Variations in Whistle Characteristics of Bottlenose Dolphins (*Tursiops truncatus*) in Cardigan Bay, Wales.

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In Partial Fulfilment

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Master of Science

In

Marine Environmental Protection

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by

Katy Thompson

In Collaboration with

the Sea Watch Foundation

Declaration & Statements

This work has not previously been accepted in substance for any degree and is not being concurrently submitted for any degree.

This dissertation is being submitted in partial fulfilment of the requirement of M.Sc. Marine Environmental Protection.

This dissertation is the result of my own independent work / investigation, except where otherwise stated.

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Variations in Whistle Characteristics of Bottlenose Dolphins (*Tursiops truncatus*) in Cardigan Bay, Wales.

Abstract

Bottlenose dolphins have complex social structures which require a wide range of auditory communication. Whistles are long ranging vocalisations which vary within different social contexts. Whistle convergence has previously been seen in groups of strongly bonded individuals as a result of vocal mimicry, causing similarities in whistle characteristics such as frequency and whistle complexity variables. Other sources of whistle variation can be caused by behaviour and the environment. Whistles of the Cardigan Bay population were investigated by comparing whistles characteristics produced by different groups of dolphins both within and between dolphin groups. The variation was then correlated to behavioural and environment contexts. This was completed via *Ad libitum* and line transects surveys and subsequent multi and univariate analysis.

Whistle variation between groups was larger than within groups; this was attributed to shared whistle repertoires of different social groups. Frequency variables were responsible for the variation between groups whilst variation within groups was attributed to whistle complexity. Frequency characteristics of peak, maximum and minimum frequency increased in areas of increased boating activity, decreased depth and whilst in tighter group formations. The increased frequencies indicate increased excitement or distress due to the presence of boats, which may result in tighter group formations, in particular those with calves. Overall whistle rates were low which may also be resultant of high calf numbers in Cardigan Bay. Low whistle rates reduces the risk of adult male conspecifics locating calves and reduces energy costs for lactating females. In addition, the high familiarity between individuals of the sample area may indicate a large amount of vocalisation is not required. Despite the small dataset it can be concluded that whistle variation does occur in Cardigan Bay however increasing surveying effort will give a full representation of whistles of the dolphin population in the different environments within Cardigan Bay.

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List of Abbreviations

ANOVA	Analysis of Variance
ANOSIM	Analysis of Similarities
BEST	Bio-Env. and Stepwise Tests
CoV	Coefficient of Variants
dB	Decibels
EC	European Commission
EUNIS	European Nature Information System
kHz	Kilohertz
m	Metres
ms	Milliseconds
>	More Than
MDS	Multi- dimensional Scaling
%	Percent
PRIMER	Plymouth Routines in Multivariate Ecological Research
SAC	Special Area of Conservation
SIMPER	Similarity Percentages

1.0 Introduction

1.1 Background

The high intelligence of cetaceans, has allowed them to form complex fission-fusion societies which have varied social structures and relationships (Connor et al. 2000; Connor, 2007). The most studied odontocete species is the bottlenose dolphin (*Tursiops truncatus*), which lives in large, changeable groups. Small groups split off from the larger population in order to feed, mate and socialise (Connor, 2007). These smaller groups comprise of similar aged and sexed individuals or mother - calf pairs, and can last from months to years, thus forming strong individual relationships (Shane *et* al. 1986; Sayigh *et* al. 1990). A result of this complex social structure is the high level of communication, which develops in the form of both visual and auditory signals. Auditory communication is the most efficient, as it can be used over larger distances (Janik, 2000). In addition the amount of information carried by vocalisations is higher than that of visual cues with information being conveyed via variation in vocalisation characteristics, the decibel level and prosodic features (Herzing, 1996)

1.2 Types of Vocalisations

Bottlenose dolphin vocalisations can be classified into three main types: burst pulsed clicks, echolocation clicks trains, and tonal whistles. Burst pulsed clicks are broadband signals of approximately 50μs, with frequencies varying from 2->200 kHz. As a result, they have low directionality and are therefore associated with social behaviour as a means to convey emotive information (Lammers, *et* al. 2003). Emotive communication can come in the form of buzzes, such as the genital buzz in which an individual is buzzed around the genital region during mating or when disciplining calves. Such communication can also come in the form of squawks during aggressive behaviour (Herzing, 1996). By comparison echolocation clicks are used to locate prey and for navigation purposes. High levels of information are conveyed by creating longer interclick intervals, in order to allow interpretation of the signal (Au, 1993). Echolocation click trains are high frequency broadband clicks which travel long distances and can distinguish small details of objects. As a result they are most prominently used in hunting pelagic fish and squid species, rather than for communication between conspecifics (Au, 1993). These clicks are transmitted from the dolphin as sound beams into the water column. The sound beams rebound off objects such as target prey species, returning to the dolphin as echoes which the animal then processes (Au, 2009). The time taken for the click to return and the strength of the signal delivers information on the objects location, size and additional environmental data (Au, 2009). The amount of background noise, the objects size and range, and whether the aim is to discriminate or detect the target can cause the dolphin to change characteristics of the click train such as the rate, amplitude and waveform (Au, 1993; Au, 2009).

By comparison to clicks, whistles are longer ranging vocalisations which are split into two groups: variant whistles and signature whistles (May-Collado and Wartzok, 2008). Variant whistles are used during activities when higher levels of synchronisation are required, such as during travelling and foraging. This has been demonstrated with groups of dolphins showing a wider range of harmonics and higher amplitudes of whistles when moving towards prey rather than away (Lammers and Au, 2003). The high directionality of whistles makes them ideal for group synchronisation as they convey information on group positions and direction over large distances. In comparison signature whistles are unique whistles developed by individuals in order to identify themselves to others within the group (Tyack, 1986). Such whistles are repeated regularly within the group and can be mimicked by conspecifics indicating conscious communication with specific individuals (Reiss, *et* al. 1997). This mimicking behaviour has most often been seen between mother calf pairs in order for the calf to recognise their mothers call (Reiss, *et* al. 1997).

1.3 Whistle Variation

Whistles range in frequency from 1-32 kHz, and have decibel levels of 125 - >140 dB. In addition they have harmonics which occur at multiples of the fundamental frequency (Caldwell, *et al.* 1990; Lammers, *et al.* 2003). Whistles are therefore classed as continuous narrow banded tonal sounds, produced by changes in sound waves of sinusoidal signals (Lammers, *et al.* 2003). Whistles can vary in frequency characteristics (kHz) such as start frequency, end frequency, minimum frequency, maximum frequency, frequency range and peak frequency. The whistle complexity comprises duration (ms) and the number of inflection points, defined as the point at which the slope of the whistle changes direction (i.e. modulation) (Caldwell, et al. 1990; Au, 2000). Frequency variables and whistle complexity characterise whistles and are incorporated in the whistle contour, which is defined as the change in peak frequency over time (Caldwell, et al. 1990). Whistle contours can be categorised as multi point (more than one inflection point), ascending-descending, ascending (upward sweep), descending (downward sweep), descending-ascending and constant (Azevedo, *et al.* 2007) (Figure.1).

The frequent use of different types of whistles varies between individuals and populations, as demonstrated between populations in Portugal and South America. The majority of whistles from the Portuguese population were upsweep in contrast to the down sweep or balanced whistles found in populations in South America (dos Santos, *et al*. 2005; Azevedo, *et al.*2007). Whistle characteristics can also vary between conspecifics as shown in the large level of variation around the average whistle duration in a resident population in Portugal where the average whistle duration was 553.3ms with a large standard error of 393.9ms (Azevedo, *et al.*2007).

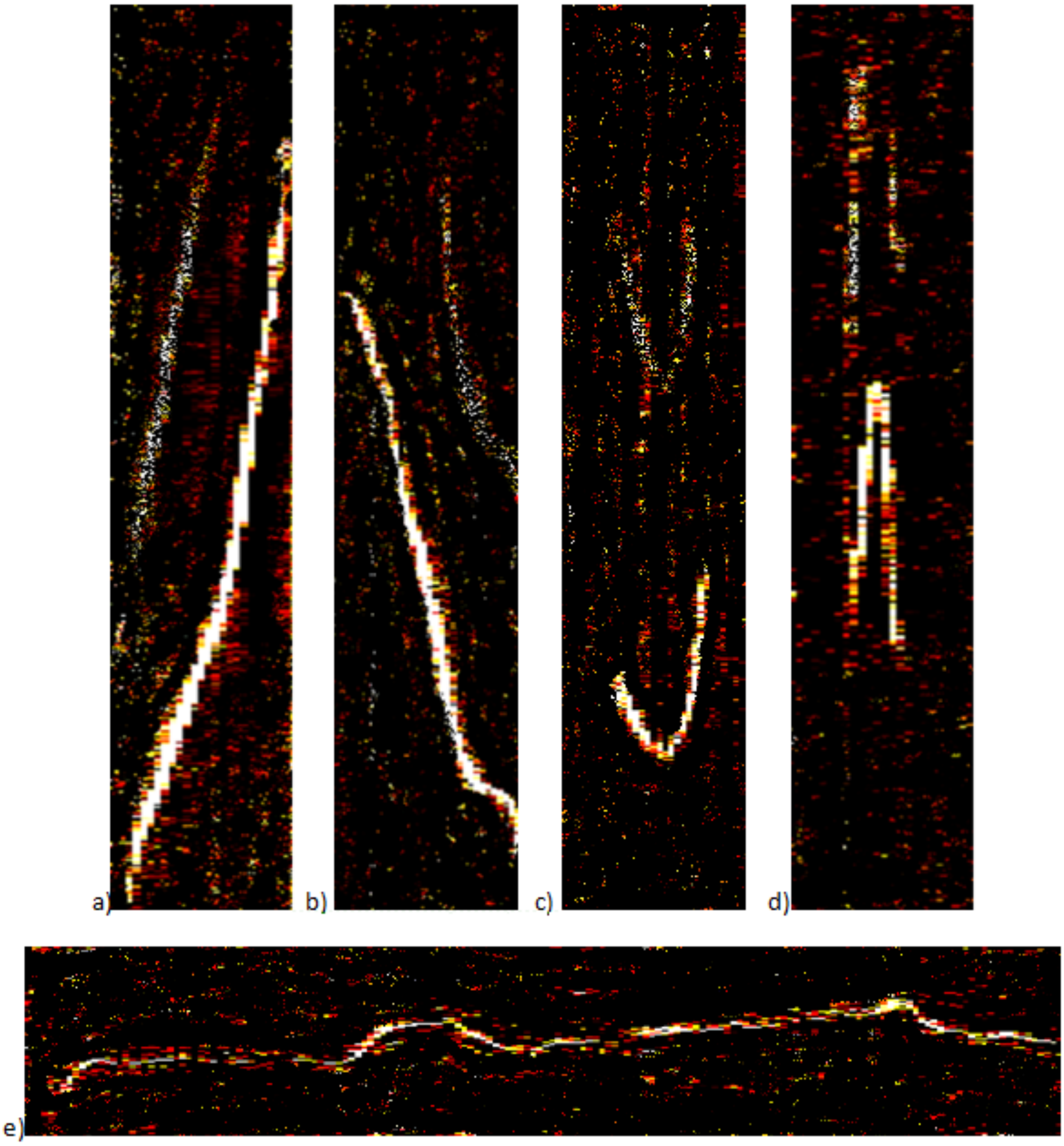

Figure 1*: Spectrogram from the Ishmael software of the different types of whistles and their harmonics a) Upsweep b) Down sweep c) Descending-ascending d) Ascending –descending e) Multipoint*

1.3.1 Whistle Variation in Response to Behaviour

Variation in vocalisations can occur in response to the type of activity being undertaken, with feeding and socialising showing the largest variation (dos Santos, *et al.* 2005). Variation in vocalisations whilst feeding is suspected to be a result of the increased group coordination that is required. Whilst during socialising the combining of various social alliances each with a set whistle repertoire increases the range of whistles produced (Smolker and Pepper, 1999). The rate at which whistles are produced can also vary in response to behaviour, group size, community composition and the environment. Average whistle rates of individuals in a bottlenose dolphin population in South America increased from 0.28 per minute to 0.45 per minute during surface feeding (dos Santos, *et al*. 2005). Such increases in whistle rates can again be explained by the need for increased cohesion whilst feeding on mobile prey. The increase in error demonstrates individual variation in whistle production, as not all group members will vocalise. Such a strategy decreases the chance of confusion through the overlapping of whistles (dos Santos, *et al*. 2005). Quick and Janik (2008) found that whistles rates peaked for group sizes of 16-30 individuals, after which vocalisations decreased. Whistle rates were lowest whilst travelling; this is perhaps a way of conserving energy when vocalisations are not necessary, especially when travelling in tight formations. Furthermore, quiet travelling may increase the detection of predators, prey, boats and other dolphin groups (dos Santos and Almada, 2004). The highest whistle rates were observed during non-polarised movement (dolphins not moving in the same direction or in formation), with rates peaking at group sizes of 11-15 individuals. In contrast, whistle rates whilst socialising were much higher within smaller group sizes and rapidly decreased with increased group size. This may have been a result of the majority of social interactions occurring within a few individuals (Quick and Janik, 2008). On average whistle rates during socialising were reduced compared to other activities, which could be in part due to the use of burst-pulsed clicks for communication in social contexts thereby reducing the need to produce whistles (Herzing, 1996). The use of prosodic features of sound such as rhythm, silence and intensity in social situations will also contribute to the reduction in the amount of whistles whilst socialising (Herzing, 1996).

1.3.2 Group Whistles

Groups of bottlenose dolphins that are geographically separated are expected to have different whistle characteristics, in accordance with varying environmental conditions and different social settings. This is demonstrated in populations along the Texas coastline which displayed larger differences in whistle structure between those populations which were farther apart (Ding, *et al.* 1995). Differing environmental conditions at the different locations may be the cause of such large variation in whistles. Higher frequencies, longer durations and a greater number of inflections are associated with areas of higher anthropogenic background noise (Wang, *et al.* 1995). Environmental aspects including depth, sediment and habitat can also influence whistles as a result of differing foraging methods. Dolphins in deep-water environments which hunt pelagic prey require larger groups of dolphins which in turn necessitate the increased numbers of whistles to co-ordinate the group (Ingram and Rogan, 2002). In other environments the water visibility may be low therefore an increase in whistle production enables animals to keep in touch with conspecifics and also them to navigate (Fertl and Wursig, 1995). Variation in whistles characteristics has also been observed in groups of bottlenose dolphins of differing group compositions within the same geographic region (McGowan *et al*. 1998). Groups of similarly sexed or aged individuals (alliances) have been shown to share whistles repertoires through vocal mimicry. Such behaviour has been observed in male alliances in Australia, with a group of three males showing increased strength of social bonds as they matured, in addition to their whistles converging. Convergence was to such an extent that individuals could no longer be recognised from their vocalisations (Smolker and Pepper, 1999). Such convergence of whistles allows for the identification of groups based on the group's repertoire. However there has yet to be sufficient investigations on the extent of variation in whistles, between and within social groups of the same population, including the factors which contribute to any such variation. Future investigations will also have to incorporate the role of signature whistles in group variance in wild bottlenose dolphins.

1.4 Signature Whistles

Signature whistles are unique individual whistles, emitted at frequencies between 7-15 kHz with durations of less than one second (Tyack, 1986). Whistles are frequency modulated (i.e. varying in frequency but with constant amplitude) which allows signature whistles to convey enough information for individual dolphins to correctly identify the producer without the use of voice features such as e.g. rhythm and intonation (Janik, *et al*. 2006). This means that dolphins are able to recognise an individual's whistles rather than discriminating between the whistle characteristics, meaning whistles can be used to either address or relate to individuals (Janik, *et al*. 2006). The development of a signature whistle occurs during the first year of life with calves as young as a month old exhibiting them (Tyack, 1986). This development is acquired by imitation and learning rather than genetic transmission, with calves modelling their signature whistles on whistles of their conspecifics, modifying them to make their own version (Janik, 2000; Janik, *et al.* 2006). Differences occur between the sexes of the calves, with male calves having similar signature whistles to their mothers in contrast to female calves whose whistles are dissimilar (Sayligh, *et al.* 1990). This is due to females often associating with their mothers once maturity is reached, therefore by having a different whistle from their mothers confusion may be prevented (Fripp, *et al.* 2005). Calves have also been observed to model their whistles on unfamiliar individuals in order to avoid confusion between the individuals that it associates most with (Fripp, *et al*. 2005).

