The Effect of Boat Noise and Depth of Water on the Frequency of Echolocation of bottlenose dolphins, (*Tursiops truncatus*) in Cardigan Bay

Elizabeth Shaw

Submitted in part candidature for the degree of B.Sc. Zoology, Institute of Biological, Environmental and Rural Sciences, Aberystwyth University

MODULE **BS32930 – P**ROJECT

I certify that except where indicated, all material in this thesis is the result of my own investigation and references used in preparation of the text have been cited. The work has not previously been submitted as part of any other assessed module, or submitted for any other degree or diploma.

NAME (Capitals) …………………………………………….………..

Signed …………………………………………………………………..

Date …………………………………………………………………..

Acknowledgements

ABSTRACT

As visibility in the marine environment can be poor, cetaceans communicate, navigate and forage acoustically. Anthropogenic noise can propagate over long distances underwater in the marine environment and there is increasing evidence and concern that noise generated by boats in particular, may lead to signal masking in cetaceans. Here I investigate the effect of boat noise on the frequency of echolocation in bottlenose dolphins in Cardigan Bay. This study shows that the bottlenose dolphins (*Tursiops truncatus*) of Cardigan Bay show plasticity in the frequency of echolocation and are able to reduce this masking effect by altering the frequency of echolocation (Hz) when boats are present. Dolphins have significantly lower echolocation frequencies when boats are present. The number of clicks per second was also significantly lower when boats were present. In contrast, there was a significant negative correlation between distance from New Quay harbour, where peak levels of boat activity are found, and the frequency of echolocation, though there was no significant correlation between peak frequency and distance to shore. There was also a significant correlation between water depth and echolocation frequency. These findings illustrate that bottlenose dolphins in Cardigan Bay have the ability to change their acoustic signals in response to masking. Therefore, although human activity and increasing levels of boat noise may be a cause for concern, bottlenose dolphins seem to be able to find ways of avoiding signal masking.

CONTENTS

ABBREVIATION GLOSSARY

CBMWC – Cardigan Bay Marine Wildlife Centre

COG – Course Over Ground

CCW – Countryside Council for Wales

FFT – Fast Fourier Transform

GPS – Global Positioning Satellite

Hz – Hertz

MB – Motor Boat

RIB – Rigid Inflatable Boat

SAC – Special Area of Conservation

T-POD – Timed Porpoise Detector

VPB – Visitor Passenger Boat

1.0 Introduction

1.1 Sound and Communication

Sound is an energetic medium utilised by many species for the important behavioural function of communication in order to convey information; both between conspecifics or heterospecifics (Marler, 1967). The use of sound and the diversity of signals used for communication may have assisted in the evolution of sociality in the vertebrates (Cavallisforza and Feldman, 1983), as it is vital for individuals in gregarious species to convey important information about their surroundings as well as make informed decisions based on the use of signals by others (Endler, 1993). Sound as a medium of communication, is important for both inter-specific competition (e.g. nightingales, *Luscinia megarhynchos*, time their vocal calls to avoid inter-specific competition; Brumm, 2006)   and intra-specific competition (e.g. competition between males in red deer, *Cervus elaphus*; Berglund, 1995). It is also important in maintaining hierarchies within polygynous species (e.g. in elephant seals, *Mirounga angustirostris,* Bartholomew, 1961).

Prey location is another important function of sound emission, as well as orientation of an individual within its surroundings. As well as being used to communicate the whereabouts of a food source to conspecifics and coordinate group

foraging e.g. in greater spear-nosed bats, *Phyllostomus hastatus*, (Wilkinson and Boughman, 1998) sound can also be used for auto-communication, where a sound is broadcasted and received by the same individual, by echolocation. Echolocation is classed as a broadband vocal sound described as a directional beam of ultrasonic clicks (Caldwell and Caldwell, 1965). It is an adaptive method of locating prey and orientating an individual to its surroundings that has evolved separately in different groups of animals by the process of convergent evolution. The use of echolocation has been documented in bats: *Microptera*, toothed whales: *Odontocetes,* tenrecs, cave swiftlets, (*Aerodramus)* oil bird (*Steatornis caripensis*) and two orders of shrew: *Sorex* and *Blarina* (Martin, 1990).

1.2 Development of acoustical location

The ability to detect prey acoustically appears to have evolved as an adaptation to enable the capture of prey in habitats where visual prey location is difficult. For example, within Aves, acoustic senses are relied upon for prey location by the marsh hawk, to locate prey concealed in long grass (Rice, 1982) and by owls (Order: *Strigiformes*) such as barn owls (*Tyto alba*) which hunt nocturnally and have highly developed directional hearing ability (Payne, 1971). Within the mammalian kingdom, those species which rely on sound for prey location do so for similar reasons; insectivorous bats (e.g. little brown bat, *Myotis lucifugus*) use echolocation to detect the location of fast moving, air borne prey to enable them to track individual targets more efficiently than by sight (Fenton *et al*., 1998). Furthermore, it has also enabled efficient nocturnal hunting for both bats and cave-dwelling birds (Martin, 1990).

The odontocetes use sound, both as a medium for communication used in group hunting activities (Gazda *et al*., 2005) and individual recognition (Janik *et al*., 2006) between group members, as well as for echolocation for prey location and orientation. However, the sounds used for each of these functions are distinguished by different frequencies and length of bursts of sounds, with echolocation clicks being higher in frequency and more directional, than sounds used for communication which are broader to maximise acoustical space (reviewed in Clausen *et al*., 2010). It has also been noted that acoustic signaling from bottlenose dolphins can also be non-vocal, for example, from tail slapping (Grellier *et al*., 1995).

