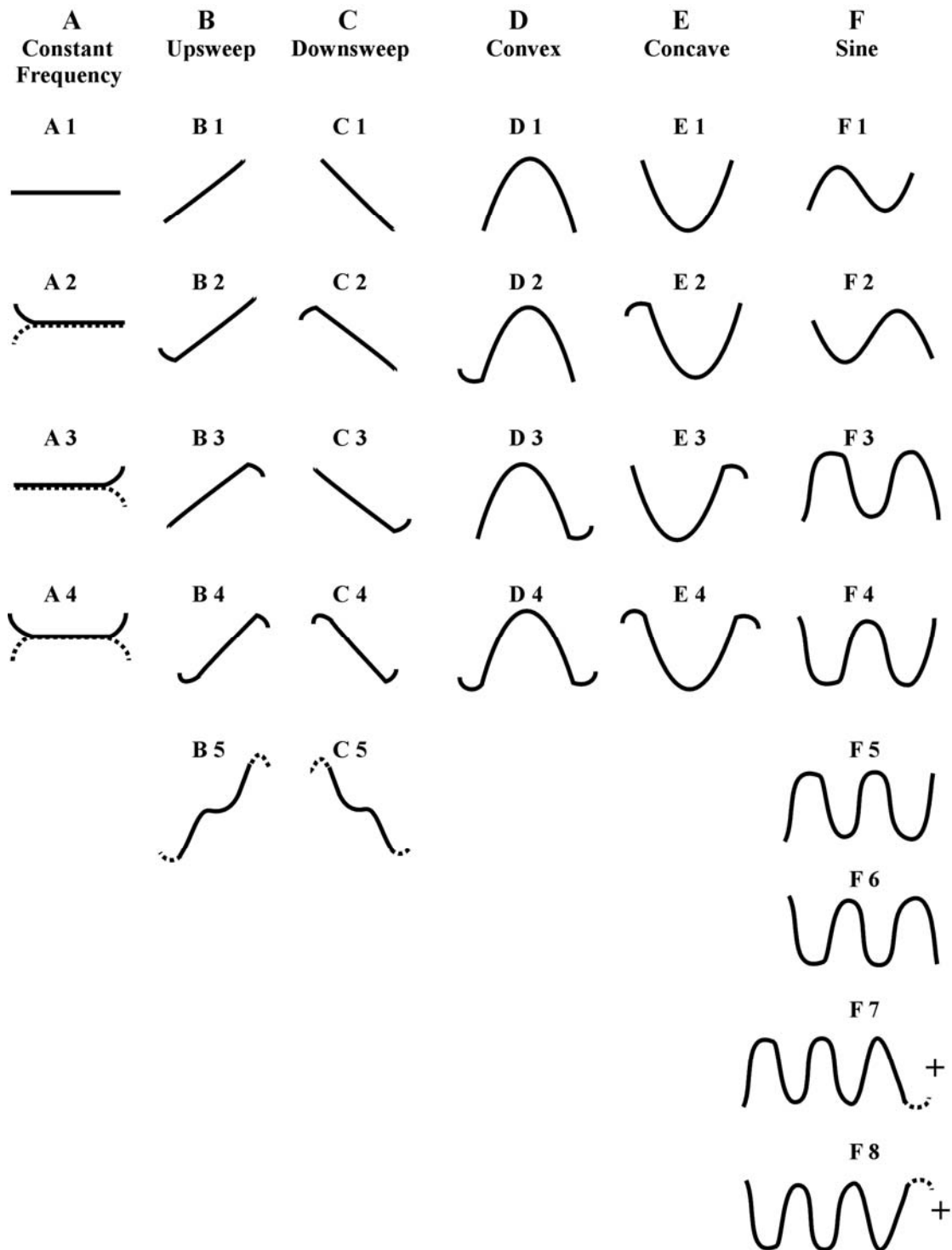


Figure 3.8. Idealised contours of the different whistle types.

Upsweeps were the most common general whistle type making up a proportion of 31.0% of all whistles, followed by downsweeps which made up 26.5%. The constant frequency type described 14.3% of whistles and convex and concave whistles made up 11.7 and 9.3% respectively. The least frequent whistle type was sine, with 7.3% (fig. 3.9). When whistles were further broken down into sub-types, it became apparent that generally the simpler sub-types were more common than the more modulated ones. For all except the sine whistles, the first sub-type (A1, B1, C1, D1 and E1) was the most frequent within its general whistle category. For the sine category the two equally simple sub-types, F1 and F2 were most common, with F2 found at higher proportions than F1 (fig. 3.10). Table 3.3 summarises the means and ranges of the whistle parameters for each overall type, as well as the proportion out of all whistle made up by each type.

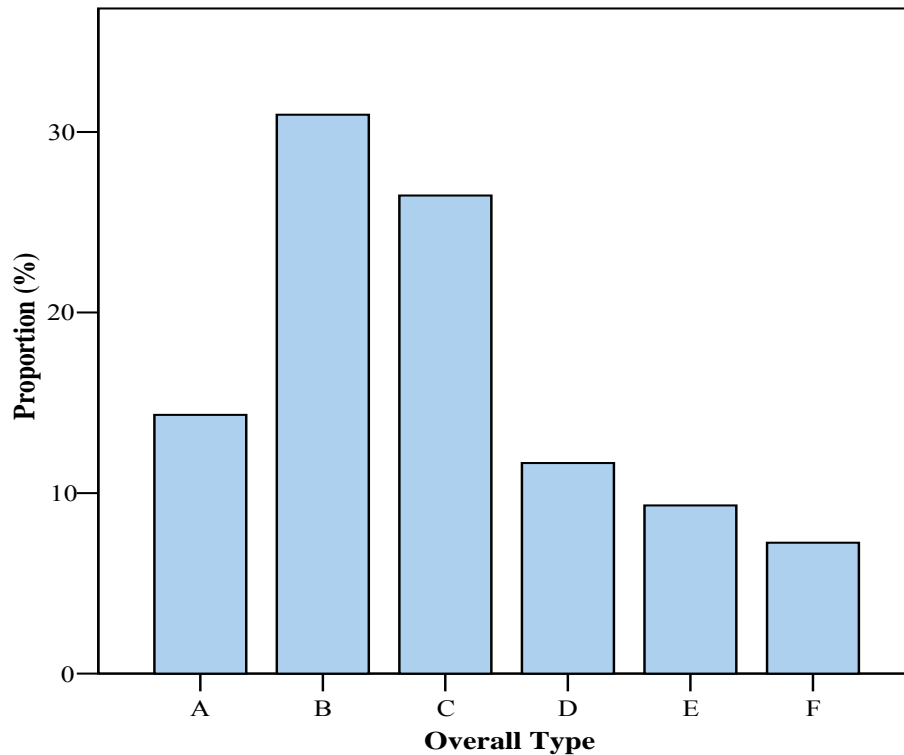


Figure 3.9. Proportional frequencies (%) of each broad whistle type in the 1,835 sampled whistles of common dolphins in the Celtic Sea.

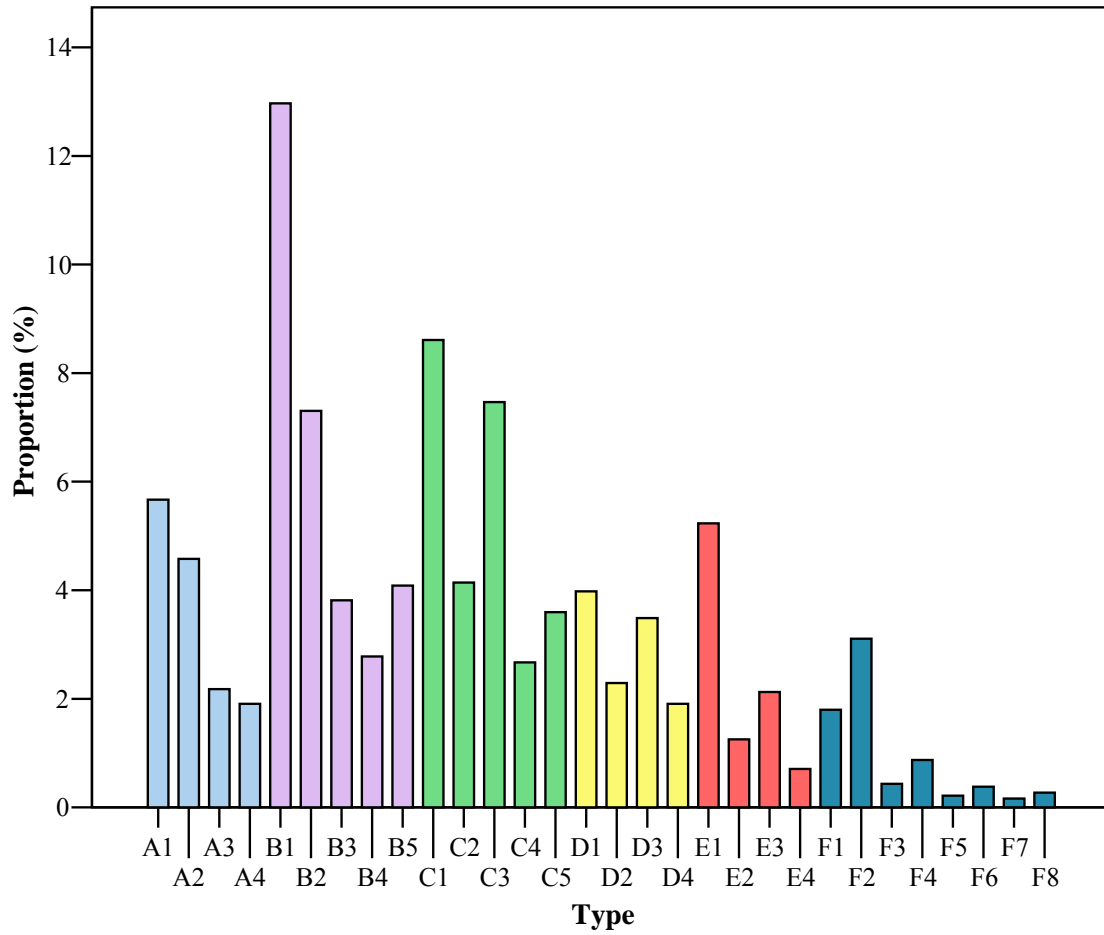


Figure 3.7. Proportions (%) of the 1,835 sampled whistles made up of each whistle sub-type, colour-coded by overall type.