Signature whistles are distinguished as the fundamental frequency of the whistle contour, which is usually the lowest frequency contour and the strongest element of the whistle (Abbott, 2009). The variation in the production of signature whistles comes in the form of intensity and rate in accordance with changes in behaviour (Caldwell, *et al.* 1990; Smolker, *et al.* 1993). Variation in signature whistle production has been observed when different social groups congregate allowing individual identification to occur (Janik, *et al*. 2006). Mimicry of signature whistles occurs during these gatherings (Janik, *et al*. 2006). Dolphins are able to imitate new sounds correctly even at their first attempt and can adopt features of different whistles (Janik, 2000). As a result signature whistles of different dolphins can be found in various group repertoires (Janik, 2000). Large numbers of signature whistles have previously been recorded when dolphins are out of sight of each other, confirming that they are used for group cohesion and identification (Janik, 2000). Other uses of signature whistles come in the form of mother-calf reunions, the mother produces continuous series of 2-124 whistles (dependant on the distance of the calf) separated by an interval of less than a minute. This behaviour occurs when the calf moves too far away or a threat is perceived (Smolker, *et al*. 1993; Herzing, 1996). In addition signature whistles are repeatedly emitted by female and male dolphins during courtship and mating activities (Herzing, 1996). Variation in the production of signature whistles by different bottlenose dolphin populations may also be a result of the level of stress a population or individual is under. Dolphins found in high stress areas, when contacting conspecifics is important, produce more signature whistles compared with those in low stress environments. (Smolker and Pepper, 1999). The different use of signature whistles and their importance remains to be fully understood, due to their production varying with populations and settings. In addition, the majority of experiments with signature whistles have been carried out on captive dolphins which cannot be comparable to wild dolphins.

1.5 Cardigan Bay Population

Cardigan Bay holds the largest population of bottlenose dolphins in the United Kingdom, with between 200 and 300 individuals using the Bay in any one year (Baines, *et al.* 2002; Pesante, *et al*. 2008; Veneruso and Evans, 2012). Seasonal migration occurs in the winter months with 57% of the dolphins in Cardigan Bay moving to northern waters such as those around Anglesey, the Isle of Man and Liverpool Bay. Longer termed movements out of Cardigan Bay occur for 42% of the population, with 80% of migrating individuals not returning the following year (Pesante, *et al.* 2008; Veneruso and Evans, 2012). Reasons for such migration may relate to the seasonal availability of food, with different prey types present at different times of the year, in addition to life history needs. Such regular migration means that the Cardigan Bay population can be described as open, with a meta-population showing strong site fidelity, in addition to transient individuals joining the population each summer (Pesante, *et al.* 2008; Feingold, *et al*. 2011; Veneruso and Evans, 2012).

Cardigan Bay has a high proportion of calf sightings indicating it is used, at least in part, as a nursery area. This could account for the strong site fidelity of some individuals, and also for the influx of others in the summer months, with calving occurring mainly between April and September (Veneruso and Evans, 2012). Mother and calf pairs are annually observed year round in the Bay due it being a shallow bay which allows mothers to forage whilst their calf accompanies them in addition to the reliable food source of benthic and demersal fish (Bristow and Rees, 2001; Gregory and Rowden, 2001) Mother-calf pairs often associate with other mother-calf pairs or female and young males. 82 % of dolphin groups in Cardigan Bay were made up of less than six individuals, with the same composition of individuals being observed on numerous surveys (Bristow and Rees, 2001; Feingold and Evans, 2012). This indicates strong bonds are formed within social groups. A select few individuals were observed to have a major role in the social structure associating with a wide range of individuals, whilst others were only connected to a small group of individuals (Pesante, *et al.* 2008). Feeding efforts are concentrated in shallow waters around headlands, small embayment's and river mouths due to aggregations of fish in those areas (Lewis and Evans, 1993; Baines, *et al.* 2000; Evans, *et al.* 2001). Feeding activity has also been seen to be concentrated in the mornings and early evening with socialising and travelling occurring between foraging events (Gregory and Rowden, 2001; Pesante, *et al.* 2008). The food prey in the summer months occurs in the form of small shoals of fish or solitary benthic species, and therefore there is not the need for larger groups whilst foraging.

Whistle vocalisation in Cardigan Bay is expected to be variable due to smaller social groups converging in the summer months each having their own repertoire. However similarities are also expected as these social groups mix throughout the year as part of the wider dolphin community. As in other dolphin populations, whistle variation is expected to be affected by environmental and social factors including activity, group composition, depth, habitat type and boat activity. Studies have yet to analyse the whistles of the Cardigan Bay population which would help in determining associative individuals, aid in collecting abundance data even when dolphins are out of sight, determine important habitats for dolphins and the reasons for this importance in addition to determining whether anthropogenic activities such as the large number of tourist boats affect the resident population.

1.6 Aim and Objectives

The aim of this study is to determine the level of variation in whistle characteristics of the Cardigan Bay bottlenose dolphin population both within and between groups, relating any variation to social and environmental characteristics. This aim will be addressed through: 1) statistically comparing whistles produced by different groups of dolphins both within the group and between different groups and 2) correlating the use of whistles and their characteristics to visual observations of dolphin behaviour and the natural environment. To achieve those objectives, the following hypotheses will be tested:

H^1 Whistle characteristics will vary in characteristics in the form of rate, duration, inflection points and frequency parameters within and between groups of bottlenose dolphins in Cardigan Bay. The variation is expected to be greater between rather than within groups.

H^2 Bottlenose dolphins in Cardigan Bay will exhibit signature whistles which will vary in characteristics, in the form of rate, duration, inflection points and frequency parameters between individuals.

H^3 Variation in whistle characteristics will be the result of different behaviours and different environmental factors.

2.0 Methods

2.1 Study Area

Cardigan Bay is a large bay located on the west coast of Wales (52.4667 °N, 004.1500 °W). There are two designated Special Areas of Conservation (SACs); the Pen Llyn a'r Sarnau SAC is located in the north of the Bay stretching from Aberystwyth to Porth-Madog and the Cardigan Bay SAC in the south stretches from Aberaeron to Cardigan (Figure. 2). This designation is for Annex I habitats and/or Annex II species, including the bottlenose dolphins (*Tursiops truncatus*), grey seals (*Halichoerus grypus*), harbour porpoise (*Phocoena phocoena*) and two species of lamprey under the 1992 EC Habitats Directive. Habitats within the SAC's which are safeguarded include sea caves, rocky reefs and sandbanks.

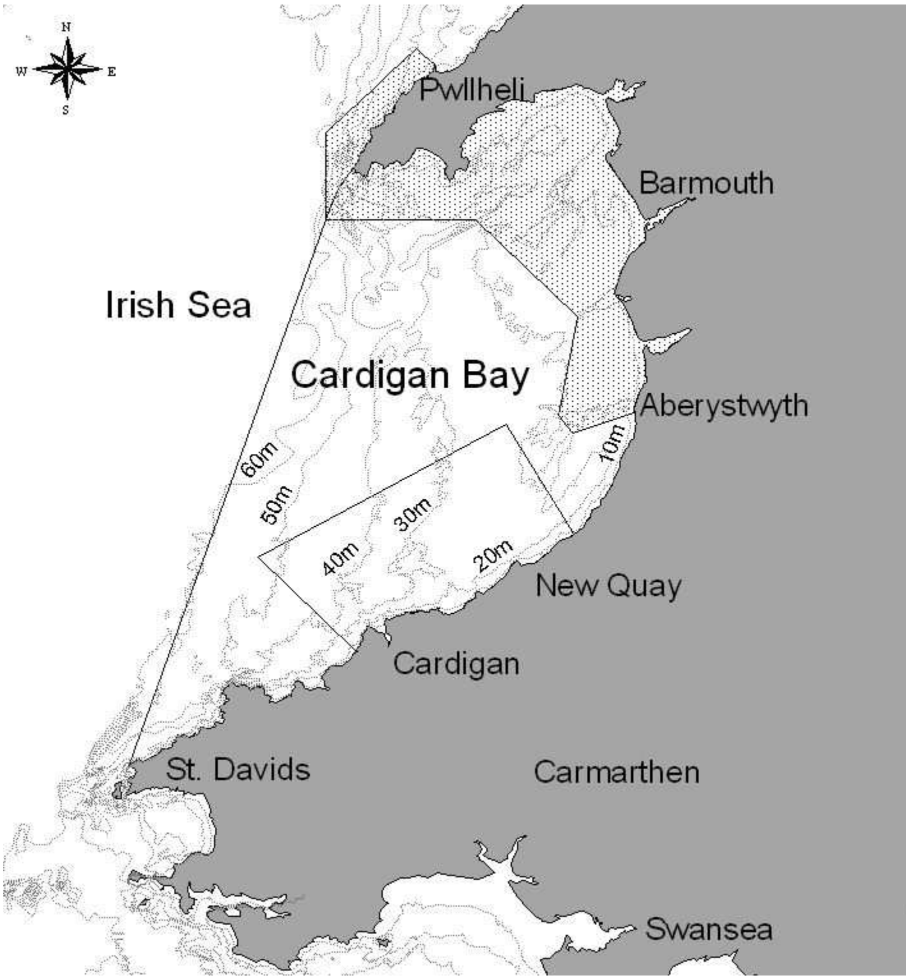

Figure 2: *A map of Cardigan Bay with the boundary for the bay marked by the line on the left. The rectangle is the Cardigan Bay SAC and the hatched polygon is the Pen Llyn a'r Sarnau SAC (*Pesante, *et al*. 2008).

2.2 Data Collection

Whistle and behavioural data was collected under similar weather conditions (Beaufort sea states <4) using a mixture of line transect and *Ad libitum* surveys on a variety of small motor boats. Once dolphins were within 100m of the boat the hydrophone was placed in the water and the recorder was set to record the underwater noise which was stored as a WAVE audio file. During the encounter the recordings were monitored via headphones and were later transferred to the acoustics software Ishmael. The recording system used consisted of a C55RS hydrophone with a linear frequency range of 0.020-50&124-250+ kHz, useable frequency range of 0.009-77 & 96-250+ kHz and a transducer sensitivity of -200 dB re 1V/µpa, as well as an Olympus L5-11 EU recorder which had a sampling rate of 96 kHz (Figure 3). Where possible the engine was turned off whilst recording in order to reduce background noise. However, some sampling was undertaken whilst on Sea Watch line transect surveys and therefore the opportunity to turn the engine off was limited. In addition, during the encounter, the dolphins travelled in varying directions therefore, in order to record the most whistles, the boat had to move to stay with them. During acoustic data collection three minute behaviour samples were recorded including: group composition, group size, behaviour, geographic position, time, group formation, directionality, whether there were other groups of dolphins in sight, distance of the dolphin group to the boat and surfacing mode.

Photo identification was also collected on board in order to identify the individuals in the dolphin group. Individual bottlenose dolphins can be recognised by the shape of the fin, distinctive pigmentation or scars and in particular missing parts such as nicks, notches or natural deformities found in the trailing edge of the dorsal fin. These markings occur as a result of interactions with conspecifics, predators or vessels and are unique to the individual. Photographs were taken perpendicular to the fin and at close range (<40 m), in order for the characteristics to be highly visible. The aim was to photograph each individual at least five times, making sure both the left and right side of the fins were photographed. These photographs were then compared to previously taken images within Sea Watch's Photo – ID catalogue (Feingold and Evans, 2012) in order to identify each particular individual. A total of 13 surveys (Table 1) were carried out in Cardigan Bay with the majority of the effort being concentrated near New Quay due to the combination of the lack of boat availability from other harbours and bad weather conditions.

Table 1: *The date and time spent recording per survey*

Survey	***Date***	***Time Spent Recording (hh:mm:ss)***
1	29/05/12	00:26:55
2	11/06/12	00:19:29
3	12/06/12	00:37:44
4	13/06/12	00:06:13
5	18/06/12	01:16:16
6	05/07/12	00:21:01
7	09/07/12	00:11:26
8	12/07/12	00:11:33
9	21/07/12	00:14:22
10	24/07/12	00:22:04
11	25/07/12	00:17:47
12	26/07/12	00:41:44
13	19/08/12	00:34:10

In order for signature whistles to be recorded, a parabolic reflector and a pole were attached to the hydrophone allowing us to direct it towards specific individuals. Recordings of signature whistles had to be completed with the engine off and in close proximity to the person completing the photo ID in order for the correct individual to be identified whilst it was vocalising, therefore sampling could only be carried out on Sea Watch's rib, *Gallois*. In addition, forms recording behaviour were also completed at the same time as whistle recordings were being taken.

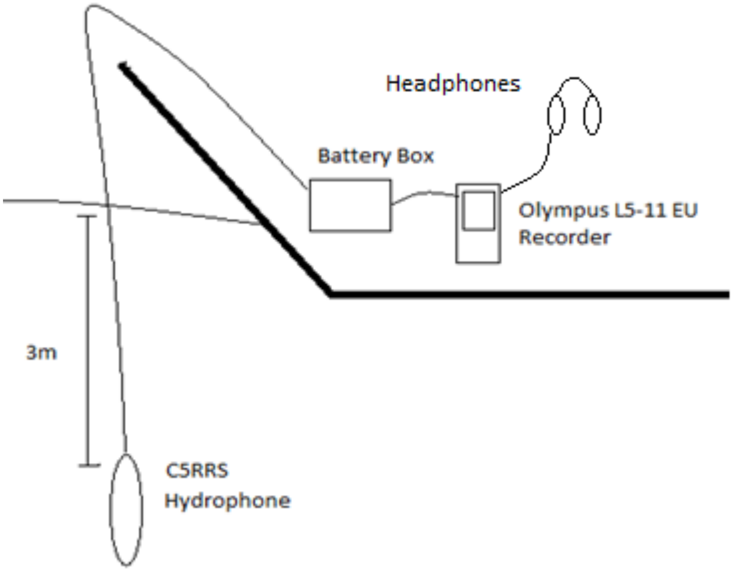

Figure 3: *A diagram of the equipment set-up when on a survey boat.*

2.3 Data Analysis

2.3.1 Whistle classification

Whistle classification was completed using the software Ishmael (Mellinger, 2001). Sound files were displayed as a spectrogram in a Hamming window of 512 frame size, within a frequency range of 0-24 kHz. The display frame duration was set at 0.56 sec/cm, pausing the recording at the end of the screen thereby measurements can be taken over frequency and time. The contour of the whistles and the number of inflection points was identified by visual observation, whilst the whistle characteristics in the form of start frequency (kHz), end frequency (kHz), maximum frequency (kHz), minimum frequency (kHz), peak frequency (kHz), and duration (ms) was produced by Ishmael. The whistles were classified into ascending (whistles rising in frequency), descending (whistles falling in frequency), multi – point (multiple changes in direction), ascending-descending (initial rising in frequency followed by one inflection point, then falling in frequency) and descending-ascending (initial falling in frequency followed by one inflection point then rising in frequency).

2.3.2 Statistical Analysis

2.3.2.1 Hypothesis 1

PRIMER v.6 (Plymouth Routines in Multivariate Ecological Research) was used in order to compare whistles between and within dolphin groups (Clarke and Gorley, 2006). However due to the large variability in the number of whistles recorded per group, five whistles from each group were randomly selected for analysis. Encounter no. 43 only had one whistle recorded and therefore was not involved in the analysis as this would skew the results. The data was transformed in PRIMER using square roots to normalise the data, and a Bray-Curtis resemblance matrix was created to maintain the invariance within the data (Clarke and Ainsworth, 1993). An MDS (Multidimensional Scaling) plot was created with this matrix in addition to an ANOSIM (Analysis of Similarities) test to determine the differences and similarities within the samples. An additional MDS plot was created excluding whistle no. 392 in order to show the spread of data more clearly. Subsequent univariate analysis was completed for each whistle characteristic in order for a value judgement to be attached to the general response found in the ANOSIM result (Warwick and Clarke, 1991). Each whistle characteristic was tested by the Levene's test for homogeneity; these were subsequently tested for between and within group variance. The characteristics which passed the test for homogeneity were then tested in an ANOVA *t* test (Analysis of Variance) whilst the variables that did not pass, were tested via a non-parametric Kruskal-Wallis test. Any significant results were tested via a post hoc Tukey test to determine where differences between encounters occurred. The resemblance matrix was also used to undertake a SIMPER analysis in order to show the top whistle characteristic contributing to the similarity and dissimilarity between and within groups. The top three characteristics contributing more than or equal to 15% to the total cumulative dissimilarity between encounters were all processed in univariate tests. In addition, the coefficient of variation was calculated for each frequency characteristic for each encounter in order to show the level of variation within the data.

2.3.2.2 Hypothesis 2

Due to the difficulty of successfully collecting signature whistle data, only one specific whistle from an individual male was collected and therefore no statistical analysis could be undertaken. Therefore, unfortunately, Hypothesis 2 could not be tested.

2.3.2.3 Hypothesis 3

The environmental data on depth (m), habitat type, boat activity, behaviour, group formation, group size and group composition were correlated to the whistle variation using a BEST analysis. This was completed in PRIMER to determine which environmental factor contributes most to the variation within groups (Clarke and Gorley, 2006). The factors which had the highest correlation were tested against the whistle characteristics produced from the SIMPER analysis (as explained above in section 2.3.2.1) using univariate analysis. The characteristics which passed the Levene's test of homogeneity were subsequently tested via an ANOVA, whilst the characteristics which did not pass, were tested via a Kruskal-Wallis test. Any significant results were tested via either a post-hoc Tukey test or Mann- Whitney U test to determine for which environmental factor, the whistle characteristic varied the most. Whistle rates and whistle types were also tested against each environmental factor via univariate tests of either ANOVA or a Kruskal-Wallis, with significant results being post hoc tested in order for the greatest difference between variables to be shown.

3.0 Results

A total of 22 dolphin encounters occurred over the two month study period, 17 of which had recorded whistles. From these 17 encounters, there were a total of 402 whistles recorded yielding an average number of whistles per encounter of 22.3. The number of whistles produced per group varied from no whistles being recorded to 77 whistles (Figure 4). The total recording time was 420 minutes, resulting in an average whistle rate for the whole sample of 1.05 whistles per minute. Group sizes sampled ranged from single individuals to groups of 22 individuals (Figure 5). The total number of different identified individuals sighted was 65, with another 48 individuals being sighted which were unidentified (did not match any records in Sea Watches Photo ID catalogue). There was no relationship between group size and the rate of whistles (Figure 6); the high levels of variance around the mean suggest that the production of whistles changes but this change is not dependent upon group size. Varying types of behaviour were also observed with the most common being travelling, feeding and socialising. Other behaviours such as bow riding and percussive and aerial displays were less frequent.

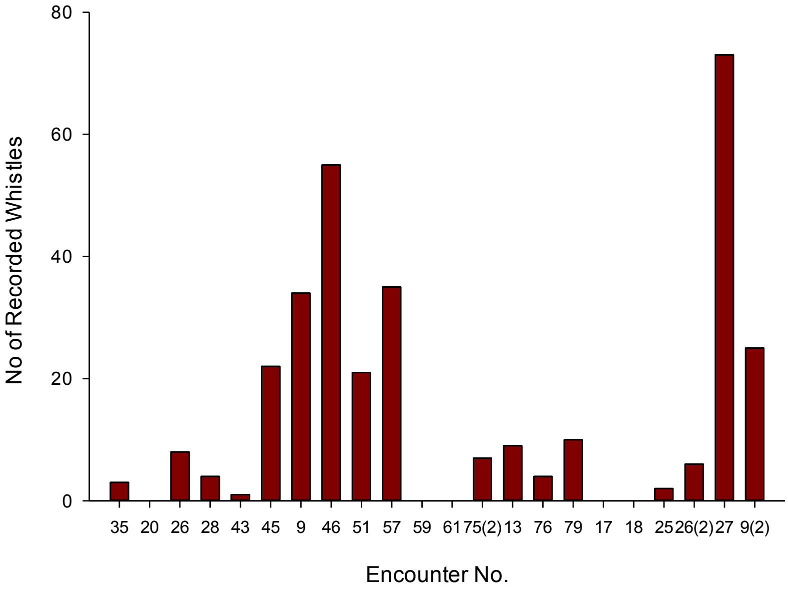

Figure 4: *Total number of recorded whistles at each dolphin encounter*

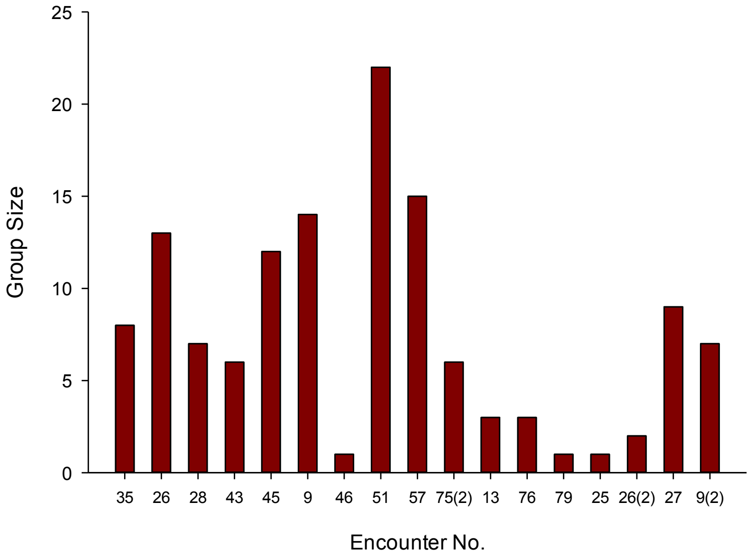

Figure 5: *Total number of individuals sighted at each dolphin encounter.*

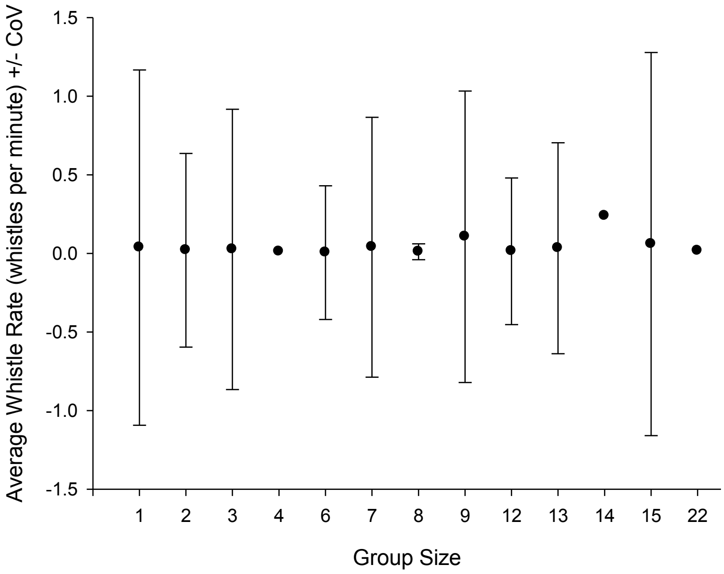

Figure 6: *The average whistle rates for each group size observed ± coefficient of variation*

Average whistles characteristics ± coefficient of variation for the whole data set were as follows; start frequency 8.28±0.38 kHz, end frequency 11.03±0.34 kHz, frequency range 4.59±0.58 kHz, minimum frequency 7.42±0.32 kHz, maximum frequency 12.002±0.28 kHz, peak frequency 9.63±0.48 kHz, duration 0.61±0.74 seconds and number of inflection points 0.69±1.3. Such frequency variables vary between the encounters, with the greatest variation in the whistle duration and no. of inflection points. This is especially seen in encounter no. 26(2) for whistle duration and throughout all encounters for the number of inflection points (Figure 7). The average start frequency for most encounters was higher than the average end frequency, constituting a majority of whistles (53.8%) being classed as ascending. Descending whistles were the second most common contributing 20.5%, followed by multipoint (10.9%), descending-ascending (9.1%) and ascending – descending (5.7%) (Figure 8). The type of whistle shows a significant difference between encounters, with encounter no. 28 contributing most to the difference (Table 2).

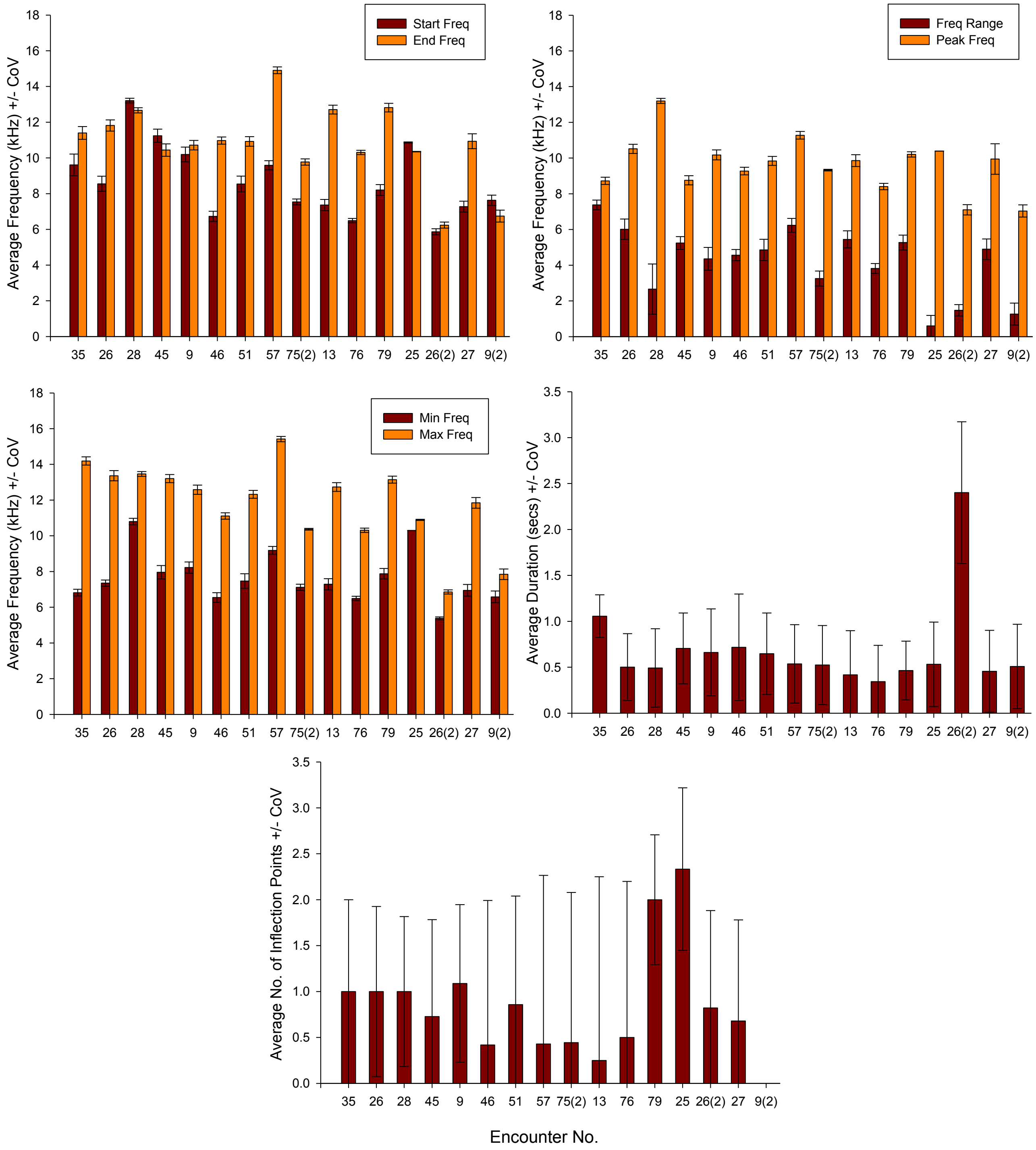

Figure 7: *Average whistle characteristics for each dolphin encounter ± coefficient of variation.*

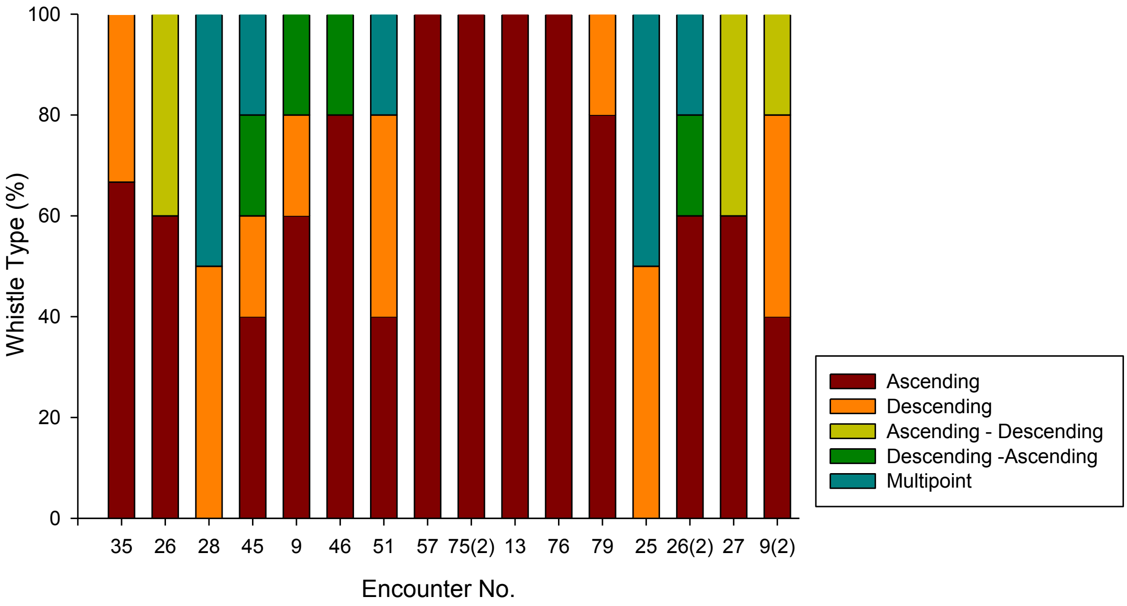

Figure 8*: The percentage of the occurrence of different classifications of whistles during each dolphin encounter.*

Table 2*: Kruskal-Wallis results table testing whistle types between the encounters in addition to the significant results from post hoc Mann Whitney U tests for each encounter.*

Variable	***df***	***Chi²***	***p***
Whistle Types	15	26.138	0.037
Encounter		***U***	***p***
28 v 57		0	0.016
28 v 75		0	0.016
28 v 13		0	0.016
28 v 76		0	0.029

3.1 Whistle Variation Between and Within Dolphin Groups.

Multivariate analysis demonstrated that the whistle characteristics of different dolphin groups showed similarities (ANOSIM: R^2: 0.32 p: 0.01). This is supported by Figure 9 where there is no significant grouping between encounters.

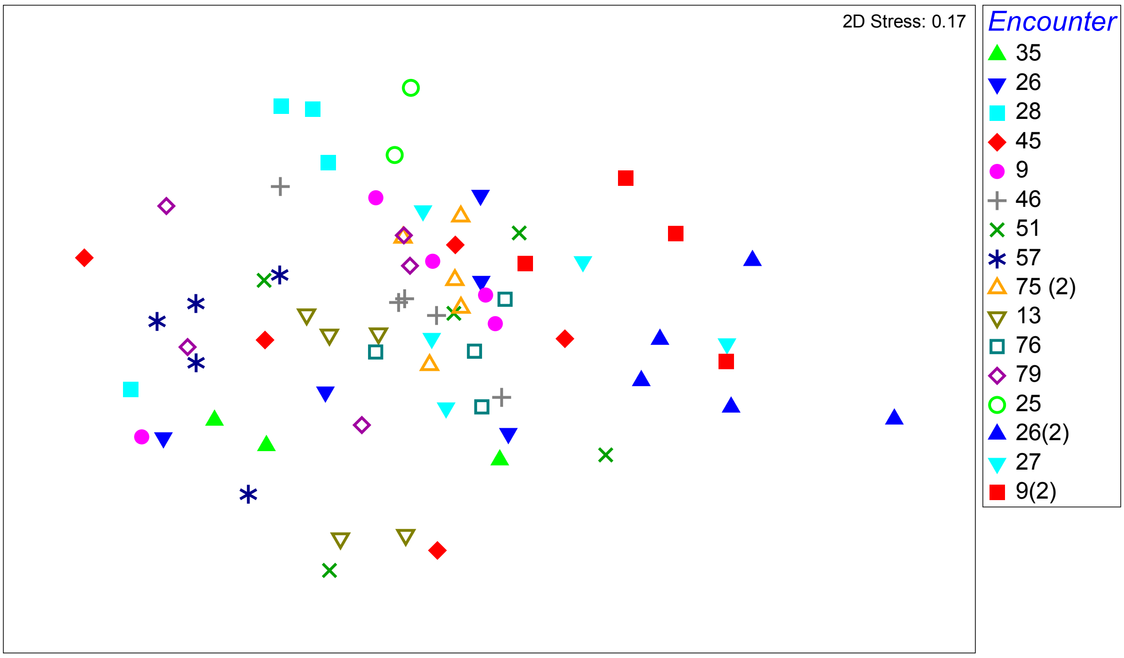

Figure 9: *MDS plot of individual whistles based on whistle characteristics excluding whistle 392, each symbol represents a different dolphin encounter.*

Univariate analysis revealed each whistle variable showed significant differences between the different encounters, with the exception of start frequency and the number of inflection points (Table 3). Peak frequency, duration and maximum frequency showed the strongest significant difference. Such results are supported by a SIMPER analysis with peak frequency (23.3 %), minimum frequency (21.6 %), and maximum frequency (15 %) proving to contribute most to the dissimilarity between groups with frequency range (2.5 %) contributing the least.