Table 3.3. Fraction of all whistles made up by each broad whistle type and means and ranges (below mean in parenthesis: minimum-maximum) of the different variables by whistle type.

Type	Fraction (%)	Duration (s)	Start Freq (Hz)	End Freq (Hz)	Min Freq (Hz)	Max Freq (Hz)	Mean Freq (Hz)	Freq Gradient (Hz/s)	Abs Freq Gradient (Hz/s)	Freq Range (Hz)	Inflections	Steps
A	14.3	0.440 (0.048-1.160)	11,138 (6,246-19,911)	11,001 (5,647-19,792)	10,539 (4,928-19,492)	11,571 (6,422-20,031)	11,031 (5,898-19,732)	-330 (-11,641-15,967)	2,192 (0-15,967)	1,032 (117-4,178)	0.10 (0-3)	0.02 (0-1)
B	31.0	0.588 (0.051-1.852)	9,534 (4,323-16,642)	14,524 (7,421-22,271)	9,261 (4,323-15,503)	14,677 (7,421-22,449)	11,876 (5,812-17,620)	10,276 (957-72,372)	10,276 (957-72,372)	5,416 (873-17,227)	0.26 (0-5)	0.15 (0-2)
C	26.5	0.615 (0.071-1.602)	15,075 (7,562-23,514)	9,808 (4,071-19,468)	9,417 (4,071-19,186)	15,305 (7,562-23,514)	12,019 (6,275-19,807)	-9,901 (-52,544-1,479)	9,901 (1,479-52,544)	5,888 (911-15,481)	0.32 (0-3)	0.16 (0-3)
D	11.7	0.849 (0.097-1.836)	10,508 (3,555-20,052)	10,088 (4,146-18,884)	9,181 (3,555-18,884)	16,136 (5,740-22,983)	12,719 (4,763-20,377)	-463 (-9,897-7,799)	2,056 (0-9,897)	6,955 (822-17,147)	1.30 (0-7)	0.12 (0-2)
E	9.3	0.698 (0.056-1.598)	13,954 (7,866-21,408)	13,670 (8,398-21,281)	9,273 (5,210-15,451)	14,695 (8,398-21,408)	11,556 (7,184-17,142)	203 (-14,370-20,895)	2,623 (0-20,895)	5,422 (815-11,917)	1.13 (0-4)	0.12 (0-2)
F	7.3	1.013 (0.068-2.017)	13,233 (5,399-23,461)	11,733 (4,318-20,942)	8,848 (4,318-16,487)	16,265 (8,652-23,461)	12,261 (8,073-16,905)	-1,385 (-12,617-20,812)	5,099 (40-20,812)	7,417 (738-14,666)	2.87 (0-10)	0.20 (0-3)

3.2.2. Relationship between Whistle Characteristics and Behaviour

To determine whether there were significant differences in the means of whistle characteristics between encounters where different behaviours had been recorded (Travelling, Foraging, Socialising, Bow-riding, two different behaviours, three different behaviours or four different behaviours), a non-parametric Kruskal-Wallis test was used because the variables were not normally distributed. It showed significant differences in mean duration ($X^2=18.779$; $df=6$; $p<0.05$), maximum frequency ($X^2=18.808$; $df=6$; $p<0.05$), mean frequency ($X^2=15.089$; $df=6$; $p<0.05$), frequency gradient ($X^2=12.693$; $df=6$; $p<0.05$), frequency range ($X^2=20.788$; $df=6$; $p<0.05$) and steps ($X^2=17.929$; $df=6$; $p<0.05$).

It was not possible to analyse correlations between the whistle type and behaviour using crosstabulation and the Pearson Chi-Square statistic because more than 20% of the cells had expected counts less than 5 which makes this test unreliable (Francis, 2001).

To examine the influence each individual behaviour had on whistle characteristics, encounters were coded by whether each behaviour (travelling, foraging, socialising and bow-riding) had been recorded or not (yielding a binary variable for each). Non-parametric Mann-Whitney U-tests were used for this analysis. They found:

- No significant differences in the means of any whistle variable between encounters where bow-riding was recorded and encounters where no bow-riding occurred.
- For travelling (yes/no) there were significant differences in the means of maximum frequency ($Z=-2.214$; $N=1,826$; $p<0.05$), frequency range ($Z=-1.973$; $N=1,826$; $p<0.05$) and steps ($Z=-2.627$; $N=1,826$; $p<0.05$). The mean MaxF and FR were higher when the dolphins were not travelling (Mean MaxF=14,940Hz, SD=3,116; Mean FR=5,492Hz, SD=3,243) than when they were (Mean MaxF=14,609Hz, SD=3,130; Mean FR=5,167Hz, SD=2,354) and there were on average more steps in the whistles when travelling occurred (mean steps=0.14, SD=0.41) than when no travelling was recorded (mean steps=0.08, SD=0.293).

- The mean number of steps also differed significantly depending on foraging ($Z=-3.573$; $N=1,826$; $p<0.001$), with more steps recorded (mean steps=0.17, $SD=0.451$) when foraging occurred than when there was no foraging (mean steps=0.10, $SD=0.337$).
- Most differences were found for socialising. Mean duration ($Z=-3.393$; $N=1,826$; $p=0.001$) was higher when the dolphins were socialising (mean duration=0.693s, $SD=0.321$) than when they were not (mean duration=0.632, $SD=0.328$). Mean minimum frequency ($Z=-2.584$; $N=1,826$; $p<0.05$) was also higher when socialising was recorded (mean MinF=9,655Hz, $SD=1,957$) than when it was not (mean MinF=9,384Hz, $SD=2,070$). And the whistles had on average significantly more inflections ($Z=-2.136$; $N=1,826$; $p<0.05$) when no socialising was recorded (mean inflections=0.66, $SD=0.979$) than when socialising did occur (mean inflections=0.59, $SD=1.007$).

Looking at each behaviour individually allowed crosstabulation and Pearson chi-square correlation analysis between the presence or absence of each behaviour and the whistle type. There was no significant correlation between overall whistle type and presence or absence of bow-riding or travelling. Overall whistle type was significantly correlated with whether the animals were foraging or not (Pearson: $X^2=11.188$; $df=5$; $p<0.05$) although a Cramer's V value of 0.078 indicates that this is a relatively weak correlation (fig. 3.11). There was also a significant correlation between overall whistle type and socialising (Pearson: $X^2=22.448$; $df=5$; $p<0.001$) and the Cramer's V value for this correlation was 0.111, thus slightly higher than for foraging but still relatively weak (fig. 3.12). When these analyses were carried out for the 30 sub-types of whistles, rather than just the overall types, all individual behaviours were significantly correlated to whistle type (Bow-riding: $X^2=46.856$; $df=29$; $p<0.05$; Cramer's V=0.160; Travelling: $X^2=55.853$; $df=29$; $p<0.05$; Cramer's V=0.175; Foraging: $X^2=43.005$; $df=29$; $p<0.05$; Cramer's V=0.153; Socialising: $X^2=56.874$; $df=29$; $p=0.001$; Cramer's V=0.176).

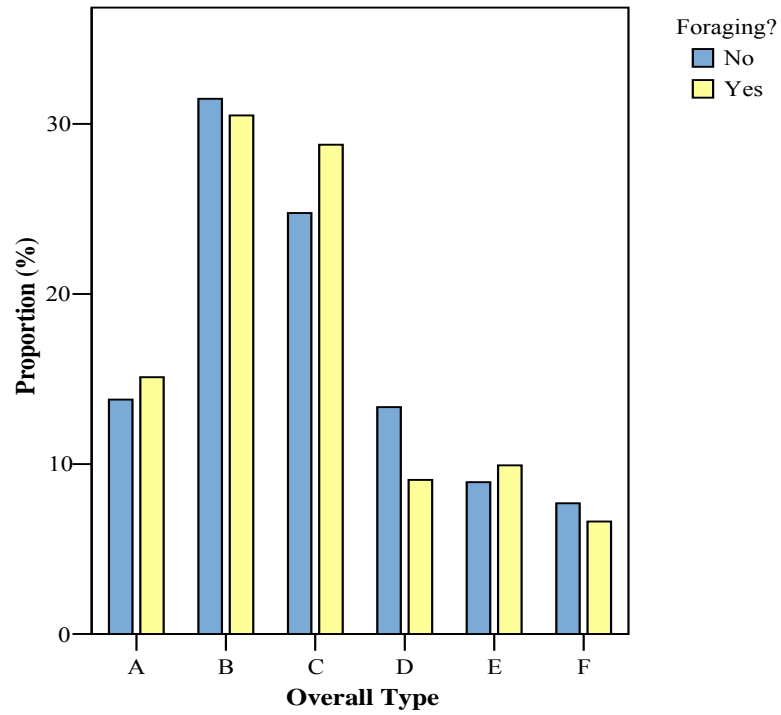


Figure 3.11. Proportions (%) of each broad whistle type, in cases when dolphins were foraging (yellow) and when they were not (blue).

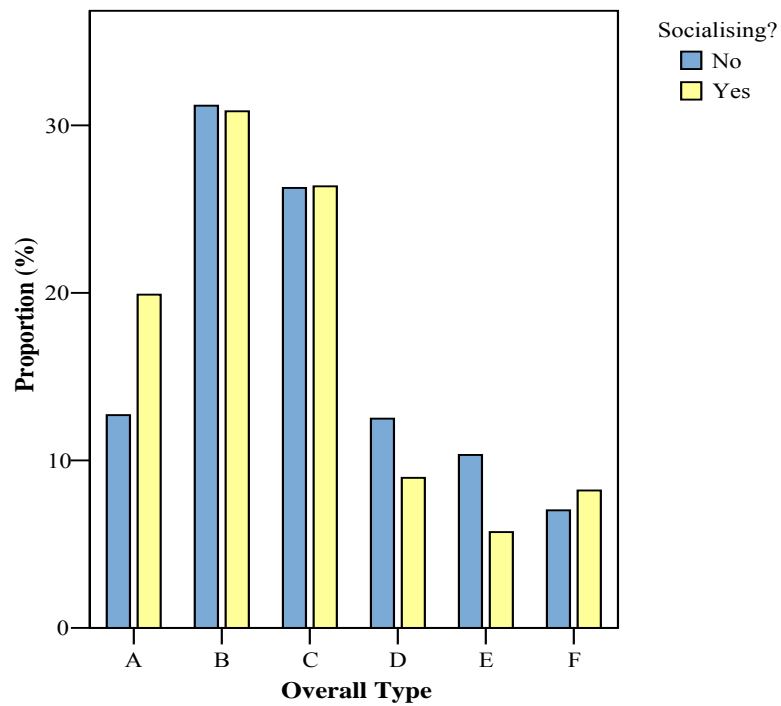


Figure 3.12. Proportions (%) of each broad whistle type, in cases when dolphins were socialising (yellow) and when they were not (blue).

3.2.3. Relationship between Whistle Characteristics and Group Size

Group sizes were pooled together into the categories: <5, 5-10, 11-20, 21-50, 51-100 and >100 to get roughly similar sample sizes (200-471) for each category. An exception was the <5 category which had a sample size of only 14 but it was felt that this was still a biologically important category to include. Non-parametric Kruskal-Wallis tests showed that only the mean frequency gradient (FG) was significantly different ($X^2=12.180$; $df=5$; $p<0.05$). While the absolute value of the frequency gradient was not significantly different, for groups of 5-10 animals it was positive, so on average the whistles had a rising slope, while for groups of >50 animals it was negative, so whistles were overall falling in frequency (fig. 3.13). For the other group sizes it had an intermediate distribution around zero. Crosstabulation and Pearson's Chi-Square analyses found no significant correlations between group sizes and overall whistle type ($X^2=33.385$; $df=25$; $p>0.05$). For whistle sub-types, these tests could not be used as more than 20% of the cells had expected counts less than 5.

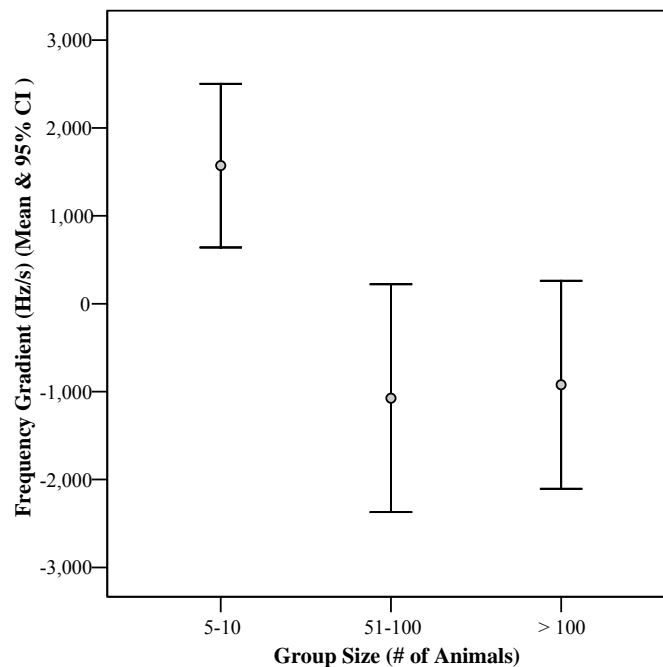


Figure 3.13. Error bar graph illustrating differences in mean frequency gradient between dolphin groups of 5-10 animals and groups of >50 animals.

3.2.4. Relationship between Whistle Characteristics and Encounters

To determine whether mean whistle variables were significantly different between individual encounters, the non-parametric Kruskal-Wallis test was used. It showed that the means of all of the variables were significantly different between encounters:

- Duration: $X^2=174.605$; $df=33$; $p<0.001$
- SF: $X^2=80.402$; $df=33$; $p<0.001$
- EF: $X^2=64.010$; $df=33$; $p=0.001$
- MinF: $X^2=117.589$; $df=33$; $p<0.001$
- MaxF: $X^2=101.426$; $df=33$; $p<0.001$
- MeanF: $X^2=102.646$; $df=33$; $p<0.001$
- FG: $X^2=66.781$; $df=33$; $p<0.001$
- AFG: $X^2=64.804$; $df=33$; $p=0.001$
- FR: $X^2=145.875$; $df=33$; $p<0.001$
- Inflections: $X^2=110.374$; $df=33$; $p<0.001$
- Steps: $X^2=120.015$; $df=33$; $p<0.001$

Correlation analyses between encounters and whistle types could not be used because data were not sufficient; more than 20% of cells had expected counts less than 5.

Encounters were then grouped together into survey days to check for significant differences between data from different days. The Kruskal-Wallis test showed that all whistle variables, except for frequency gradient and absolute frequency gradient had significantly different means for different survey days:

- Duration: $X^2=64.725$; $df=5$; $p<0.001$
- SF: $X^2=15.912$; $df=5$; $p<0.05$
- EF: $X^2=23.427$; $df=5$; $p<0.001$
- MinF: $X^2=21.101$; $df=5$; $p=0.001$
- MaxF: $X^2=34.013$; $df=5$; $p<0.001$
- MeanF: $X^2=36.587$; $df=5$; $p<0.001$
- FG: $X^2=9.861$; $df=5$; $p>0.05$
- AFG: $X^2=8.533$; $df=5$; $p>0.05$
- FR: $X^2=28.732$; $df=5$; $p<0.001$
- Inflections: $X^2=27.090$; $df=5$; $p<0.001$
- Steps: $X^2=65.272$; $df=5$; $p<0.001$

Correlation analysis showed that broad whistle types were also significantly correlated with survey day (Pearson $X^2=83.090$; $df=25$; $p<0.001$) although a Cramer's V value of 0.095 indicated only a weak correlation.

3.3. Comparison between Celtic Sea and English Channel Whistles (Part C)

3.3.1. English Channel Whistle Characteristics and Types

From the English Channel recordings, a total of 435 whistles were marked. These were measured and categorised in the same way as the Celtic Sea whistles. Table 3.4 summarises the means, ranges, and standard deviations of the whistle parameters of the English Channel whistles.

Out of the overall whistle types, the upsweep was the most frequent among the English Channel whistles, making up a proportion of 30.3%. The next common whistle types were the downsweep with 23.9% and the constant frequency type with 16.8%, followed by the convex and sine types which made up 13.1% and 10.1% respectively. The least common type was the concave type which only represented 5.7% of the whistles (fig. 3.14). Looking at the individual sub-types, a similar pattern to that found for Celtic Sea whistles was apparent, that is, the least modulated first sub-type (or in the case of the sine category the first two equally simple sub-types) were the most frequent sub-types within each overall type (fig. 3.15).

Table 3.4. Range, Mean and Standard Deviations for the different characteristics measured of English Channel common dolphin whistles.