Table 3: *Univariate results for each whistle characteristic tested against each encounter.*

ANOVA	***df***	***MS***	***F***	***p***
Minimum Frequency	15, 57	9.682	2.719	0.003
Peak Frequency	15, 57	18.117	4.105	<0.001
Duration (log10)	15, 57	0.156	3.878	<0.001
Kruskal-Wallis	***df***	***Chi Squared***		***p***
Start Frequency	8	11.071		0.198
End Frequency	8	20.926		0.007
Frequency Range	8	20.870		0.007
Maximum Frequency	8	24.015		0.002
No. of Inflections	8	8.279		0.407

The F values for the ANOVA analysis showed that there is more variation between groups than within groups (Table 3). Analysis for non-parametric tests in the form of Chi-squared values suggests there are differences in the median values between groups (Table 3).

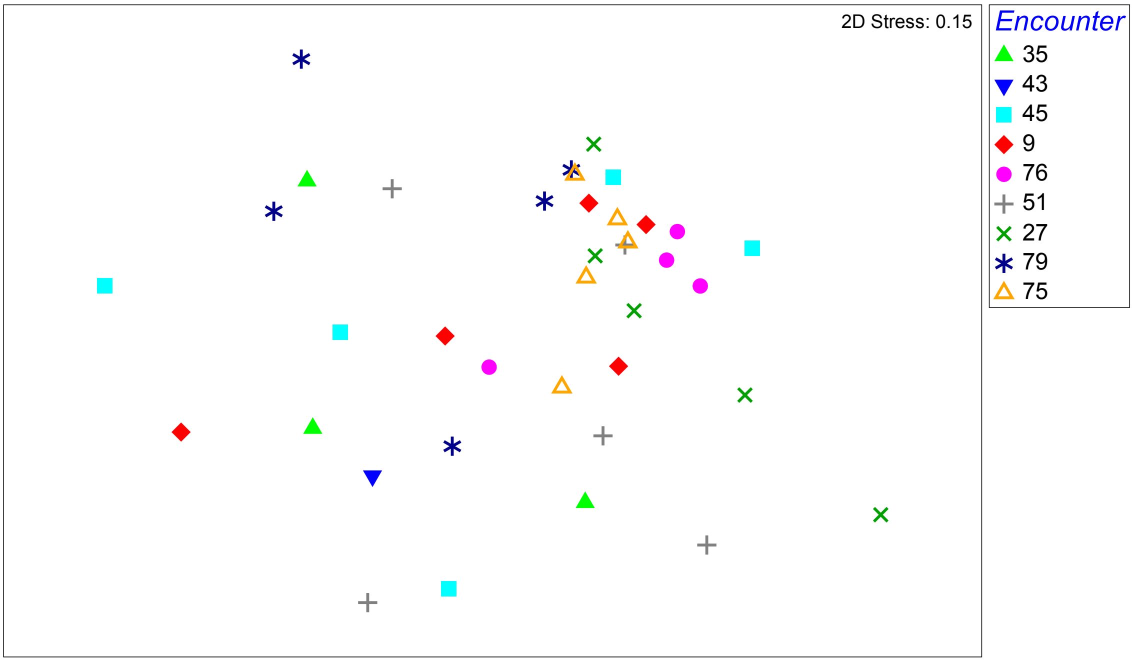

Figure 10*: MDS plot of whistles from encounters which shared individual dolphins.*

The number of shared individuals between different encounter is low, with only 1 or 2 individuals being shared between certain encounters (Table 4). As a result there is a lack of grouping of encounters with shared individuals (Figure 10).

Table 4*: The dolphin encounters that shared individual dolphins and the number of shared individuals.*

Encounter	*No of Shared Individuals*
35; 43	2
35; 45; 9	1
45; 9	2
76; 27	1
35; 26	1
51; 27	2
79; 27	1
75; 51; 76	1
75; 76	1

3.2 Whistle Variation within Different Environmental and Social Settings.

Dolphin groups were seen in varying habitats. However the majority were recorded near New Quay headland in shallow water (0-10m) (Figure 12), in areas of high boat activity (Figure 11) and in high energy circalittoral seabed, circalittoral fine sediment and infralittoral fine sediment (Figure 13).

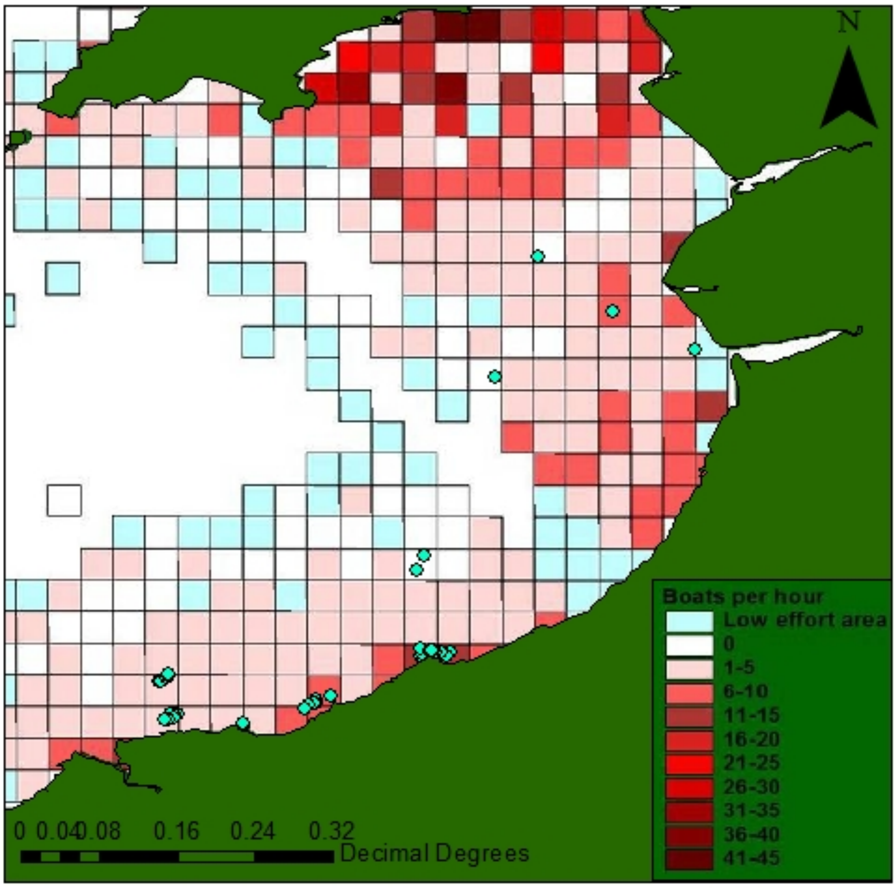

Figure 11: *A map of the level of boat activity within Cardigan Bay in addition to dolphin sightings from which whistles were recorded represented by the blue circles.* (Lohrengel *et* al. 2012)

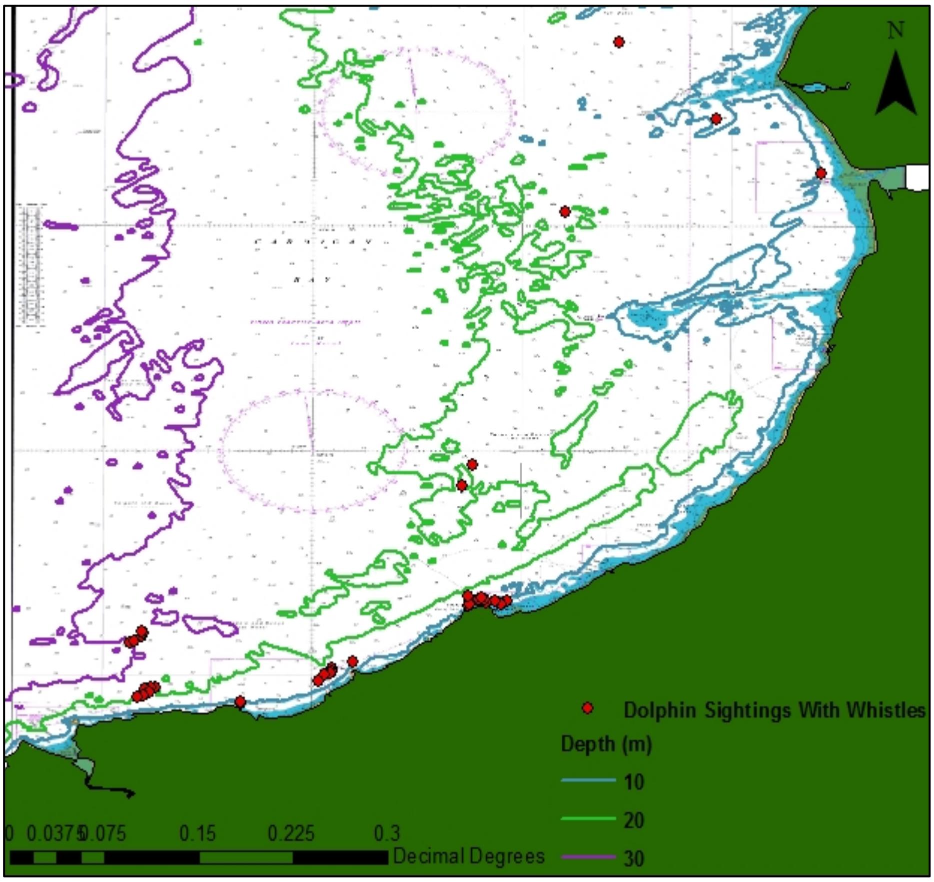

Figure 12: *A map of the depth contours in Cardigan Bay in addition to dolphin sightings from which whistles were recorded* (Marine Digimaps).

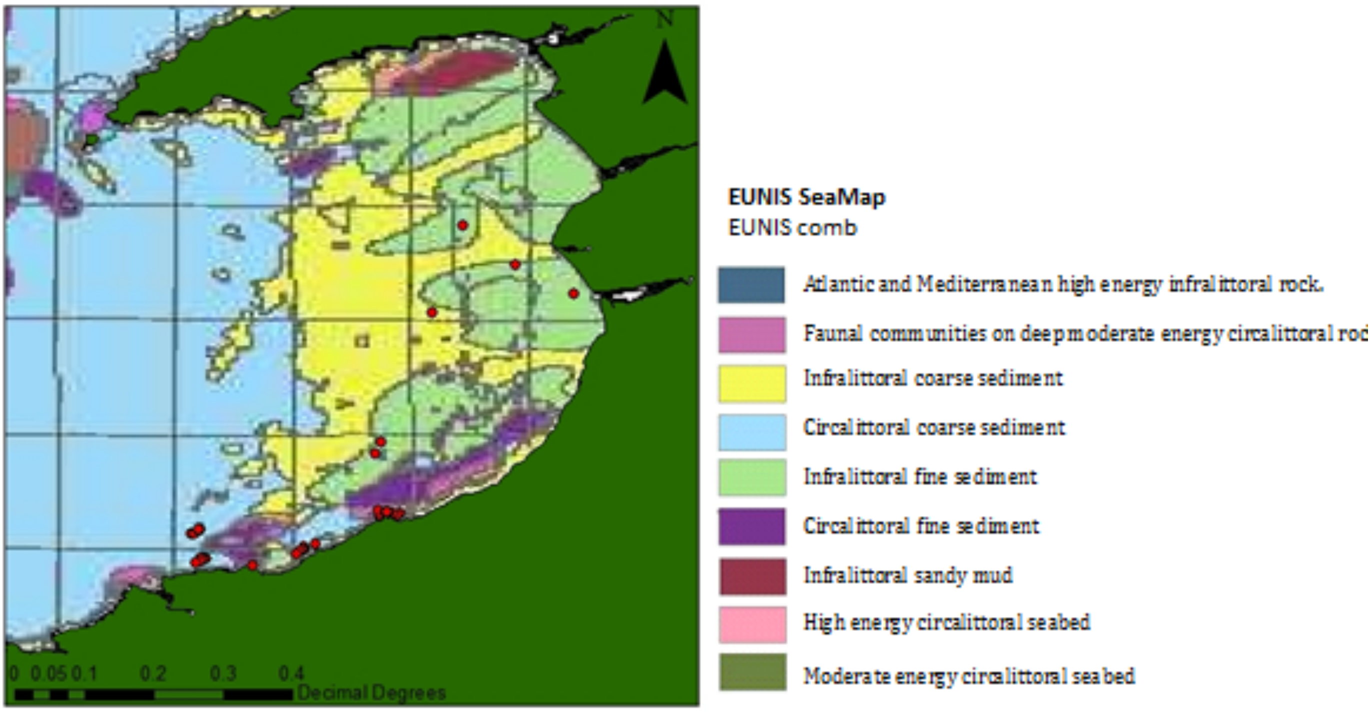

Figure 13: *Habitat Map of Cardigan Bay determined via EUNIS (European Nature Information System) the red circles represent a dolphin sighting from which whistles were recorded. A full version of the map and associated key can be found in Appendix D.*

In addition to natural environments, social settings also differed between encounters with group formation, group composition and main behaviours being the most changeable. A BEST analysis showed that depth, boat activity and group formation had the strongest correlation with the variability in whistles between groups (Table 5).

Table 5: *Results from a BEST analysis showing the environmental factor which most affects the variation in whistles.*

Variables	***Correlation***	***Number of Variables***
Depth, Boat Activity, Group Formation	0.252	3
Depth, Boat Activity, Group Formation & Group Composition	0.248	4
Depth & Group Formation	0.234	2

During periods when individuals were in close proximity to each other, the average frequency of whistles was significantly higher than that of more widely spaced individuals (Figure 14; Table 6). The greatest difference was seen between tight group formations and patchy or dispersed formations (Table 7). This relationship was especially obvious within the minimum frequency and maximum frequency (Table 7). In comparison the average number of inflection points and duration increase when the dolphin group is more widely dispersed. This result was not significant, and is probably a result of the large variation around the mean for both variables (Figure14).