	Minimum	Maximum	Mean	Standard Deviation
Duration (s)	0.093	1.886	0.643	0.324
Start Frequency (Hz)	5017	27945	12641	3946
End Frequency (Hz)	4519	26124	12476	3970
Minimum Frequency (Hz)	4519	21080	9801	2462
Maximum Frequency (Hz)	8160	27945	15835	3283
Mean Frequency (Hz)	5757	22249	12669	2369
Frequency Gradient (Hz/s)	-44241	41157	509	11632
Absolute Frequency Gradient (Hz/s)	0	44241	8363	8091
Frequency Range (Hz)	121	20513	6034	3419
Inflections	0	6	0.56	0.912
Steps	0	3	0.10	0.335

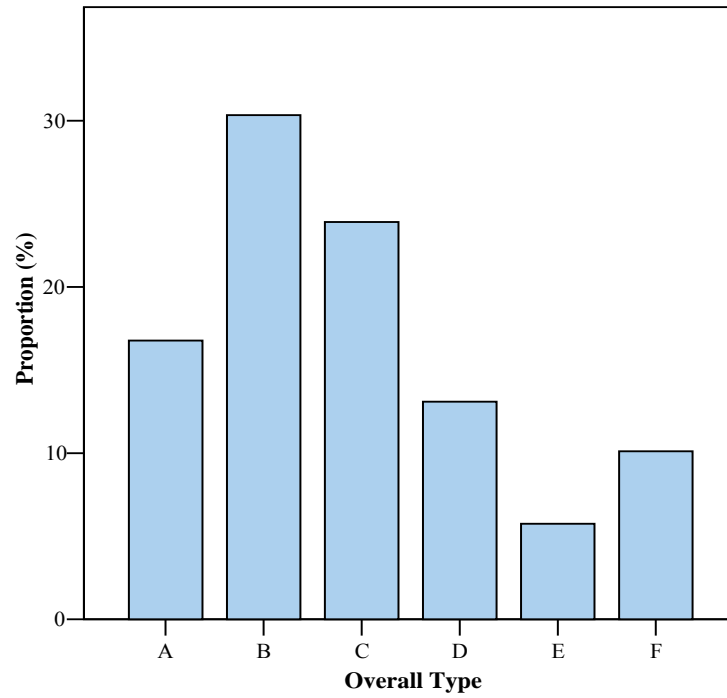


Figure 3.14. Proportional frequencies (%) of each overall whistle type in the 435 sampled whistles of common dolphins in the English Channel.

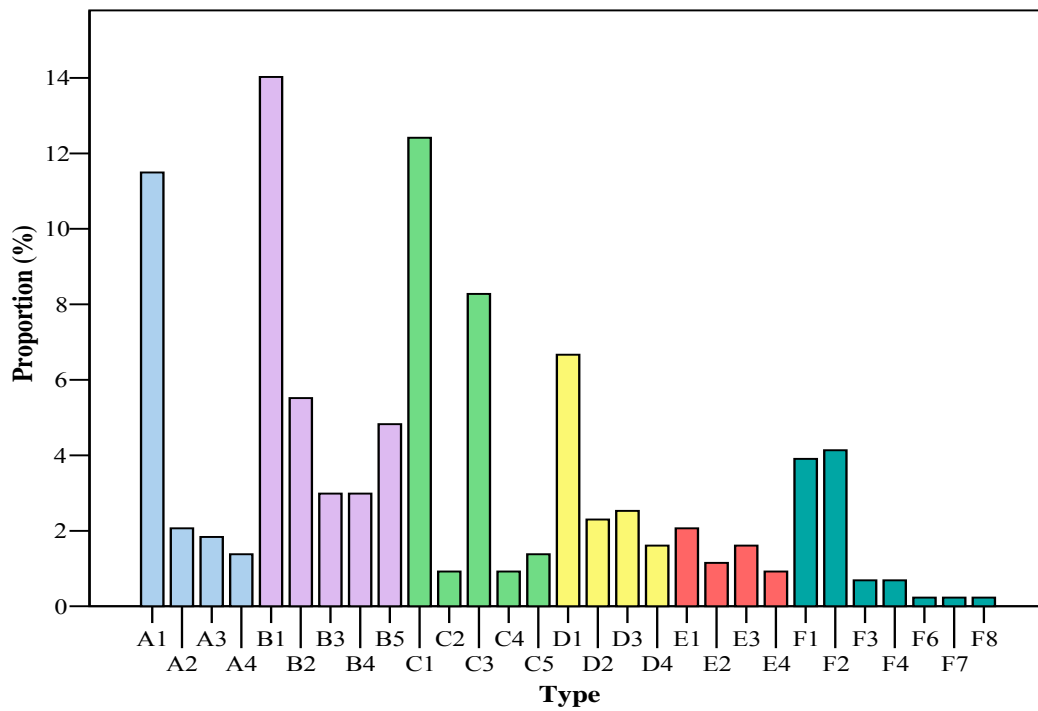


Figure 3.15. Proportions (%) of the 435 sampled whistles made up of each whistle sub-type, colour-coded by overall type.

3.3.2. Celtic Sea versus English Channel Whistle Comparisons

Since only 435 whistles were available from the English Channel, a random subset of 435 whistles was taken from the Celtic Sea whistles to achieve equal sample sizes for the comparisons between the two locations. Most of the whistle variables had an approximately normal distribution. Therefore, to look for significant differences in the means of each variable between the two sampling locations, a t-test (which is robust to slightly skewed distributions as sample sizes were equal for both locations (Francis, 2001)) was used, assuming equal variances where this was confirmed by Levene's test, or not assuming equal variances if they were significantly different. Significant differences were found in the means of start frequency ($t=-2.033$; $df=852.646$; $p<0.05$), end frequency ($t=-2.131$; $df=842.580$; $p<0.05$), minimum frequency ($t=-2.303$; $df=868$; $p<0.05$), maximum frequency ($t=-4.839$; $df=868$; $p<0.001$), mean frequency ($t=-4.911$; $df=858.321$; $p<0.001$), absolute frequency gradient ($t=-3.179$; $df=840.974$; $p<0.05$), frequency range ($t=-3.073$; $df=868$; $p<0.05$) and inflections ($t=2.863$; $df=829.402$; $p<0.05$). In other words the means of all variables except for duration, frequency gradient and steps were significantly different between the two locations. For all the frequency related variables in which differences were determined, the English Channel whistles consistently had higher mean frequency values than those from the Celtic Sea (fig. 3.16-3.22). The mean number of inflections was higher for Celtic Sea whistles (fig. 3.23).

Using a nested ANOVA (to determine whether the differences between locations were larger than the differences between encounters within locations) or a discriminant function analysis (DFA) (to establish whether it would be possible to classify whistles into correct location groups based on whistle parameters) was not possible as the parameters did not consistently meet the assumptions of normality and homogeneity of variance and transformations did not solve this problem.

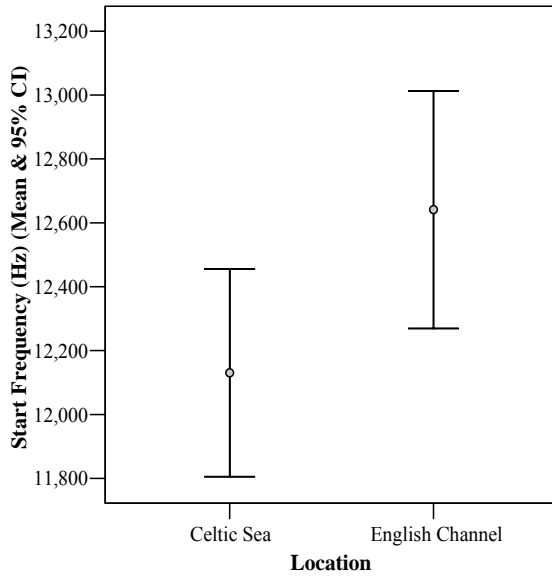


Figure 3.16. Error bar graph showing mean and 95% CI of start frequency by location.

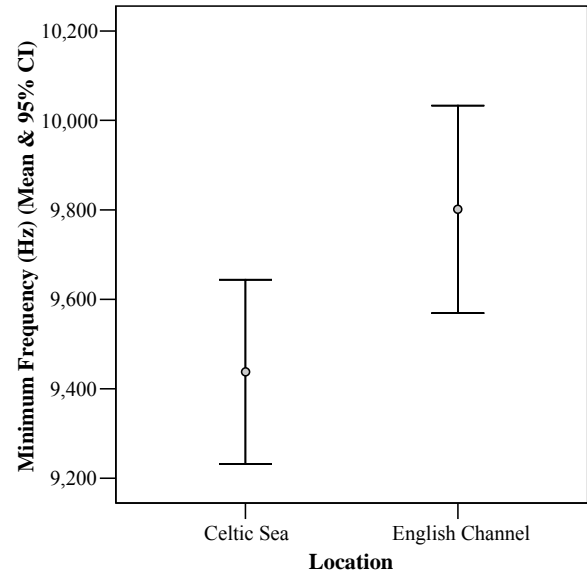


Figure 3.18. Error bar graph showing mean and 95% CI of minimum frequency by location.

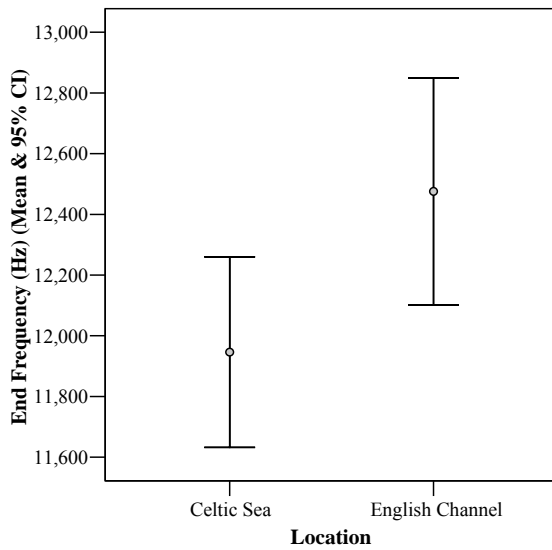


Figure 3.17. Error bar graph showing mean and 95% CI of end frequency by location.