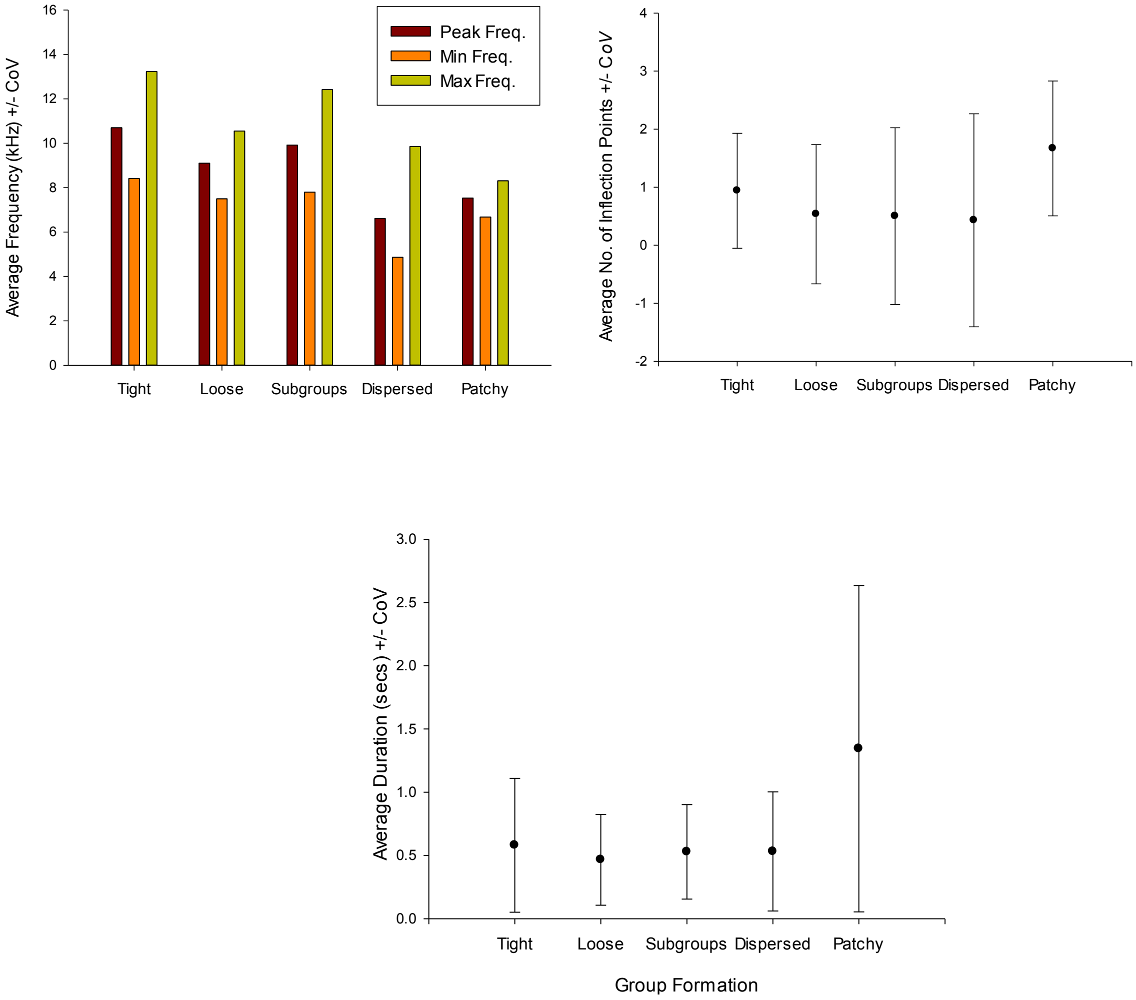

Figure 14*: The average frequency for the whistle variables contributing >15% to the total cumulative percentage of dissimilarity between dolphin groups in addition to the no. of inflection points and duration in relation to different group formations ± CoV*

Table 6: *Univariate results for the whistle variables contributing >50% to the total cumulative percentage of dissimilarity between and within dolphin groups against Group Formation.*

Source	***df***	***MS***	***F***	***p***
No. of Inflection Points (log)	4, 29	0.314	1.599	0.201
Minimum Frequency	4, 68	17.495	4.276	0.004
Maximum Frequency	4, 68	48.327	5.653	0.001
Peak Frequency	4, 68	30.043	5.067	0.001
	df	***Chi^2***		***p***
Duration ***(Kruskal-Wallace)***	4	1.561		0.816

Table 7: *Results from a post-hoc Tukey test for whistle variables that show a significant relationship with Group formation*

Variable	***Formation***	***Standard Error***	***p***
Minimum Frequency	Tight v Dispersed	0.917	0.002
	Loose v Dispersed	0.926	0.045
	Subgroups v Dispersed	0.861	0.010
Maximum Frequency	Tight v Patchy	1.21832	0.001
	Subgroups v Patchy	1.13083	0.005
Peak Frequency	Tight v Dispersed	1.10341	0.004
	Tight v Patchy	1.01454	0.022
	Subgroups v Dispersed	1.03682	0.18
	Patchy v Subgroups	0.94169	0.097

Frequency variables increased during levels of boating activities of 1-10 boats per hour but decreased at higher and lower intensities (Figure 15). Only the relationship between boat activity and maximum frequency showed any significant relationship (Table 8). The largest difference was between 0 boats per hour compared to the other levels of boat activity (Table 9). Maximum frequency showed a smaller average frequency for no boat activity whilst peaking at activity levels of 1-5 boats (Figure 15). Such a relationship is also displayed in the average peak frequency; however this relationship was not significant (Table 8).

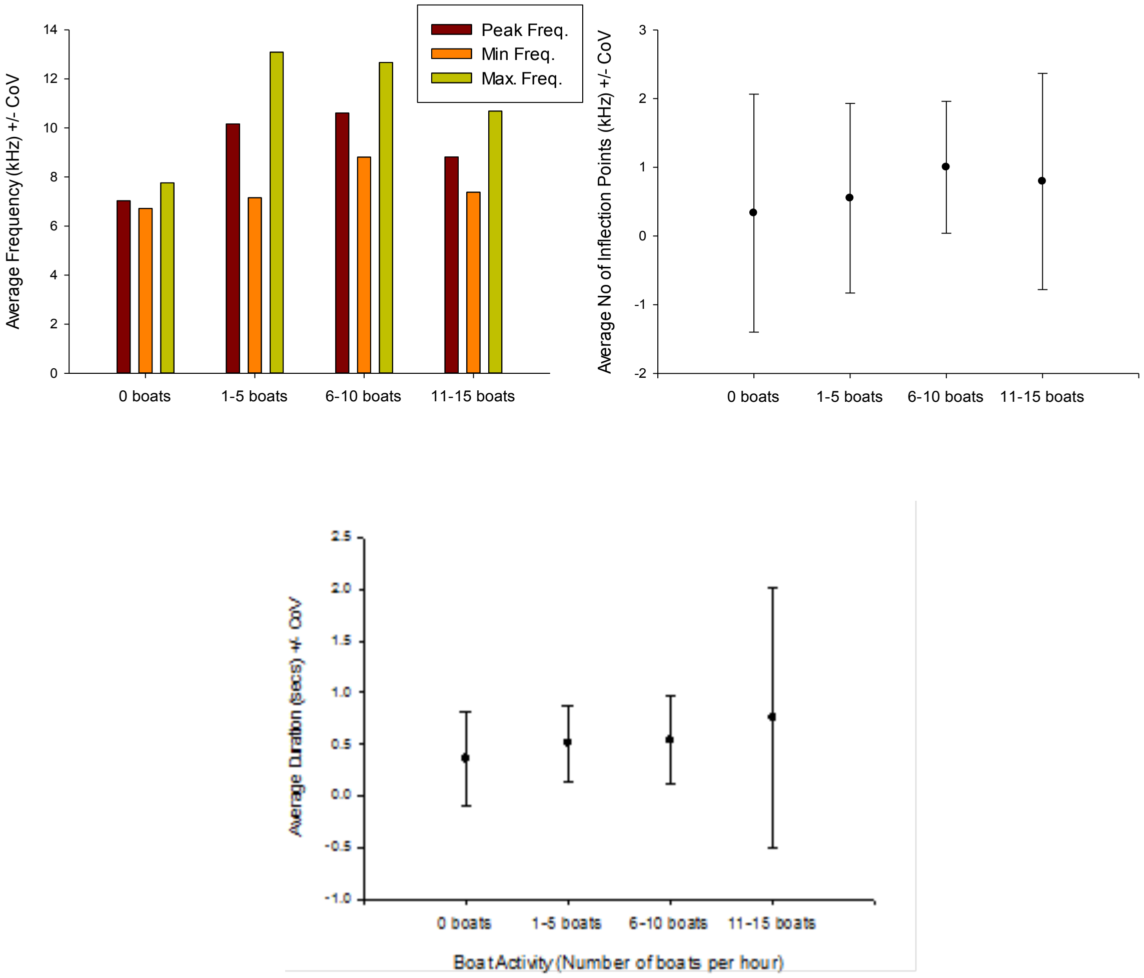

Figure 15: *The average frequency for the whistle variables contributing >15% to the total cumulative percentage of dissimilarity between dolphin groups in addition to the no. of inflection points and duration in relation to different levels of boat activity ± CoV.*

Table 8: *Univariate results for the whistle variables contributing >50% to the total cumulative percentage of dissimilarity between and within dolphin groups against Boat Activity.*

Source	***df***	***MS***	***F***	***p***
No. of Inflection Points (natural logarithm)	3, 67	0.754	0.672	0.572
Minimum Frequency	3, 67	9.475	2.305	0.085
Maximum Frequency	3, 67	44.297	5.275	0.003
Duration	3, 67	0.276	0.589	0.672
	df		***Chi²***	***p***
Peak Frequency ***(Kruskal-Wallis)***	3			0.055

Table 9: *Significant results from a post-hoc Tukey test for top whistle variables with Boat Activity*

Variable	***Boat Activity***	***Standard Error***	***p***
Maximum Freq.	0 v 1-5	1.79414	0.021
	0 v 6-10	1.84361	0.047
	1-5 v 11-15	0.81660	0.023

All whistle variables decrease at deep depths (Figure 16). This is supported by the results from the Tukey test, which show the only significant result to be between 21-30 m and the other depth ranges (Table 10). Larger variation occurs at depths of 21-30 m, which could be attributed to the smaller data set as only three encounters occurred at these depth ranges (Figure 16). Maximum frequency is greatest at shallower depth ranges, whilst minimum and peak frequencies are the same for both 0-10m and 11-20m. The no. of inflection points show high levels of variation around the average, indicating no relationship between depths for this characteristic (Table 11).

Table 10: *Univariate results for the whistle variables contributing >15% to the total cumulative percentage of dissimilarity between and within dolphin groups against Depth.*

Source	***df***	***MS***	***F***	***p***
No. of Inflection Points (natural logarithm)	2, 31	0.630	3.435	0.045
Minimum Frequency	2, 70	20.335	4.629	0.013
Maximum Frequency	2, 70	41.853	4.240	0.018
Peak Frequency	2, 70	34.741	5.358	0.007
	df	***Chi^2***		***p***
*Duration (**Kruskal-Wallis**)*	2	4.035		0.133

Table 11: *Significant results table from a post-hoc Tukey test for top whistle variables with depth.*

Variable	***Depth***	***Standard Error***	***p***
Minimum Frequency	0-10m v 21-30m	1.540	0.025
	11-20m v 21-30m	1.514	0.010
Maximum Frequency	0-10m v 21-30m	2.30876	0.014
	11-20m v 21-30m	2.26938	0.027
Peak Frequency	0-10m v 21-30m	1.87112	0.006
	11-20m v 21-30m	1.83921	0.005

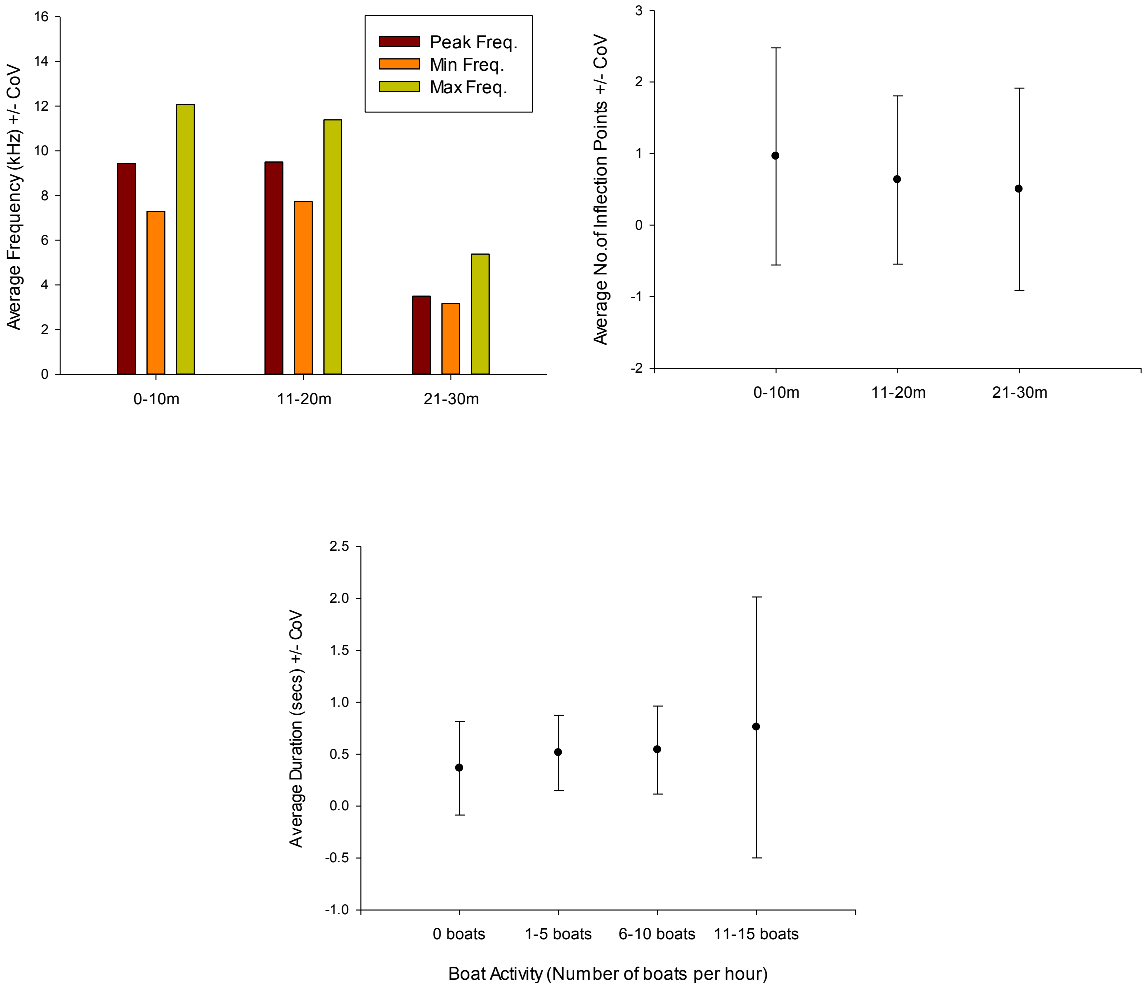

Figure 16: *The average frequency for the whistle variables contributing >15% to the total cumulative percentage of dissimilarity between dolphin groups in addition to the no. of inflection points and duration in relation to different depths ± CoV*

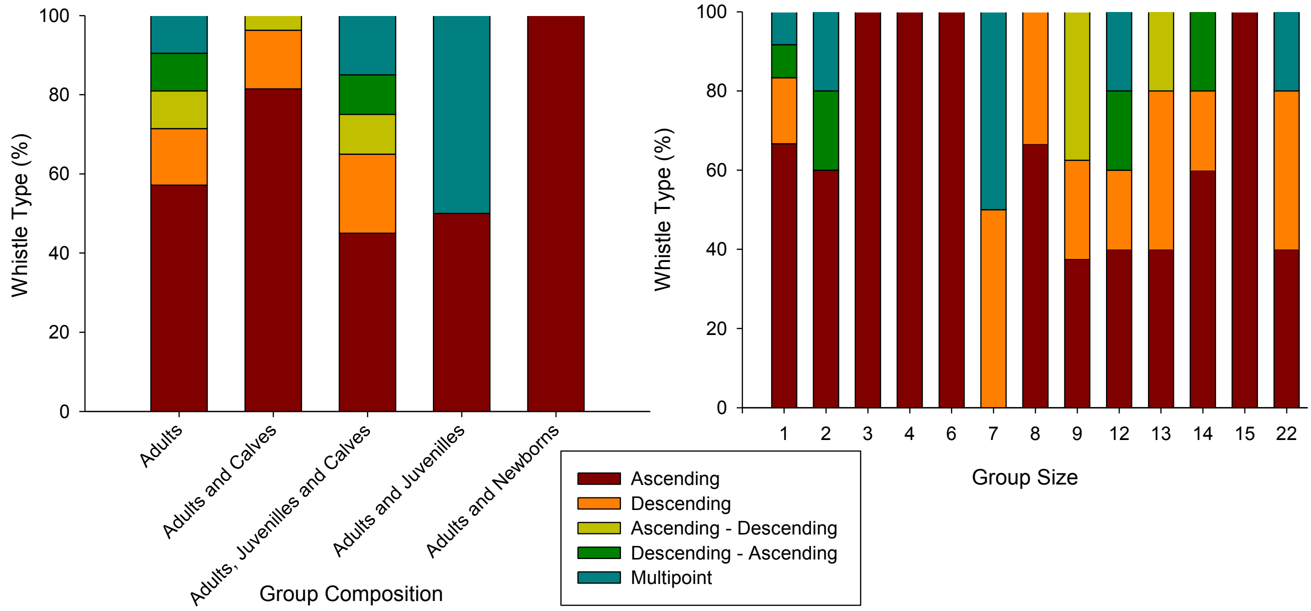

Figure 17*: The average percentage of whistle types produced at each different Group composition (left) and Group size (Right).*

Table 12*: Results from univariate testing for the production of different whistle types against all environmental and behavioural factors.*

Variable	***df***	***MS***	***F***	***p***
*Depth (**ANOVA**)*	2, 70	0.685	0.411	0.664
*Behaviour (**ANOVA**)*	3, 69	2.242	1.391	0.253
	df	***Chi^2***		***p***
*Habitat Type (**Kruskal Wallis**)*	7	12.556		0.084
*Boat Activity (**Kruskal Wallis**)*	4	9.182		0.057
*Group Formation (**Kruskal Wallis**)*	4	2.749		0.601
*Group Composition (**Kruskal Wallis**)*	4	10.895		0.028
*Group Size (**Kruskal Wallis**)*	12	23.669		0.023
*Between Encounters (**Kruskal Wallis**)*	15	26.138		0.037

Analysis was completed for whistle rates in relation to various environmental factors. However this yielded no significant results and no visible relationships (Appendix. A). On the other hand, the types of whistle produced varied with environmental and behavioural contexts (Figure 17). The only variables that showed significant results were group composition and group size (Table 12). Post hoc testing with Mann Whitney U showed that the most significant differences were between groups composed of adults vs. groups of adults and calves or adults, juveniles and calves (Table 13). Such post hoc testing also showed significant differences between group sizes of one individual and groups of seven individuals; no other relationships were found between different group sizes (Table 13).