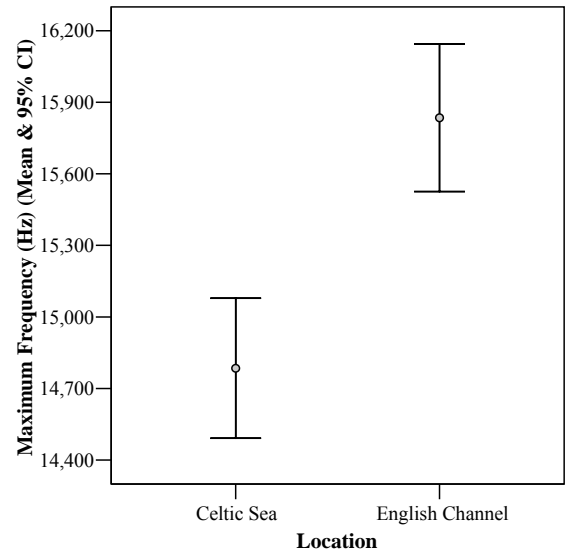


Figure 3.19. Error bar graph showing mean and 95% CI of maximum frequency by location.

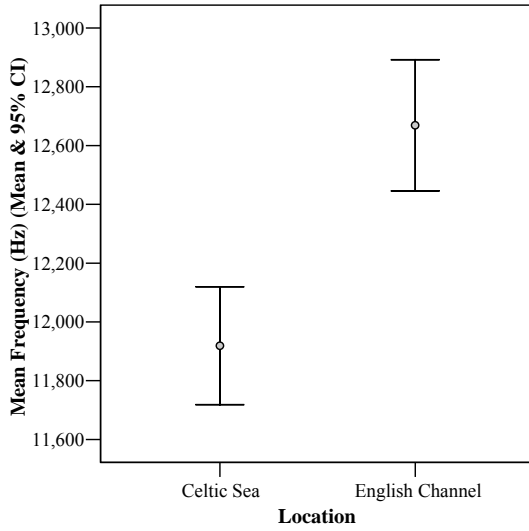


Figure 3.20. Error bar graph showing mean and 95% CI of mean frequency by location.

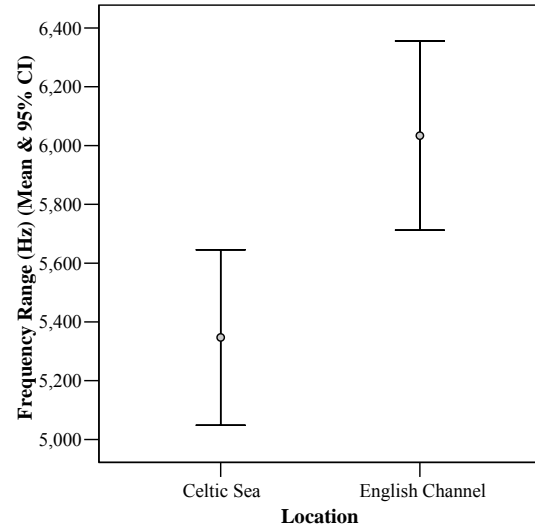


Figure 3.22. Error bar graph showing mean and 95% CI of frequency range by location.

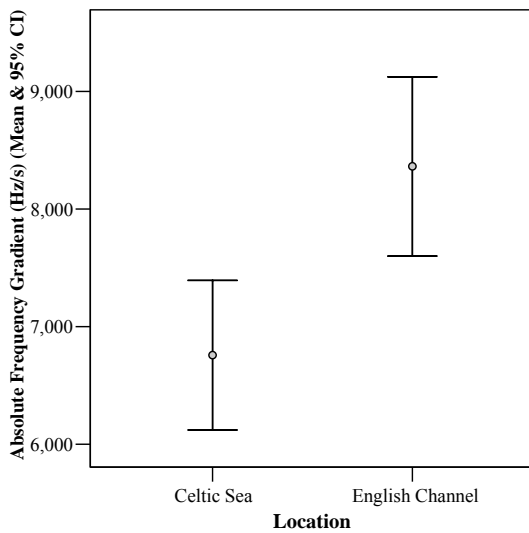


Figure 3.21. Error bar graph showing mean and 95% CI of absolute frequency gradient by location.

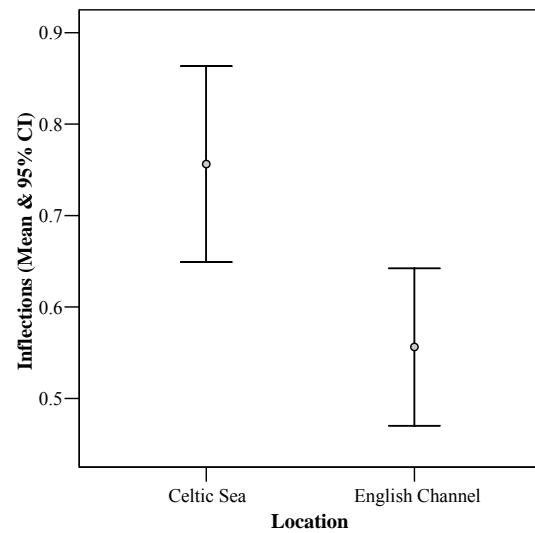


Figure 3.23. Error bar graph showing mean and 95% CI of the number of inflections by location.

The broad whistle type was not significantly correlated to the sampling location (Pearson $X^2=10.295$; $df=5$; $p>0.05$), although figure 3.24 shows slight variations in the percentages each type makes up between locations. Particularly type E (concave) seems to be relatively less common in the English Channel, while type A (constant) seems slightly more common. Correlation analyses could not be used for the whistle sub-types as insufficient data was available (more than 20% of cells had expected counts of less than 5).

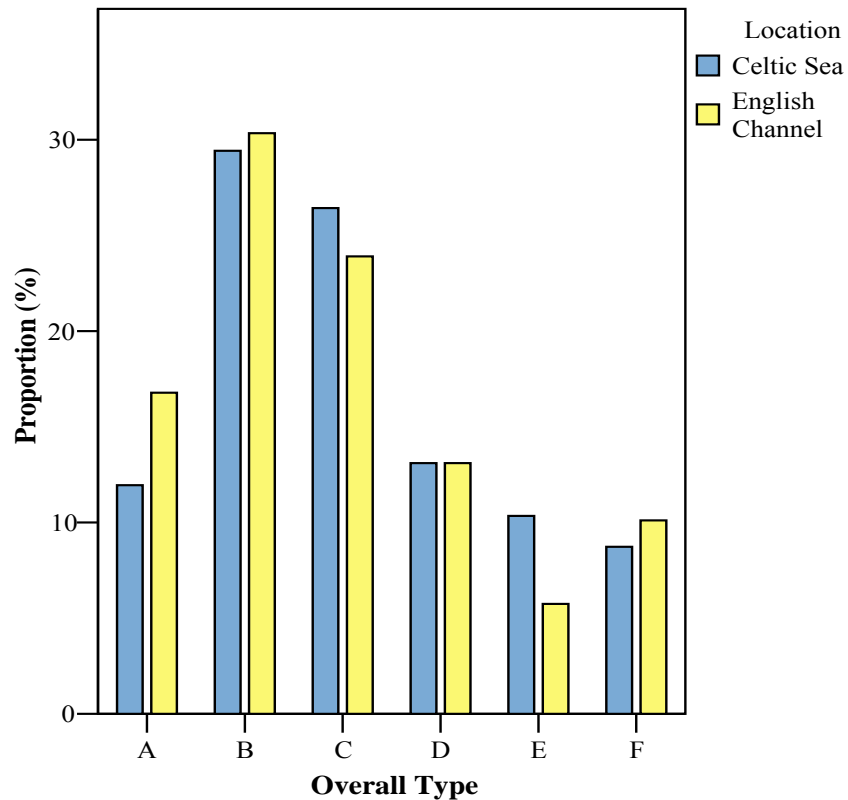


Figure 3.24. Proportions (%) of each broad whistle type, in dolphin whistles from the Celtic Sea (blue) and from the English Channel (yellow).

For all statistical outputs referred to in the previous sections see CD-ROM appendix 7.4.

4. Discussion

4.1. Acoustic Survey Methodology (Part A)

In this study, there were only seven cases (out of 366 ten-minute-intervals) where common dolphins were detected visually but not acoustically. In four of those, the animals were seen at an estimated distance of over 1 km from the vessel. The exact distance at which dolphins can be detected acoustically is not known, it depends on many factors such as, for example, the background noise, the source level of the vocalisations, and the type of hydrophone used. Generally, however, it is thought that dolphin vocalisations can be picked up from a distance of no more than 1 km (Richardson et al. 1995). Thus it is likely that this was the reason why these four sightings were not recorded acoustically.

Another possible disadvantage of acoustic surveying is that animals may be silent (Goold, 1996; Evans and Hammond, 2004). Goold (1996) noted that this is not usually a problem with common dolphins. They are generally regarded as highly vocal (Carwardine, 1995). Still, this probably accounts for the remaining three cases in which animals were seen but not detected acoustically. In two out of those three, only a solitary animal was seen and in the third case it was a pair of two individuals. Intuitively it makes sense that a single dolphin on its own has no need to produce social sounds, and a group of two that may well be in close visual contact are also less likely to vocalise than a larger group of animals. These small group sizes are not encountered very often in common dolphins, and in this study the average group size was 23 (on the basis of encounters rather than sightings).