Table 13: *Significant results from post hoc Mann Whitney U tests for production of whistle types against environmental and behavioural factors.*

Variable		***U***	***p***
Composition	Adults v Adults and Calves	202	0.034
	Adults and Calves v Adults, Juvenile and Calves	157	0.004
Group Size	1 v 7	7	0.042

4.0 Discussion

The findings from this study demonstrate bottlenose dolphins in Cardigan Bay vary whistle characteristics in the form of frequency variables and complexity. Statistical analysis of such characteristics suggests larger differences among whistles occur between social dolphin groups than within groups, although a degree of intragroup variability has been observed. Differences in whistle characteristics may be, in part, due to the local environment and behaviour at the time of recording. The following sections focus upon the results that warrant further discussion, these include; inter and intragroup variation, boat activity's effect on whistle variables, whistle variation in response to larger depth ranges, changes in whistles as a result of different group formations, the lack of variation in whistle rate and environmental effects of whistle type.

4.1 Whistle Variation Between and Within Dolphin Groups

The findings of this study demonstrate that whistles vary in their characteristics, however the level of variation is not large enough to show significant grouping in the MDS plot. Such similarities in whistle characteristics could be a result of dolphins modifying their whistles to match calls made by other known dolphins (Datta and Sturtvant, 2002). Bottlenose dolphins from the Cardigan Bay population have home ranges which cover the whole bay (Veneruso and Evans, 2012) therefore individuals associate with many other dolphins. Whistle matching with a number of individuals will result in a shared whistle dialect (Datta and Sturtivant, 2002). Despite the apparent lack of grouping, there was a significant difference between dolphin groups which could be an indication of smaller group repertoires as previously described by Datta and Sturtivant (2002); Connor (2007); Miller, *et al.* (2007). The presence of such groups is supported by the greater variation found between than within dolphin groups.

Variation within groups may indicate the production of individual whistles; however this could not be proven due to the difficulty in unequivocally locating the individual dolphins that were vocalising (Quick *et al.* 2008). The large proportion of whistles which were classed as ascending coupled with the low number of inflection points, indicate a lack of complexity in the whistle. This suggests they could be used for signalling rather than for individual identification (Ansman, *et al.* 2007). Similar results were found in dolphin populations from the Sado Estuary, Portugal and in Australia. Smolker and Pepper, (1999) hypothesised that low signature whistle production was a result of low stress environments. This could also be said for Cardigan Bay due to the sheltered nature of the bay in summer months, the availability of food and the lack of natural predators. Such findings contradict Quick and Janik (2008) who stated signature whistles contribute 39 - 52% to total whistles recorded from wild dolphins; however this finding could be a result of the different environmental setting with their population residing in an exposed deep water habitat.

Variation in whistles within groups was driven by complexity factors such as duration and inflection points, as previously shown by Morisaka, *et al.* (2005). This was suspected to be a result of the dolphin's ability to modulate such characteristics in order to convey emotional levels and individual identities. In comparison, the variation between groups was dependent upon frequency variables such as maximum frequency, minimum frequency and peak frequency which are more stable characteristics (Morisaka, *et al.* 2005). This stability could indicate that they are limited by sound production organs and are possibly affected by behavioural or environmental influences at the time of recording (Morisaka, *et al*. 2005). In contrast to the findings of this paper captive dolphins from the Gulf of Mexico showed greatest intergroup differences for start and end frequency. Such differences in populations could be a result of the varying environmental settings (McCowan, *et al*. 1998).

Whistle variation between groups could be attributed to group alliances and their shared whistle repertoires. Alliances between specific individuals (Connor, 2007) could not be identified from the encounters during this study, as individuals were not seen repeatedly within the same group, except for certain mother-calf pairs. However there were a number of groups consisting of adults, juveniles and calves, indicating the presence of female bands which comprise of adult females and their more recent offspring (Miller, *et al*. 2007). The present of such groups was indicated by older calves without the presence of their mother, exhibiting alloparental care. This occurs for mothers to stray from their calves in order to feed (Reidman, 1982). Female bands have strong social bonds and high familiarity between individuals meaning they spend vast amounts of time together, which may cause a convergence of whistles within the group.

There was no evidence of male alliances within Cardigan Bay. There were numerous adult only groups however the sex could not be identified. In addition, no behaviour specific to male only groups was observed such as herding and aggressive displays (Möller, *et al.* 2001). A large number of dolphins sighted were classed as previously unidentified (not matched with Sea Watch's Photo ID catalogue); as a result, reoccurring social groups may have been unrecorded. Previous studies on the Cardigan Bay population found it to be a fission-fusion society, as most other studies of this species have also concluded (Pesante, *et al.* 2008). A recent study regarding the social network of the Cardigan Bay population demonstrated that individuals form moderate sized groups but few very strong associations in areas of high vessel activity. In comparison, larger groups are found in areas of low boat activity which have few very strong associations (Richardson, 2012). Due to the spatial scaling of our sampling the majority of recorded whistles were from areas of increased boating activity. The high boat activity could therefore explain the lack of grouping between encounters shown in multivariate analysis, whilst also accounting for the slight differences which were found between groups (this is discussed in section 4.2). An increase in survey effort in both the number of surveys and spatial scale would improve our understanding of the level and types of social groups in Cardigan Bay.

4.2 Whistle Characteristic Variation as a result of Boat activity

Whistle frequencies increased during intermediate boating activity of 1-5 and 6-10 boats per hour. Such increases in frequencies may be a result of increased excitement, with positive responses such as swimming towards the boat and bow riding being commonly observed for bottlenose dolphin populations (Reynolds, *et al.* 2000). On the other hand, it could also be a sign of distress, possibly produced by mothers in order to call to calves (Kuczaj, *et al.* 2012). The numbers of inflection points and whistle duration peaked with higher boating activities; however the variation in the production of such characteristics is high. This could indicate the dolphins were communicating emotional information or perhaps conveying individual identification with conspecifics (Morisaka *et al.* 2005). The presence of such communication is an additional sign of stress or excitement which are classed as disturbance calls (Buckstaff, 2004)

Vessel noise is a result of air bubbles collapsing near the blades of the propellers and can be increased or decreased depending on the rate of propeller rotation (May-Collado and Wartzok, 2008). Increasing the propeller rate increases the frequency of the vessel noise. The reduction of frequencies displayed by the Cardigan Bay population during higher boat activity may be a result of engine noise masking the dolphin's acoustic signals (Buckstaff, 2004). Such masking has been observed in Florida with whistles being produced at a frequency range of 3.23 kHz and watercraft noise ranging from 0.5-12 kHz, whilst in this locality, the decibel level has been recorded to be 26 dB above the ambient noise level (Buckstaff, 2004). Lowering whistle frequencies in response to boat traffic has also been observed in Indo-Pacific bottlenose dolphin populations. However, this population also demonstrated a decrease in the amount of modulation (number of inflection points), indicating a lack of emotional information being conveyed (Morisaka, *et al.* 2005). Lower frequencies increase the distance the vocalisation can travel whilst a lower number of inflection points means the vocalisation is less likely to be masked (Baron, *et al.* 2008). Despite this, other dolphin populations' show increases in whistle characteristics (including modulation and duration) in the presence of multiple boats (May-Collado and Wartzok, 2008). Differences between geographically distinct populations could be a result of the types of boats used in the area. The sizes and speed of the vessel can cause different noise levels in addition to different frequency ranges (Ansman, *et al.* 2007; May-Collado and Wartzok, 2008). In inshore Cardigan Bay the majority of vessels used are small tourist boats, sea angling boats, yachts or speed boats with relatively small engines producing higher frequencies therefore having the potential to mask dolphin whistles (Evans, *et al*. 1992). We can therefore assume that the whistles of the Cardigan Bay dolphins are affected by boat activity; this relationship, however, does not seem to affect their general behaviour towards boats. Increased information is required on the level and frequencies of engine noise in Cardigan Bay before firm conclusions can be reached.

4.3 Whistle Characteristic Variation as a result of Group Formation

Whistle frequencies increased when dolphin groups were spaced closely together, such as in tight or sub grouped formations. The increased frequencies may be an indication of excitement or of being distressed as discussed above (section 4.2.). The higher frequencies with boat activity combined with the tighter group formation may indicate individuals become distressed during the approach of boats, with the higher frequencies being a signal to decrease the amount of distance between individuals (Nowacek, 2005). Increased whistle frequencies and whistle production has especially been seen in groups with calves indicating distress signals are increased during possible dangerous situations (Jones and Sayigh, 2002). By comparison, in dispersed or patchy formations the number of inflection points and duration increased, indicating varying information is being communicated. The varying information produced could be a result of conspecifics not being in visual contact with each other, therefore more information on position, behaviour, direction and emotional state needs to be conveyed (Lammers, *et al*. 2003). The dolphins of Cardigan Bay therefore produce whistles for group synchronisation in addition to a warning or excitement signal, the significance of the result is probably attributed to the high number of calves in the bay as well as the high boating activity.

4.4 Whistle Characteristic Variation as a result of Depth

Comparisons with whistle variation at different water depths gave significant results for all variables. Decreased maximum, minimum and peak frequency occurred when dolphins were in deeper water (21-30m) meaning the frequency range was low. In previous studies, frequency range has been observed to increase in deeper habitats rather than in shallower habitats, with this being attributed to signal absorption by sea grasses (Buckstaff, 2004). In addition, sound propagation has been recorded to be low when water depth is less than half of the wavelength of the whistle meaning sound production in shallow waters was deemed less effective (Buckstaff, 2004). This is due to sounds rebounding from the seafloor and other natural features e.g. reefs (Janik, 2000). Such inhibitors may affect the methods of vocalising such as changes in frequencies, in order to effectively hunt prey in the different environments. For example decreased frequencies travel further than higher frequencies therefore the presence of low frequencies in deeper water would be more effective for hunting pelagic prey as it can be found over larger distances (Baron, *et al.* 2008). Wursig and Wursig (1979) also found such a relationship, with smaller groups feeding on benthic fish in shallow inshore environments, and larger groups hunting pelagic prey in deeper waters (Gregory and Rowden, 2001). Such strategies have previously been seen in Cardigan Bay and therefore could account for the significant relationship between whistle variation and depth (Evans, *et al.* 2001; Baines, *et al.* 2002). However caution should be taken, as the largest depth range had a small sample size compared to the other depth ranges, meaning the significant result may be caused by the unequal dataset.

4.5 Whistle Rates and Types of Whistles

In previous studies, the rate of whistles has been dependent upon behavioural or environmental states, with rates increasing during feeding, socialising and whilst in areas of high disturbance (Quick and Janik, 2008). In contrast, the findings from this study showed that the rate of whistle production in Cardigan Bay did not vary with environmental or behavioural states; this unusual result could be attributed to the small sample size. However there were large amounts of variation around the mean whistle rate, indicating whistle rates in Cardigan Bay do vary yet the small sample size stops relationships with external factors being shown.

The overall rate of whistle production is significantly lower than that of other dolphin populations in Florida and Portugal (Lopez and Shirai, 2009). The possible reasons for such low whistle rates may be a result of the small spatial scale of sampling; most sampling occurred near New Quay. As a result the individuals that were recorded will be familiar with their conspecifics and surroundings, meaning the need to vocalise is reduced (Jones and Sayigh, 2002; Quick and Janik, 2008). Low whistle rates combined with the lack of dependency on group size may indicate a hierarchy within dolphin groups of Cardigan Bay, allowing specific individuals to vocalise at certain times (Quick and Janik, 2008). Conservative vocalising may be advantageous as it expends less energy, in addition to preventing confusion between signals (Jones and Sayigh, 2002). Previous studies have found decreased whistle rates are seen in smaller group sizes (Quick and Janik, 2008), which may also explain the low whistle rates in the present study with the majority of dolphin groups being moderately to small sized (3-8 individuals). Low whistle rates have also been regularly seen in groups which contain calves, this is due to the increased familiarity within female bands meaning the need to vocalise is reduced. In addition the lack of vocalisation within these groups is a method to reduce the risk of predation as well as the energy demands of lactating females (Jones and Sayigh, 2002). The high levels of calves in

Cardigan Bay could be indicative of the low whistle rates, and whilst there is no evidence of predation within the Bay there has been evidence of adult males practicing infanticide on harbour porpoises. Thereby inferring that infanticide does occur which could be a possible reason for the reduced vocalisations (Patterson, et al. 1998).

Whistle types within this study were seen to vary with group size and composition; this has yet to be observed in any other studies on dolphin whistles. Previous studies observed the range of whistle types increased during activities where dolphins become excitable such as feeding (dos Santos, *et al.* 2005). The large amount of ascending whistles and high levels of feeding observed concurs with previous studies which state the occurrence of ascending whistles is indicative of feeding (Akiyama and Ohta, 2007). However, there was no significant result obtained for whistle type and behaviour, which could be a result of the small numbers of certain whistle types (e.g. ascending – descending and multipoint) within particular environmental and behavioural contexts. The data does not therefore represent the whole population resulting in relationships not being displayed within the results. Further data collection is recommended in order for the accurate representation of the results to be displayed.

4.6 Data Considerations

Due to the large range of vocalisations recorded for each encounter the amount of whistles used in analysis was significantly reduced in order to create a balanced design for statistical testing-resulting in a small sample size. This small sample size means the findings of this study may not be fully representative of the population and therefore they should be viewed with caution. Further collection and analysis of whistles should continue to increase the number of whistles, in addition to environmental and behavioural data. Furthermore, the method for recording whistles does not allow us to distinguish which dolphin is vocalising, meaning the number of dolphins actually vocalising within a group is unknown. Whistles may therefore be attributed to more dolphins than is correct e.g. in a group of seven dolphins, one assumes that the majority are vocalising and yet there may only be two. This means one may be comparing whistles of the same individual (Oswald, *et al*. 2003) thereby giving false representation of whistle variation between and within dolphin groups. Development of equipment in the form of increased numbers of hydrophones in order to measure locality will cancel out such errors in the data.

4.7 Additional Research

Possible research following on from the findings of this thesis should include extending the period of study in order to collect data over the winter months, for both the individuals that remain in Cardigan Bay and individuals which migrate to north Anglesey. This may provide data from a greater range of environments, including those which are deemed stressful. Relationships with whistle production and season have been previously observed (Jacobs, *et al*. 1993). Vocalisations increased during winter months, whilst whistle production increased during travelling and feeding in the summer months compared to the winter when they increased during socialising. In addition to changes in seasons long term collection of data may indicate temporal changes in whistle production (Morisaka, *et al.* 2005). This could be an indication of changes in the social structure of the dolphin population or environmental changes. Such information particularly in relation to human activities may be useful in assessing the usefulness of the SAC designations.