The opposite case, that visual sightings were missed while dolphins were detected acoustically, was far more frequent and made up 30% of all 10-minute-intervals. Interestingly, sea state, which is generally considered a major factor limiting sightability (Evans and Hammond, 2004), did not have a significant effect on whether sightings were missed. An explanation for this may be that much of the field work was carried out in sea states 2 or less (this was the main criteria for scheduling field work in the first place), so

sampling did not cover the full range of sea states evenly. The chance of missing a sighting was however significantly correlated to whistle density (number of whistles per minute) as well as whistle intensity (clear versus faint) in the recording. This indicates that the chances of detecting common dolphins visually are higher for larger groups of animals (assumed to be implied in higher whistle density) and for smaller distance of animals from the vessel (assumed to be implied in clearer whistle intensity). This finding supports generally accepted hypotheses that the detectability of cetaceans decreases with increasing distance from the transect line and is positively related to school size (Evans and Hammond, 2004). These results indicate that acoustic survey techniques may greatly increase the chances of detecting common dolphins compared to visual techniques alone.

An advantage of acoustic surveying is that it is not dependent on daylight and can cover the entire 24 hours of a day. Goold (2000) made use of this by recording common dolphins in the Celtic Sea continuously throughout the entire diel period and found that the level of acoustic contact peaked at night time. In the present study, surveys were only run during the day and consistent coverage from all survey days in the analysis was only available between the hours of 9am and 5pm, so these night-time peaks could not have been determined. A weak pattern was apparent, that whistle densities as well as sighting rate were highest in the afternoon and morning, with a low-point around noon (1100-1200 hrs), but this was not statistically significant.

A major problem with acoustic surveying of cetaceans is that it is very difficult to reliably estimate numbers of individuals from vocalisation rates, especially when the animals occur in large groups (Goold, 1996). The present study did find a significant regression between whistle density and group size, which yielded an equation that allows predicting group size from whistle density. However, this was only a moderately strong relationship and group size could only explain 22.6% of the variation in whistle density. Whistle density is also influenced by confounding factors such as the distance of the animals. The multiple regression which included the factor mean distance in addition to group size as predictors could explain 33% of the variation in whistle density, more than the regression with group size alone, even though group size was the more important predictor variable. However, this multiple regression is not useful in real life applications. The purpose of developing this kind of regression equation is to estimate group size from

passive acoustic survey data where no visual records are available. Thus, data on the distance of the animals would not be available either and could not be included in an equation.

Van Parijs et al. (2002) conducted a similar study and developed a regression equation to predict school sizes of Pacific humpback dolphins (*Sousa chinensis*) from the number of calls recorded. They did manage to find a fairly strong linear regression with an R^2 of 0.85 including all data or even $R^2 = 0.92$ if the three worst-fit-data points were removed. A possible reason for why their analysis gave better results than the present study may be that humpback dolphins usually occur in much smaller group sizes than common dolphins. The maximum group size recorded by Van Parijs et al. was 15 animals. Increasing group size makes it more difficult to reliably estimate the number of animals, as well as to reliably count the number of whistles (especially from a large group of a highly vocal species such as common dolphins). Thus, it is possible that larger group sizes tend to make the relationship more “noisy”. This hypothesis is supported by the fact that the three data points that Van Parijs et al. removed from their analysis because they gave the worst fit to the model were all from groups of more than 10 dolphins.

So in conclusion, based on the results of the present study, the relationship between group size and whistle density, while significant, is not considered strong enough to serve as a reliable method of estimating group sizes from acoustic survey data. It may be possible to develop reliable models for species with smaller group sizes but more research is needed to make this method more widely applicable.

4.2. Whistle Repertoire of Celtic Sea Common Dolphins (Part B)

The 1,835 whistles recorded of common dolphins in the Celtic Sea covered a frequency span from 3.56 kHz to 23.51 kHz, with most whistles occurring between 9 and 15 kHz. The shortest recorded whistle was 0.05 seconds long and the longest lasted 2.02 seconds. On average the whistles were around 0.65 seconds long. Common dolphin whistles in the Celtic Sea were of a relatively simple structure as the average whistle had only 0-1 inflections and no steps. This was further shown by the relative abundances of whistle types. The simplest first sub-types (or the first two equally simple sub-types for overall type F) were the most common within each broad whistle type. Overall, the upsweep was the most frequent type, followed by the downsweep.

4.2.1. Variation between Encounters

All of the whistle parameters measured, showed statistically significant differences between different encounters. Several explanations for this may be considered. Firstly, this result may indicate variation between each group of dolphins, possibly in the form of dialects. However, this is considered unlikely as common dolphins are thought to live in fluid fission-fusion societies of changing groups, while the establishment of dialects between groups would require highly stable group associations (Tyack, 1986). Bazúa-Durán and Au (2004) found “whistle-specific subgroups” in Hawai’ian spinner dolphins and suggested that these may represent dialects, though not as distinct as those commonly known of killer whales. However, this is a slightly different situation as the spinner dolphin whistle-specific subgroups were independent of location and recording day, whereas the significant variation found in the present study was between encounters, thus not only linked to different groups but also different recording sessions. It is likely that the differences may not have been caused by group specific whistle characteristics but rather by differences related to the recording context, such as behaviour, group size, or the presence and possible over-sampling of individual-specific vocalisations such as signature whistles (Oswald et al. 2003).

Behaviour was significantly correlated to some whistle characteristics, for example when animals were travelling, the mean maximum frequency and frequency range were lower and there was on average more steps in the whistles than when no travelling was observed. Higher average numbers of steps were also measured when dolphins were foraging. During socialising, the mean duration of whistles was longer, mean minimum frequency was higher and whistles had on average fewer inflections. Furthermore, the mean frequency gradient was significantly different between small groups of 5-10 animals, in which case it was positive indicating relatively more overall upsweeping whistles, and large groups of over 50 animals, where the frequency gradient was negative, implying more downsweeping whistles. However, there was no significant correlation between group size and relative abundances of the different whistle types. Behaviour and group size thus do influence certain whistle parameters but it is not clear whether they account for all the variation between different encounters.

The other possible explanation is high variation between individuals. This would be expected if the majority of the vocalisations of each animal were signature whistles. Caldwell and Caldwell (1965) determined that over 90% of the calls of captive bottlenose dolphins were highly stereotyped whistles specific to each individual. It is not known how much of the whistle repertoire of free-ranging common dolphins consists of signature whistles. In the present study, the author did come across highly stereotyped whistles that were repeated several times in close succession which makes it likely that these were signature whistles. However, the majority of whistles were not clearly recognisable as such. Also, the finding that the simplest whistle sub-types, that is simple upsweeps, downsweeps or constant whistles without much further modulation, were the most frequent types recorded, suggests that a large part of the repertoire of common dolphins in the Celtic Sea consists of non-signature whistles.

A major problem with these kinds of acoustic studies, and possibly the main reason for the high variance between encounters, is the non-independence of data. An underlying assumption of most statistical tests is that sampled data are independent of each other, meaning that the value of one sample point or observation is not related to or influenced by the value of another observation in the sample (Fowler et al. 1998). Currently it is practically impossible to determine which individual from a pod of

dolphins in the wild is vocalising, therefore it is likely that recordings often include more than one whistle from each individual and it cannot be guaranteed that each whistle used in the analysis is from a different animal (Oswald et al. 2003). In the present study, to avoid over-sampling particular groups and the individuals in them, a maximum of 100 whistles was used from each encounter, randomly selected if more than 100 whistles had been marked. However, this is unlikely to have removed all over-sampling and data cannot be expected to be completely independent. This should be kept in mind when examining the results of this and other acoustic studies of social cetaceans.

4.3. Geographic Variation in Whistle Parameters (Part C)

The whistle parameters measured for the Celtic Sea common dolphin whistles were similar to those described by Wakefield (2001) in the same general study area, based on recordings of common dolphins from 1994. For the comparison, Wakefield's "before" data was used, i.e. recordings from times before seismic surveys rather than during or after. The means of frequency parameters of whistles from Wakefield (2001) and the present Celtic Sea data were all within 1 kHz of each other except for maximum frequency which was 2 kHz higher in the present study. Mean duration was also slightly longer in the present study. Overall, the whistle characteristics were considered fairly consistent between Celtic Sea recordings from 1994 and 2005 (Wakefield, 2001 and present study respectively) (table 4.1).

Table 4.1. Mean and standard deviations (in parenthesis under the mean) of whistle parameters of short-beaked common dolphins in different locations and recorded with different high bandwidth limits. English Channel values marked with an asterisk (*) were significantly different from the corresponding Celtic Sea whistle characteristics in the present study. Two asterisks () marked values in the Oswald et al. (2004) study that were significantly different for different upper bandwidth limits.**

	Celtic Sea 24 kHz bandwidth limit (Present Study)	Celtic Sea 24 kHz bandwidth limit (Wakefield, 2001)	Eastern Tropical Pacific Ocean 24 kHz bandwidth limit (Oswald et al. 2004)	Eastern Tropical Pacific Ocean 40 kHz bandwidth limit (Oswald et al. 2004)	English Channel 48 kHz bandwidth limit (Present Study)
Start Frequency	12.03 * (3.47)	11.17 (2.70)	12.3 (4.3)	12.9 (5.2)	12.64 * (3.95)
End Frequency	11.97 * (3.25)	11.04 (2.43)	13.8 ** (4.8)	14.1 ** (5.4)	12.48 * (3.97)
Minimum Frequency	9.45 * (2.06)	9.44 (1.74)	8.7 (2.3)	8.6 (2.3)	9.80 * (2.46)
Maximum Frequency	14.69 * (3.13)	12.67 (2.73)	16.7 ** (3.5)	17.7 ** (4.6)	15.84 * (3.28)
Mean Frequency	11.89 * 2.05	10.96 (1.82)	-	-	12.67 * (2.37)
Frequency Gradient	0.38 (9.73)	-	-	-	0.51 (11.63)
Absolute Frequency Gradient	6.97 * (6.79)	-	-	-	8.36 * (8.09)
Frequency Range	5.24 * 3.25	-	-	-	6.03 * (3.42)
Duration	0.65 (0.33)	0.53 (0.31)	0.70 (0.42)	0.75 (0.44)	0.64 (0.32)
Inflections	0.64 * (0.98)	Median = 0	1.8 (1.5)	1.8 (1.5)	0.56 * (0.91)
Steps	0.13 (0.39)	-	1.2 (1.7)	1.2 (1.7)	0.10 (0.34)

The comparison between the common dolphin whistles recorded in the English Channel and a random sub-sample of the Celtic Sea whistles found significant differences in the number of inflections, as well as all frequency parameters except from mean frequency gradient (table 4.1). The significant differences between almost all frequency parameters seem to indicate variation caused by geographic separation of the common dolphins of these two locations, since frequency parameters have generally been found to vary mostly between rather than within populations (Azevedo and Van Sluys, 2005; Morisaka et al. 2005a).

It has to be considered in this case, that the recording sampling rates varied between the two locations, that is, in the Celtic Sea, frequencies were recorded up to 24 kHz while in the English Channel, the upper bandwidth limit was 48 kHz. Thus, whistles higher than 24 kHz would have been missed in the Celtic Sea, but recorded and analysed in the English Channel. This may have increased the mean values of English Channel data, which were indeed higher for all frequency parameters in the English Channel than in the Celtic Sea (table 4.1). The highest frequency measured of an English Channel whistle was 27.945 kHz, which certainly would have been cut off by the Celtic Sea recording equipment. In the Celtic Sea, the highest frequency was 23.514 kHz, close to the bandwidth limit of the equipment. However, out of the 435 analysed English Channel whistles, only 5 had maximum frequencies above 24 kHz, so it is unlikely that these 5 whistles significantly influenced the mean value of 435 whistles. Also, the parameter minimum frequency, which was significantly different as well, should not have been influenced by the upper bandwidth limit. Oswald et al. (2004) compared the whistles of four dolphin species, including *D. delphis*, recorded with different bandwidths. They found that increasing the upper bandwidth limit only had a significant effect on maximum and ending frequency (table 4.1). Furthermore, increasing the upper bandwidth limit to over 24 kHz only resulted in minor changes in whistle variables and correct classification between species, compared to increasing it from 20 to 24 kHz. They concluded that 24 kHz seems to be a sufficient upper bandwidth limit to describe the majority of dolphin whistles (Oswald et al. 2004). A further bias related to sampling with higher bandwidth limits is possible because more harmonics were present in the English Channel recordings, and thus it is possible that in some cases harmonics rather than the

fundamental contours may have been marked accidentally. However, the author took care to avoid this. In conclusion, these results do seem to represent a real difference between whistles from the two sampling locations, rather than a bias introduced by different sampling techniques.

Differences between the whistle characteristics of the same species in separate locations may be caused by several different factors. Firstly, the two locations may be used differently by the animals, for example one might be used as feeding ground and the other as breeding/resting/socialising area. Thus, different behaviours in the two areas might cause variation in the whistle characteristics. Intraspecific behavioural variation is usually shown in differences of parameters such as duration, inflections and steps, as these are more freely modulated by the animals (Rendell et al. 1999; Bazúa-Durán and Au, 2004; Morisaka et al. 2005a). While the mean number of inflections was significantly lower in English Channel whistles than in Celtic Sea whistles, duration and steps were not significantly different. Furthermore, different behaviours (travelling, socialising, foraging and bow-riding) were all observed in common dolphins during the Celtic Sea surveys and were only found to influence certain whistle parameters, including duration and steps but not consistently all frequency parameters as was found for the between-location comparison. Differences in frequency parameters are usually associated with variation between species or between populations rather than behavioural contexts within populations, as these frequency characteristics are generally related to anatomical variables such as body size or to environmental factors such as ambient noise levels (Rendell et al. 1999; Bazúa-Durán and Au, 2004; Morisaka et al. 2005a). To the author's knowledge, no differences in body size or other anatomical features related to sound production have been reported for the common dolphins in the Celtic Sea and English Channel. It is more likely that the consistently higher mean frequency parameters of English Channel whistles compared to those from the Celtic Sea are related to differences in the background noise levels in the two areas. The English Channel and its western approaches are an area of intense fishing effort by both English as well as French trawl fisheries (De Boer et al. 2005). Furthermore there are several ferry lines regularly crossing the Channel and many trade vessels pass through it. Generally, the English Channel is considered one of the busiest areas for maritime traffic in the world

(Wikipedia, 2005). Of course this causes considerable background noise. As ship noises are mostly low in frequencies, dolphins may shift the frequencies of their vocalisations up to avoid/reduce masking, a phenomenon called the acoustic niche hypothesis (Richardson et al. 1995; Morisaka et al. 2005b). This seems a plausible explanation for the higher frequency parameters in the whistles of English Channel common dolphins.

4.4. Variations in Whistle Types and Interspecies Comparisons

The relative abundances of the different broad whistle types were not significantly different between Celtic Sea and English Channel whistle repertoires. In both locations the most common type was the upsweep (B), followed by the downsweep (C). These relative abundances were also similar to those reported by Wakefield (2001) for common dolphins recorded in the Celtic Sea in 1994 (table 4.2). It is interesting that in Hawai'ian spinner dolphins, upsweeps are also the most common type, making up almost half of the entire whistle repertoire (Bazúa-Durán and Au, 2002) (table 4.2), while in bottlenose dolphins, the relative abundances of whistle types vary with location (Bazúa-Durán, 2004). This seems to support the hypothesis that the whistle repertoires of ecologically similar species such as the common and spinner dolphins are somewhat similar as well (Au, 2000; Bazúa-Durán, 2004) (see introduction, chapter 1.3.5). A comparison of the frequency parameters also supports this theory as they were fairly similar between common dolphins (as recorded in the present study) and spinner dolphins (Bazúa-Durán and Au, 2002). The mean duration, however, was shorter in spinner dolphins (table 4.3). The variables inflections and steps could not be compared as they were measured using a different method by Bazúa-Durán and Au (2002).

Table 4.2. Relative fractions (in percent) of each broad whistle type in the whistle repertoires of short-beaked common dolphins (*Delphinus delphis*) from different locations and studies and Hawai'ian spinner dolphins (*Stenella longirostris*).

	<i>D. delphis</i> Celtic Sea (Present Study)	<i>D. delphis</i> Celtic Sea (Wakefield, 2001)	<i>D. delphis</i> English Channel (Present Study)	<i>S. longirostris</i> Hawai'i (Bazúa-Durán and Au, 2002)
Constant (A)	14.3	12.1	16.8	9
Upsweep (B)	31.0	19.4	30.3	47
Downsweep (C)	26.5	18.1	23.9	13
Convex (D)	11.7	7.1	13.1	20
Concave (E)	9.3	9.7	5.7	5
Sine (F)	7.3	4.1 (type "other")	10.1	6

Table 4.3. Means and standard deviations (in parenthesis under the mean) of whistle parameters of short-beaked common dolphins and Hawai'ian spinner dolphins.

	<i>D. delphis</i> Celtic Sea (Present Study)	<i>D. delphis</i> English Channel (Present Study)	<i>S. longirostris</i> Hawai'i (Bazúa-Durán and Au, 2002)
Start	12.03	12.64	11.40
Frequency	(3.47)	(3.95)	(3.68)
End	11.97	12.48	13.54
Frequency	(3.25)	(3.97)	(3.78)
Minimum	9.45	9.80	9.99
Frequency	(2.06)	(2.46)	(2.71)
Maximum	14.69	15.84	15.85
Frequency	(3.13)	(3.28)	(3.58)
Frequency	5.24	6.03	5.86
Range	3.25	(3.42)	(3.49)
Duration	0.65 (0.33)	0.64 (0.32)	0.49 (0.39)

4.5. General Methodology

A problem with the methodology in this study was that it was not consistent across survey days. Due to logistical constraints and equipment failures, several different hydrophones had to be used and towed at varying lengths behind the vessel. This is likely to have affected the range and quality at which whistles were recorded as shorter hydrophone cables meant that they were closer to the engine and thus exposed to higher levels of masking noise. The type of engine as well as the speed of the vessel also greatly influenced the quality of the recordings. Unfortunately, no technical details were available about the type of engine of *Llanstadwell*, the first survey vessel. But the 420hp engine of *Predator* seemed very noisy based on the subjective experience of researchers on the boat, and it seemed to have a considerable masking effect on the recordings. For example, figure 4.1 shows the spectrogram of a continuous recording period during which the vessel was stopped to haul in the hydrophone. The first half of the spectrogram shows the recording at a cruising speed of 8-10 knots, while the second half was recorded with the engine stopped. It illustrates that the engine noise has a severe masking effect and as soon as it is removed, a large number of whistles appear in the spectrogram, which were almost completely invisible/inaudible before. Therefore, to achieve the best possible quality of recordings, hydrophones should be towed as far as possible behind the vessel and at slow speeds preferably below 10 knots. If available, a vessel with a quiet engine should be used, ideally a sailing vessel. This would have the added advantage that it would likely be less of a disturbance to the animals.