Other investigations into signature whistles using an array of hydrophones would be useful in determining the role of such whistles within the Cardigan Bay population. Quick, *et al.* (2008) describe a method in which an array of hydrophones is used to locate the vocaliser even with quick changes in group composition and formation, as well being able to ignore whistles produced by dolphins groups which are further afield. Subsequent comparisons with other dolphin populations would help elucidate the factors affecting the role of such whistles. Additionally, by analysing the click data which was opportunistically recorded in relation to the whistles that were recorded, might determine the relative roles of clicks and whistles in the Cardigan Bay population. This may explain some of the results from this study as with the lack of certain whistles and whistle variation with behaviours, certain click vocalisations may increase.

5.0 Conclusions

Bottlenose dolphins in Cardigan Bay show variation in whistles and their production. Comparing whistles from different social groups displayed greater variation between groups compared to within such groups thereby agreeing with Hypothesis 1. The large variation between groups was related to the increased familiarity with dolphin groups and the possibility of a shared whistle repertoire (Datta and Sturtivant 2002; Connor 2007; Miller, *et al*. 2007). The whistle characteristics contributing to such variation come in the form of peak frequency, maximum frequency and minimum frequency. Frequency variables are limited in their variation via sound production organs meaning they are unlikely to convey emotional information, and will therefore be used for signalling to others (Ansman, *et al.* 2007). In comparison, whistle variation within groups was due to whistle duration and modulation, inferring the use of emotional signalling (Morisaka, *et al.* 2005) and the possible use of signature whistles within these groups. The use of signature whistles was deemed unlikely however due to the large amounts of ascending whistles which are associated with feeding, (Akiyama and Ohta, 2007) and the overall low number of inflection points. It was therefore deemed that a level of whistle variation was caused by environmental and behavioural contexts.

Hypothesis 3 was also proved correct with the level of variation being attributed to levels of boat activity, depth and group formation. Intermediate levels of boating activity increased the frequencies of whistle characteristics, with this being indicative of excitement or distress vocalisations (Buckstaff, 2004). This result is supported by the increased modulation and duration of whistles which demonstrates the use of emotive communication. In levels of high boating activities frequency variables decrease, as a result of vessel noise possibly masking whistles with higher frequencies (Buckstaff, 2004). Relating to boat activity was the response seen in whistle variation with group formation with whistle frequencies increasing whilst in tighter formations. Increased frequencies indicate distress/excitement calls produced as a result of an approaching boat, which may signal to form tighter groups (Nowacek, 2005). This is especially the case with mother-calf pairs. The presence of calves can also explain the small whistle rates recorded as reduced vocalisations decreases the risk of infanticide and energy uses by lactating females (Jones and Sayigh, 2002). Decreases in frequencies were observed with increased water depth which was hypothesised to be a result of dolphins exhibiting different foraging strategies for different prey types (Gregory and Rowden, 2001). However the dataset for the depth range 21-30 m is small in comparison to the other depth ranges meaning the significant result could be a result of the unequal dataset.

Data regarding types of whistles is also small and therefore not representative of the whole population, meaning the changes observed in this data should be looked at with caution. To fully understand whistle variability, increased sampling effort is required in order for the data to be a true representation of the bottlenose dolphin population; this includes sampling during the winter months in addition to in depth studies on the effects of boating activity.

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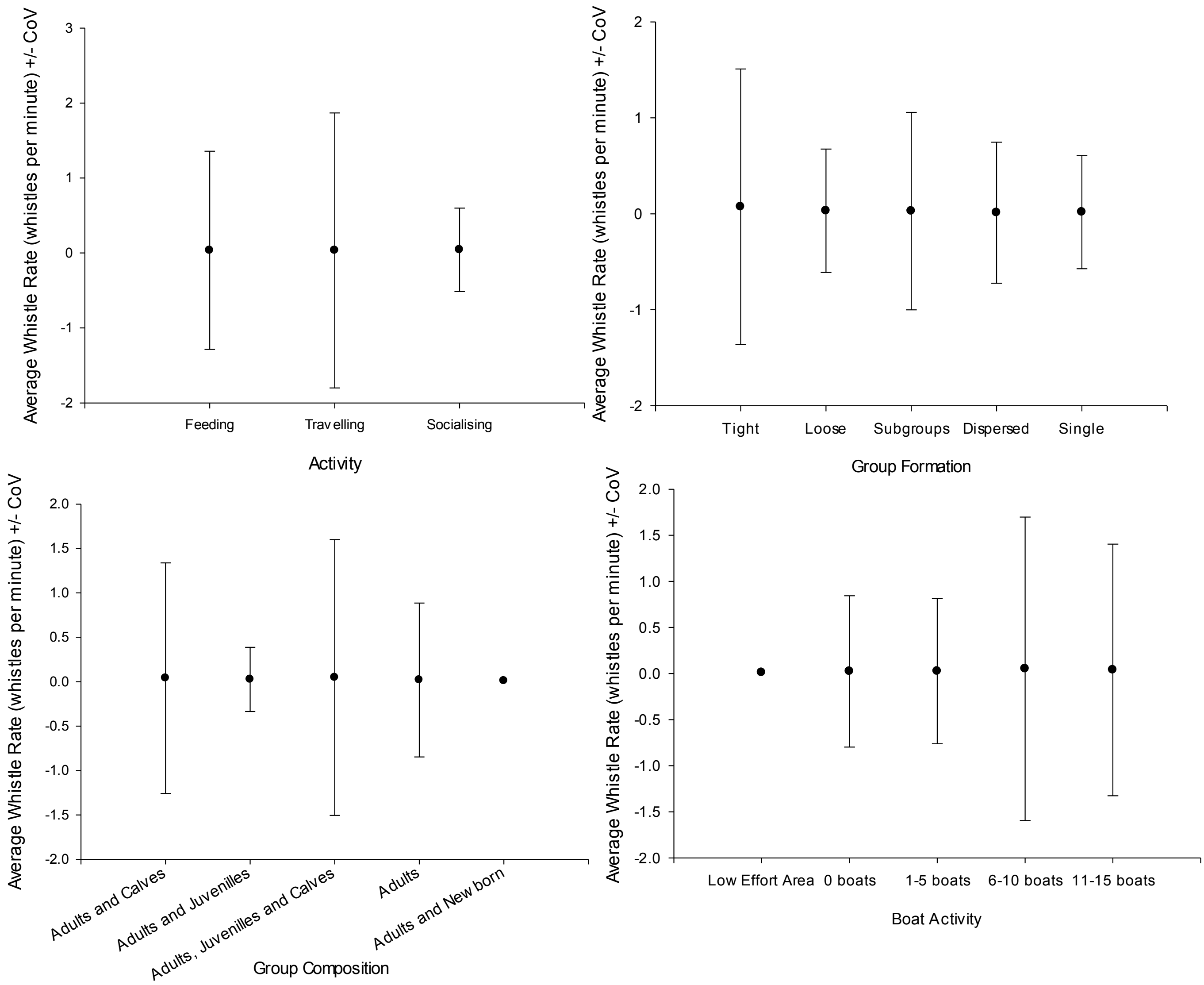
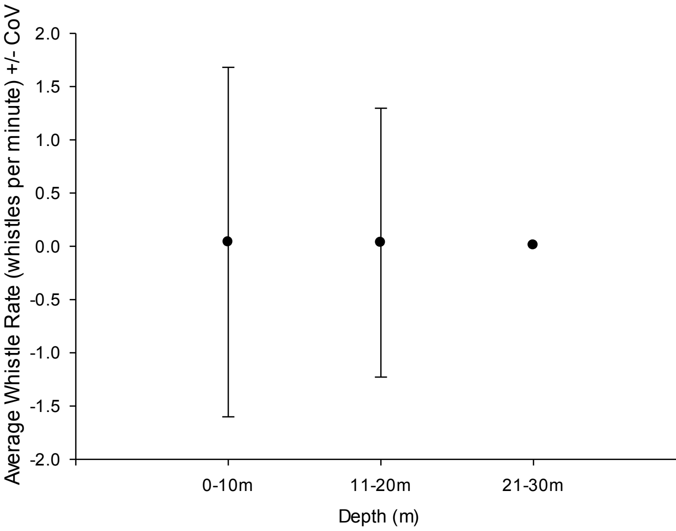
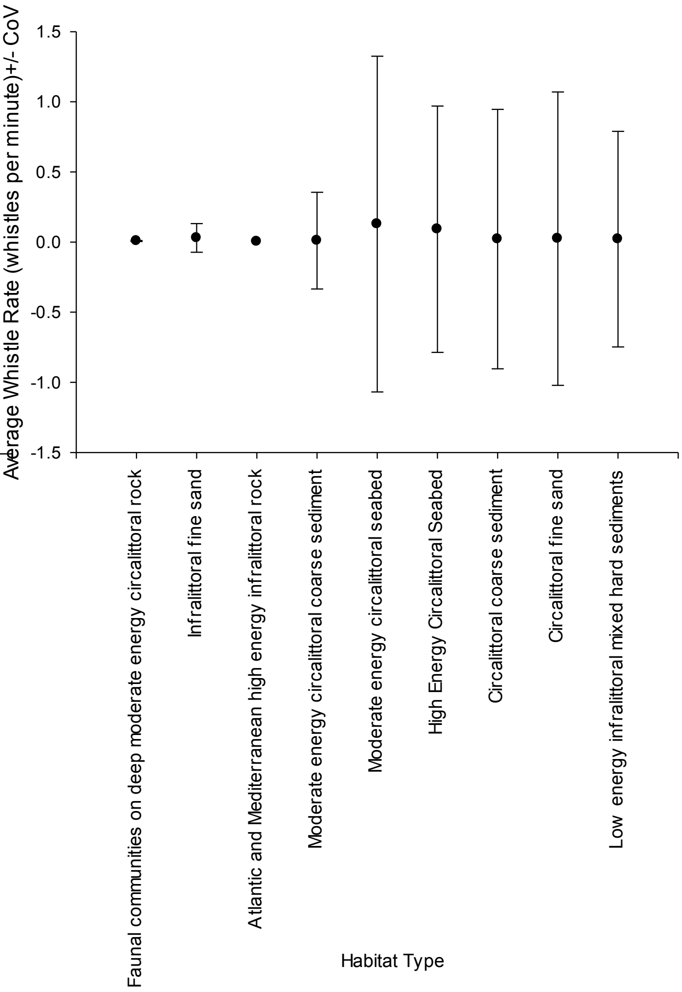
1.0 Appendices

Appendix A: Average whistle rates +/- Coefficient of Variance with each Behavioural and Environmental States



(Appendix A Continued)





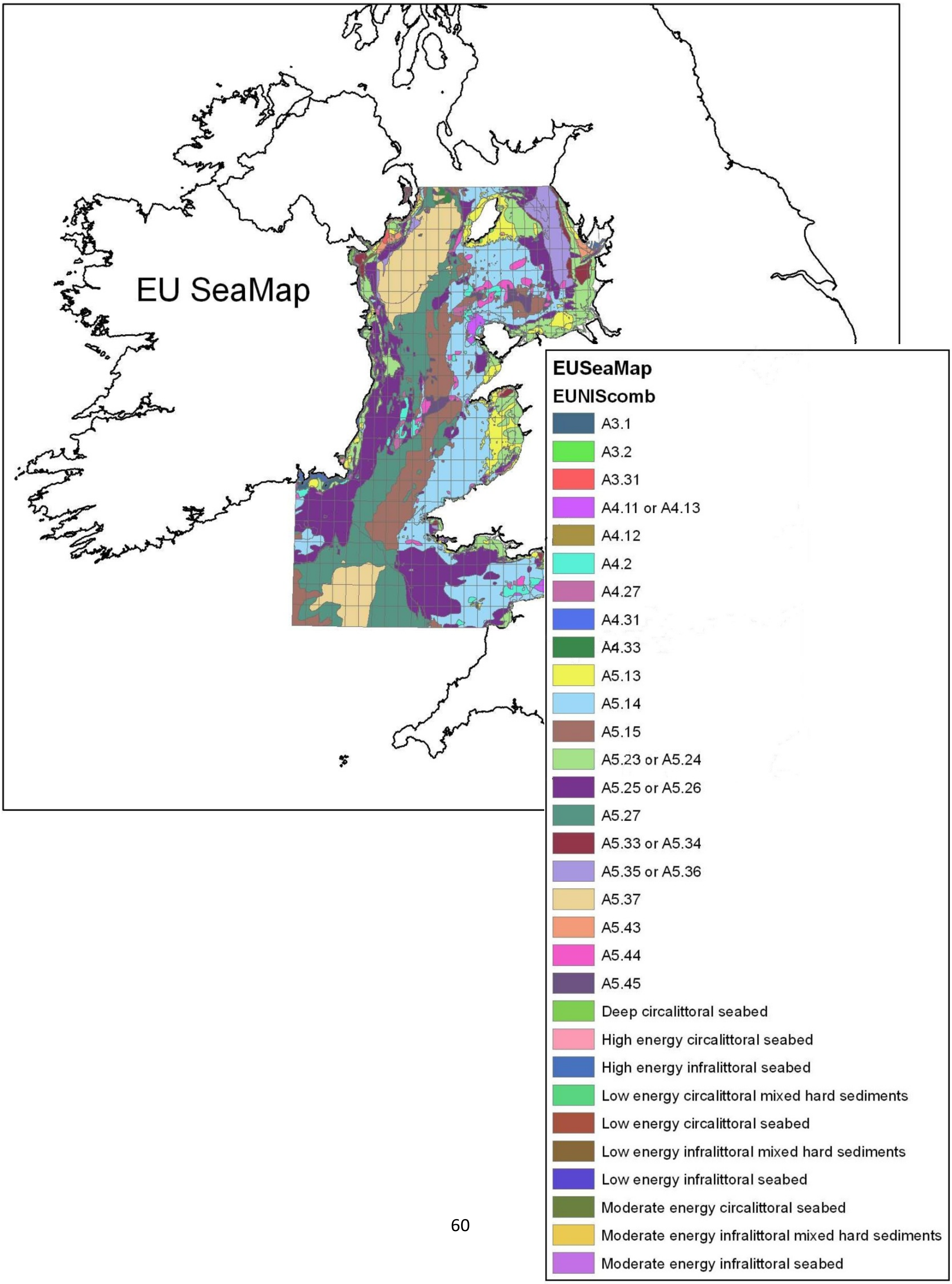
Appendix B: Range, Average and Standard Error for Each Whistle Variable During Each Encounter.

	Start Freq.	*End Freq.*	*Freq. Range*	*Min Freq.*	*Max Freq.*	*Peak Freq.*	*Duration*	*Inflection Points*
35	5.4-16.3 9.61±3.37	7.9-15.9 11.4±2.36	5.1-8.7 7.38±1.15	5.4-7.9 6.82±0.75	10.5-16.3 14.2±1.88	7.1-10.6 8.72±1.02	0.80-1.3 1.06±0.14	0-2 1.00±0.58
26	4.9-16.9 8.55±1.28	7.3-17.7 11.82±1.31	0.96-11.1 6.02±1.22	4.9-8.8 7.35±0.45	9.6-19.4 13.37±1.34	8.7-15.5 10.52±0.97	0.17-0.76 0.50±0.06	0-3 1.00±0.33
28	12.1-15.8 13.21±0.86	11.3-15.4 12.67±0.92	0.48-8.2 2.66±1.87	7.9-12.1 10.8±0.98	12.5-16.2 13.46±0.90	12.1-16.01 13.20±0.94	0.26-0.76 0.49±0.11	0-2 1.00±0.41
43	0 6.45±0.00	0 14.05±0.00	0 8.26±0.00	0 5.79±0.00	0 14.05±0.00	0 10.20±0.00	0 0.04±0.00	0 1.00±0.00
45	3.8-21.4 11.24±0.88	5.4-19.7 10.44±0.78	2.5-10.1 5.24±0.40	3.8-17.6 7.96±0.64	8.6-21.4 13.20±0.64	4.8-16 8.76±0.48	0.18-1.2 0.70±0.06	0-2 0.73±0.16
9	4.9-20.1 10.19±0.72	7.4-20.7 10.71±0.49	1.2-10.8 4.36±0.48	4.4-15.6 8.22±0.44	9.3-20.7 12.58±0.55	5.5-18.9 10.18±0.48	0.26-1.6 0.66±0.05	0-3 1.09±0.16
46	4.2-13.7 6.73±0.26	4.4-19.2 10.97±0.29	1.2-8.6 4.56±0.19	4.2-13.3 6.55±0.24	6.9-19.2 11.11±0.27	6.2-16.4 9.27±0.26	0.22-3.4 0.72±0.06	0-2 0.42±0.09
51	3.5-14.6 8.54±0.82	5.7-15.6 10.92±0.64	0.64-10.9 4.86±0.63	3.5-14.3 7.46±0.66	7.9-19.2 12.32±0.60	6.9-15.6 9.84±0.54	0.19-1.4 0.65±0.06	0-3 0.86±0.22
57	6.1-16.4 9.59±0.42	6.5-19.7 14.91±0.48	2.4-10.8 6.24±0.40	6.1-16.4 9.18±0.33	10.5-19.7 15.42±0.39	8.7-18.7 11.28±0.41	0.16-0.93 0.54±0.04	0-1 0.03±0.03
75(2)	5.7-8.9 7.54±0.47	5.9-11.1 9.77±0.66	1.8-5.4 3.25±0.52	5.7-8.8 7.12±0.46	9.8-11.1 10.37±0.18	8.8-9.9 9.33±0.16	0.27-0.78 0.52±0.09	0-2 0.43±0.30
13	3.6-11.3 7.37±0.76	8.2-19.6 12.71±1.05	1.4-8.5 5.45±0.87	3.6-11.3 7.29±0.76	8.2-19.6 12.73±1.04	5.99-17.5 9.86±1.08	0.23-0.87 0.42±0.07	0-2 0.44±0.24
76	5.5-7.4 6.49±0.39	9.0-11.99 10.31±0.62	2.4-4.7 3.82±0.53	5.5-7.4 6.49±0.39	9.04-11.99 10.31±0.62	6.85-10.43 8.41±0.75	0.2-0.51 0.34±0.07	0-1 0.25±0.25
79	5.3-13.2 8.21±0.78	7.4-18.2 12.82±0.95	1.87-8.87 5.27±0.70	5.3-13.24 7.88±0.73	10.5-18.2 13.15±0.83	9.1-14.1 10.21±0.48	0.28-0.71 0.46±0.05	0-2 0.50±0.27
25	10.6-11.1 10.86±0.25	10.3-10.4 10.35±0.09	0.35-0.85 0.60±0.25	10.26-10.3 10.3±0.03	11.11-10.7 10.89±0.22	10.38-10.4 10.39±0.01	0.71-0.36 0.53±0.17	1-3 2.00±1.00
26	5.04-7.74 5.87±0.40	4.86-7.98 6.24±0.42	0.94-2.13 1.48±0.19	4.86-5.84 5.38±0.17	5.98-7.96 6.86±0.33	5.6-6.34 6.01±0.10	0.61-5.6 2.40±0.76	0-6 2.33±0.84
27	3.74-17.9 7.28±0.26	4.09-21.7 10.93±0.53	0.76-12.9 4.90±0.33	3.74-17.9 6.95±0.27	6.64-21.7 11.84±0.42	1.91-27.78 9.95±0.99	0.11-1.22 0.46±0.02	0-4 0.82±0.10
9(2)	3.49-12.23 7.63±0.45	1.35-10.66 6.74±0.46	0.41-3.4 1.26±0.16	1.35-10.66 6.58±0.44	3.49-12.64 7.84±0.48	1.74-12.34 7.04±0.49	0.25-1.13 0.51±0.05	0-2 0.68±0.15

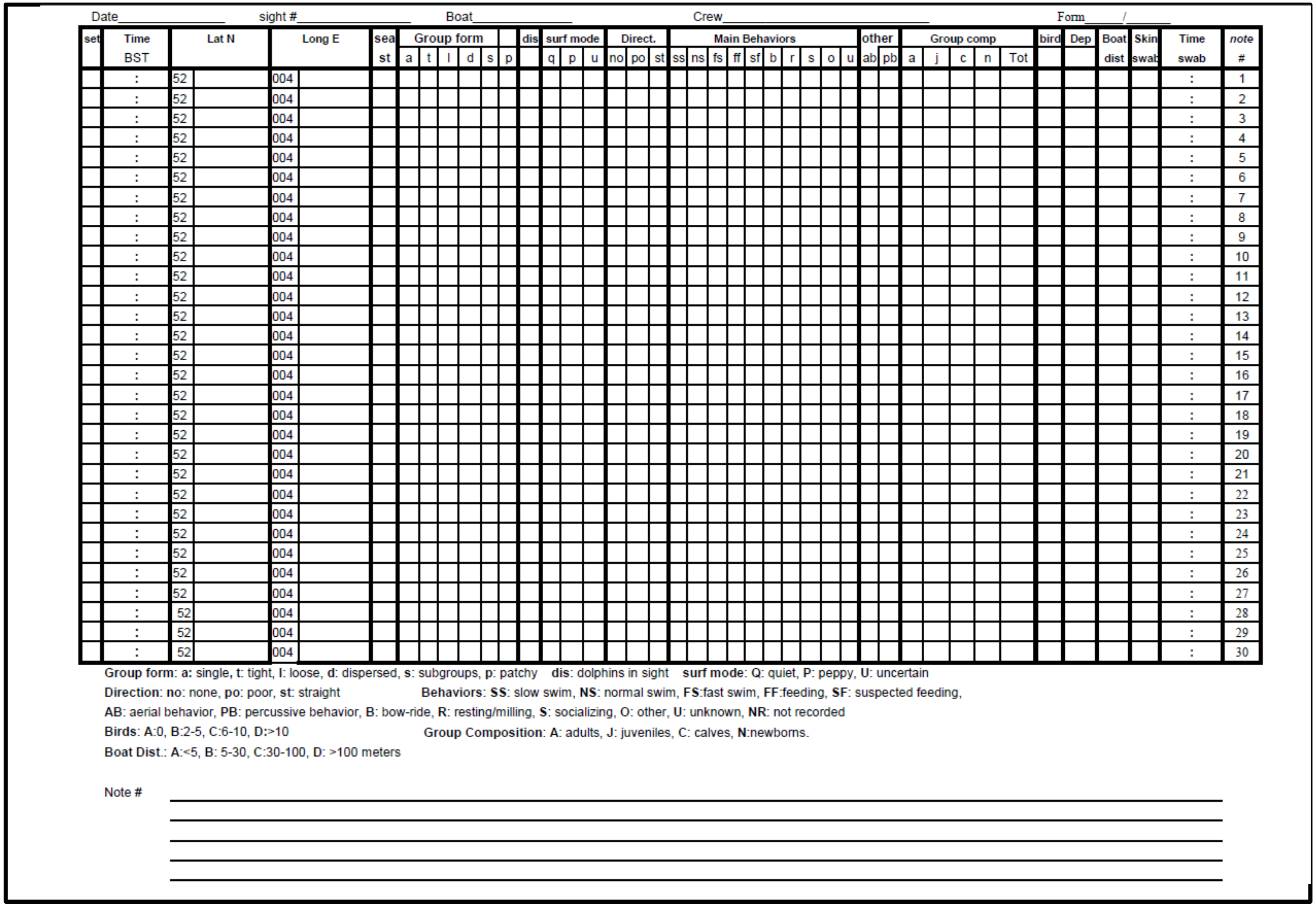
Appendix C: Latitude and longitude for the recordings from which whistles were recorded.

Encounter and Time of Recording	*Latitude*	*Latitude Decimal Degrees*	*Longitude*	*Longitude Decimal Degrees*
35 (10.44)	52” 13.005	52.21675	004” 22.526	-4.37543
26 (14.04)	52” 30.561	52.50935	004” 17.939	-4.29898
26 (14.07)	52” 38.165	52.63608333	004” 15.331	-4.25552
28 (15.28)	52” 34.75	52.57916667	004” 10.704	-4.1784
43 (08.57)	52” 10.498	52.17496667	004” 28.044	-4.4674
45 (14.40)	52” 10.264	52.17106667	004” 29.023	-4.48372
45 (14.46)	52” 10.088	52.16813333	004” 29.027	-4.48378
45 (14.50)	52” 9.986	52.16643333	004” 29.115	-4.48525
45 (14.58)	52” 9.947	52.16578333	004” 29.417	-4.49028
9 (14.43)	52” 9.692	52.16153333	004” 29.726	-4.49543
46(07.05)	52” 13.213	52.22021667	004” 21.762	-4.3627
46(07.08)	52” 13.231	52.22051667	004” 21.777	-4.36295
46(07.12)	52” 13.237	52.22061667	004” 21.775	-4.36292
51(09.29)	52” 11.372	52.18953333	004” 38.696	-4.64493
51(09.32)	52” 11.423	52.19038333	004” 38.521	-4.64202
51 (09.41)	52” 11.673	52.19455	004” 38.137	-4.63562
51 (09.45)	52” 11.782	52.19636667	004” 38.031	-4.63385
51 (09.48)	52” 11.856	52.1976	004” 38.094	-4.6349
57 (12.41)	52” 9.348	52.1558	004” 37.492	-4.62487
57 (12.45)	52” 9.338	52.15563333	004” 37.702	-4.62837
57 (12.48)	52” 9.298	52.15496667	004” 38.01	-4.6335
57 (12.57)	52” 9.148	52.15246667	004” 37.787	-4.62978
57 (13.03)	52” 9.043	52.15071667	004” 38.029	-4.63382
57 (13.06)	52” 8.95	52.14916667	004” 38.351	-4.63918
75 (17.18)	52” 13.077	52.21795	004” 22.446	-4.3741
75 (17.33)	52” 13.446	52.2241	004” 22.565	-4.37608
13 (14.14)	52” 8.648	52.14413333	004” 33.429	-4.55715
13 (14.26)	52” 8.714	52.14523333	004” 33.448	-4.55747
76 (08.48)	52” 13.239	52.22065	004” 20.716	-4.34527
79 (12.51)	52” 13.31	52.22183333	004” 22.027	-4.36712
25 (12.28)	52” 13.074	52.2179	004” 20.949	-4.34915
26 (2) (12.53)	52” 13.21	52.22016667	004” 21.286	-4.35477
26 (2) (12.59)	52” 13.192	52.21986667	004” 21.673	-4.36122
27 (11.03)	52” 13.325	52.22208333	004” 21.786	-4.3631
27 (11.11)	52” 13.362	52.2227	004” 21.888	-4.3648
9 (2) (17.41)	52” 19.326	52.3221	004” 22.331	-4.37218
9 (2) (17.56)	52” 18.389	52.30648333	004” 22.819	-4.38032
9 (2) (19.57)	52” 32.304	52.5384	004” 5.722	-4.09537

Appendix D: Full EUNIS Habitat Map



Appendix E: Boat Behaviour Form



Date_______________ sight #_______________ Boat_____________ Crew___________________________ Form_____/______

set	Time	Lat N		Long E		sea	Group form						dis	surf mode			Direct.			Main Behaviors										other		Group comp					bird	Dep	Boat	Skin	Time	*note*
	BST					st	a	t	l	d	s	p		q	p	u	no	po	st	ss	ns	fs	ff	sf	b	r	s	o	u	ab	pb	a	j	c	n	Tot			dist	swab	swab	#
	:	52		004																																					:	1
	:	52		004																																					:	2
	:	52		004																																					:	3
	:	52		004																																					:	4
	:	52		004																																					:	5
	:	52		004																																					:	6
	:	52		004																																					:	7
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	:	52		004																																					:	9
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	:	52		004																																					:	28
	:	52		004																																					:	29
	:	52		004																																					:	30

Group form: **a:** single, **t**: tight, **l**: loose, **d**: dispersed, **s**: subgroups, **p**: patchy **dis**: dolphins in sight **surf mode**: Q: quiet, P: peppy, U: uncertain

Direction: **no**: none, **po**: poor, **st**: straight **Behaviors**: **SS**: slow swim, **NS**: normal swim, **FS**:fast swim, **FF**:feeding, **SF**: suspected feeding,

AB: aerial behavior, **PB**: percussive behavior, B: bow-ride, **R**: resting/milling, **S**: socializing, O: other, **U**: unknown, **NR**: not recorded

Birds: A:0, B:2-5, C:6-10, D:>10 **Group Composition**: A: adults, J: juveniles, C: calves, **N**:newborns.

Boat Dist.: A:<5, B: 5-30, C:30-100, D: >100 meters

Note # ____

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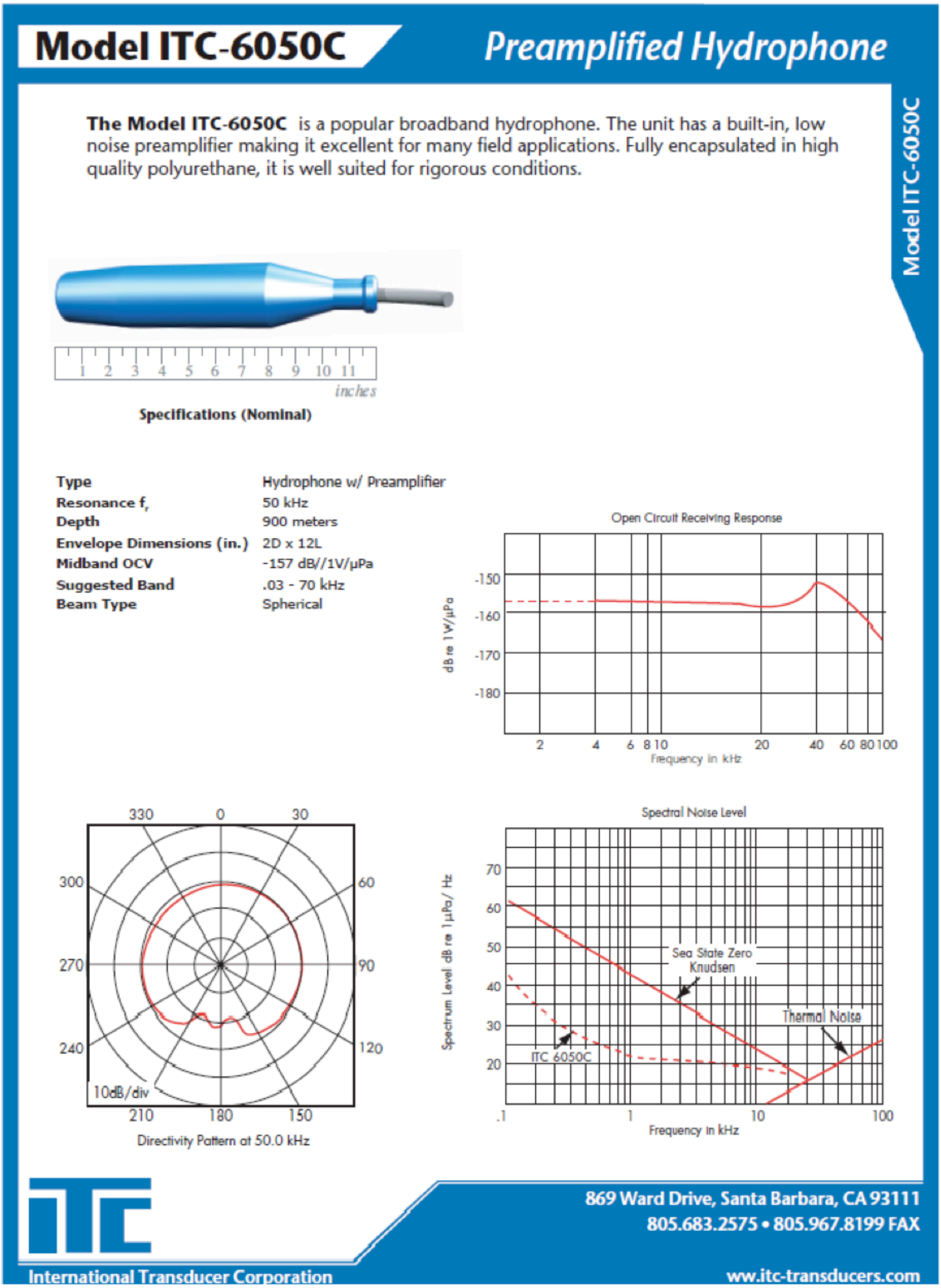
Appendix F: Hydrophone Specification



Model ITC-6050C

Preamplified Hydrophone

The Model ITC-6050C is a popular broadband hydrophone. The unit has a built-in, low noise preamplifier making it excellent for many field applications. Fully encapsulated in high quality polyurethane, it is well suited for rigorous conditions.

Specifications (Nominal)

Type	Hydrophone w/ Preamplifier
Resonance f$_r$	50 kHz
Depth	900 meters
Envelope Dimensions (in.)	2D x 12L
Midband OCV	-157 dB//1V/µPa
Suggested Band	.03 - 70 kHz
Beam Type	Spherical

Directivity Pattern at 50.0 kHz

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International Transducer Corporation

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