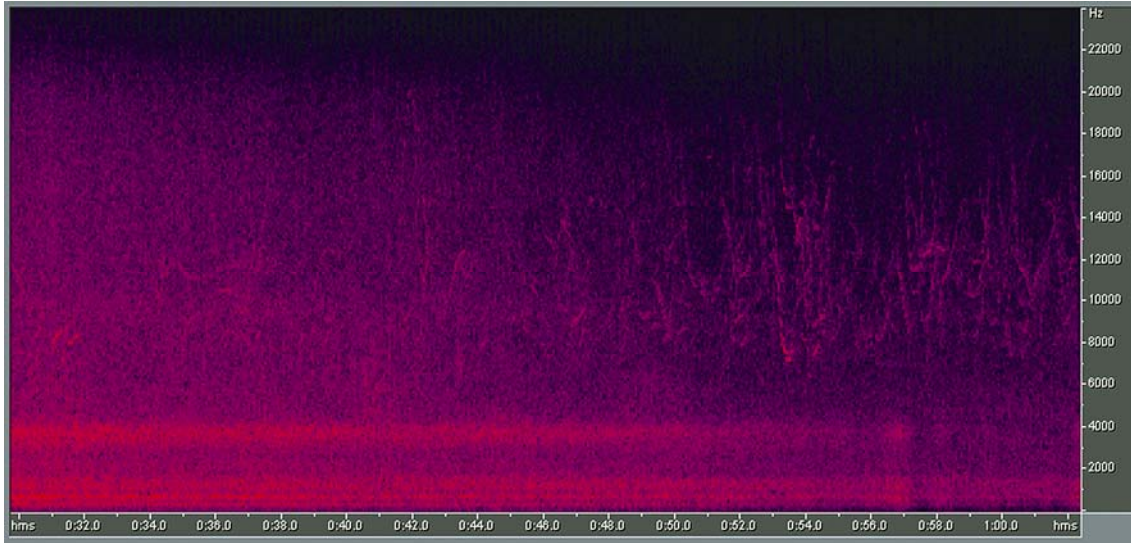


Figure 4.1. Adobe Audition spectrogram of continuous recording before and after the engine was turned off, illustrating masking effect.

Another inconsistency was the different upper bandwidth limits of Celtic Sea and English Channel recordings. These may have influenced the mean frequencies of the whistles recorded and the lower limit of the Celtic Sea equipment is likely to have cut off some whistles that had frequencies over 24 kHz. Oswald et al. (2004) showed that 8 % of the fundamental whistles of common dolphins recorded at 24 kHz upper bandwidth limit had components extending beyond this upper limit. Since this is only a small percentage of the whistles, standard DAT recorders with 24 kHz upper bandwidth limit are considered sufficient for general analyses of fundamental whistle characteristics (Oswald et al. 2004). However, if harmonic components are to be included in the analysis, a higher bandwidth limit would be necessary as these harmonics often extend far above 24 kHz, even as high as 100 kHz (Lammers et al. 2003). Even though they may have an important function in dolphin vocalisations (Lammers and Au, 2003; Lammers et al. 2003), harmonics were not considered in this study because of the limited frequency range recorded especially in the Celtic Sea data. Furthermore, the two different bandwidth limits between Celtic Sea and English Channel recordings would probably have introduced a much larger bias into the analysis of harmonics than it did for fundamentals which are mostly below 24 kHz.

A major problem with this as well as other acoustic studies of the whistle repertoire of dolphins is the lack of comparability and standardisation of methodology. This was a problem within this study (as discussed in the previous paragraph), and also between studies. Studies differ in the recording equipment used, the types of analyses carried out, the parameters measured and the subjective classification of whistle types. All of these influence the results and make them difficult to compare (Richardson et al. 1995; Bazúa-Durán and Au, 2002; Lammers et al. 2003; Oswald et al. 2004). Standard procedures clearly need to be developed.

5. Conclusion

5.1. Conclusions and Further Studies

Acoustic surveying techniques cannot fully replace traditional visual methods, mostly because group sizes of gregarious cetaceans cannot yet be accurately estimated from recordings alone. However, acoustic surveying greatly increases the chance of detection of cetaceans, especially in cases where they are at greater distances from the vessel or in smaller group sizes. Also, acoustic surveying can be used in bad weather conditions as well as at night, situations in which visual surveys are not possible or at least severely limited in their reliability. Ideally, a combination of visual and acoustic techniques should be used where logistically possible, to maximise survey efficiency and as a cross-validation of both techniques. More studies are needed to assess the relationship between whistle density and group size and to develop reliable methods of estimating group sizes based on acoustic data.

The whistle repertoire of short-beaked common dolphins in the Celtic Sea has been described in this study. Whistle characteristics varied between encounters, between behavioural contexts and between group sizes. Individual-specific variation in the form of signature whistles was observed but not considered to make up a majority of the vocalisations. Significant variation between encounters may be caused by the non-independence of data. Further methods to determine the vocalising individual within a group of dolphins need to be developed so that whistles can be related to individuals and using more than one whistle from each animal can be avoided. Also, standardised recording and analysis procedures are urgently needed to facilitate comparisons between studies.

Whistle characteristics of common dolphins in the Celtic Sea were significantly different from those in the English Channel. Most of this variation is found in frequency parameters which – though possibly slightly biased by different recording methodology –

imply geographic variation between the two sample sites. This variation is likely caused by adaptations to different ambient noise levels. Dolphins in the English Channel are exposed to high levels of low frequency ambient noise from vessel traffic and may have adapted to this by increasing the frequencies of their whistles to reduce masking. The consistent frequency variations support the hypothesis that the common dolphins in these two locations may be distinct populations. However, it could simply be the same population of dolphins responding to a different environment. Further studies of the genetic variation and the home ranges and inter-breeding between these two possible populations are needed to determine population status. If they are indeed separate populations then this has implications on the management strategies. In the western approaches to the English Channel area, where common dolphin abundance has been estimated at 9,708 animals (95% CI = 4,799-19,639; with potentially large bias caused by responsive movement by the animals), common dolphins experience high mortality rates caused by incidental catches in fishing gear (De Boer et al. 2005). These by-catch levels are large enough to pose a risk of local depletion of the species in this area, which is considered an important habitat during the winter season. This threat is particularly serious if they are in fact a distinct population (De Boer et al. 2005). Furthermore, the high levels of background noise that dolphins are exposed to in the English Channel are likely to have an impact on the animals' ability to echolocate and communicate, even if they are capable of adaptive responses such as shifting the frequencies of their sounds.

5.2. Summary of Findings

The following statements can be made based on the results of this study:

- Acoustic surveying can increase the chances of detecting common dolphins compared to visual surveys, especially in cases of smaller group sizes or where animals are at greater distance from the vessel.
- Recorded whistle density was significantly related to group size of common dolphins, however, this regression was not strong enough to provide reliable estimates of group sizes based on acoustic data.
- The whistle repertoire of short-beaked common dolphins in the Celtic Sea spanned fundamental frequencies from 3.56 kHz to 23.51 kHz with the majority of whistles between 9 and 15 kHz.
- Whistle durations of common dolphins in the Celtic Sea ranged from 0.05 to 2.02 seconds with a mean at 0.65 seconds and they had on average 0-1 inflections (mean: 0.64) and no steps (mean: 0.13).
- Upsweeps, followed by downsweeps were the most common whistle types of common dolphins in the Celtic Sea and the simpler sub-types with little further modulation were most frequent within each broad type.
- Whistle characteristics were significantly related to encounter, behaviour and group size.
- Signature whistles were observed for short-beaked common dolphins in the Celtic Sea, however they did not seem to account for a majority of the vocalisations.
- Whistle characteristics were significantly different between Celtic Sea and English Channel recordings, mostly caused by differences in frequency parameters which were consistently higher for English Channel whistles, implying possible geographic and/or interpopulation variation.
- The relative abundance of each whistle type was not significantly different between the two sampling locations.

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7. Appendix

7.1. Transect Line Waypoints for Celtic Sea Surveys

1) 16-17 May 2005:

51° 32' N, 005° 30' W to 51° 39.5' N, 006° 20' W to 51° 47' N, 005° 30' W to 51° 54.5' N, 006° 20' W to 52° 00' N, 005° 45' W

2) 22 June 2005:

51° 30' N, 006° 20' W to 51° 37.5' N, 005° 30' W to 51° 45' N, 006° 20' W to 51° 52.5' N, 005° 30' W to 52° 00' N, 006° 20' W

3) 13-14 July 2005:

51° 34' N, 006° 20' W to 51° 41.5' N, 005° 30' W to 51° 49' N, 006° 20' W to 51° 56.5' N, 005° 30' W to 52° 00' N, 006° 00' W

4) 16-17 August 2005:

51° 34' N, 005° 30' W to 51° 41.5' N, 006° 20' W to 51° 49' N, 005° 30' W to 51° 56.5' N, 006° 20' W to 52° 00' N, 005° 53' W

ACOUSTIC OBSERVER FORM

Date: _____ Start Time: _____ End Time: _____ Vessel: _____ Page: _____ of _____
 Hydrophone: _____ DAT: Mic / Line L / H Sp / Lp Rec Level:

#	Tape #	Start Time	End Time	Latitude & Longitude	Depth (m)	Start Dist (m)	End Dist (m)	Species	No. of Animals	Juv / Calves	Surface Behaviour	Comments
											For Trav Soc Bow	
											For Trav Soc Bow	
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CD-ROM Appendix

7.3. Characteristics and Examples of Whistle Types

7.4. Statistical Test Outputs

7.5. Raw Data