Another possible reason for why echolocation may have evolved is due to abiotic factors; the origin of echolocation in bats has been correlated with global warming during the Paleocene – Eocene geological period (Gingerich, 2006). This theory has been mirrored in odontocetes, by suggesting echolocation developed in conjunction with the creation of the circum – Antarctic current (Fordyce, 1980, from Lindberg and Pyenson, 2007). However, it has been argued that biotic factors may have been more important, with echolocation in odontocetes conferring a selectional advantage of nocturnal prey capture and capture of prey such as cephalopods at depths where light cannot reach (Lindberg and Pyenson, 2007).

1.3 Mechanisms of Echolocation and Physiological Adaptations

As echolocation is based solely on acoustic signalling, it follows that specialised physiological adaptations, particularly within the auditory system, are required. In

Michropteran bats, it has been reported that the larynx is involved in sound production and the ear is specially adapted, with especially large pinnae, so that information from the sound is accurately obtained, (Pye, 1960).

The ability to echolocate has evolved as a successful mechanism to find prey in the toothed whales due to the attributes of sound travel though the viscous medium (Tyack, 2008). However although other groups of mammals inhabit the same environment: Mysticeti and Pinnipeds, the ability to echolocate in these animals remains absent (Schusterman *et al*., 2000). It has been suggested that the dentition of odontocetes may be a contributing factor in sound reception and nerve conduction to the ear via vibrations (Potter and Taylor, 2001). An alternative suggestion stems from research that has shown that there appears to be homologous interspecific structures between the odontocetes, with fatty components that are responsible for the production of pulsed sounds forming the basis of echolocation, being of significant importance (Cranford *et al*., 1996).

The basic principle of echolocation in odontocetes is that the individual produces a sound in the nasal system from a complex just under the blowhole (Cranford *et al*., 1996). This is projected in a directional beam through the melon (Norris, 1968 *In* Evans and Madderson, 1973), a lipid structure in front of the nasal plug, before passing through the water and reflecting from the surroundings, back to the individual. In this way, the individual can build up an idea of the distance to particular object, its movement and its density. The signal is emitted forwards and

slightly upwards from the animal and are usually emitted within a time frame that allows each echo to return to the animal before the next is emitted (Au, 2004). In the Atlantic bottlenose dolphin (*Tursiops truncatus*), studies have indicated that echolocation signals have a short duration (less than 50-70µs), have a high intensity (up to 230dB) and a relatively high frequency (Au and Nachtigall, 1997).

The mechanism of exactly how the odontocetes have the ability to echolocate is highly complex and therefore, still poorly understood (Potter and Taylor 2001, Cranford *et al*., 1994, Evans and Madderson, 1973). This difficulty is possibly due to its close link with the evolution of the respiratory system which requires the use of the same structures used in sound production (Cranford *et al*., 1994).

1.4 Signal masking

Where acoustic communication is of such importance, both socially and functionally, to increase fitness, as well as when it is widely used within a particular niche, there is the potential for signal masking to occur. The concept of signal masking has been described as 'when the perception ability to detect and decode information from a signal is affected by another sound within the same auditory filter band' (Gelfand, 2004). Noise is the term describing any sound which is not the signal in question that interferes with the receivers' ability to distinguish between signals or distinguish the signal from background noise (Wiley and Richards, 1978), Noise is therefore the cause of auditory signal masking, and becomes a masking problem when it occurs in the frequency range that overlaps the signal (Madsen *et al*., 2006). It can

be derived from a variety of sources that can occur within a three dimensional space surrounding the individual, also referred to as: 'bio-acoustic space'. The bio-acoustical activity within in the individuals' auditory space can originate from conspecifics communicating with the individual, from eavesdropping on communication between other interacting conspecifics, the individual itself (by echolocation) or communication between heterospecifics (Parks *et al.*, 2007).

Naturally occurring biotic factors such as ambient noise from the environment, oceanographic features or geo-seismic events which can all lead to signal interference, are not the sole source of noise that may instigate signal masking (Tyack, 2008). Anthropogenic noise, which is derived from a wide variety of sources, can also mask acoustic signals. In the terrestrial environment, anthropogenic noise causing signal masking, has been widely demonstrated, particularly by urban noise masking bird song, for example: in house finches (Bermudez-Cuamatzin *et al.*, 2011) and great tits, *Parus major*, (Slabbekoorn and Ripmeester, 2008; Mockford and Marshall, 2009). Anthropogenic signal masking in birds has now been found to have a negative impact on reproductive success, with female great tits laying smaller clutches and nurturing fewer successful fledglings in noisier areas (Halfwerk *et al.*, 2011).

However, the properties of sound which travels through an aquatic environment are inherently much different to those of a terrestrial environment. Sound travels around 5 times faster through water than air (Forrest, 1994), due to the higher density of the medium and therefore, there is greater opportunity for

attenuation affects to impact upon sounds emitted for communication and echolocation. Whereas sound can be transmitted aerially up to a few kilometres, it can be propagated thousands of kilometres through the ocean (Lurton, 2002). Therefore, it can be expected that the effects of acoustical signal masking will be demonstrated to an even greater extent within the aquatic environment.

Evidence of this has already been found in the aquatic environment. For example, the possible effects of anthropogenic noise on fish have recently been highlighted, suggesting that masking sounds affect acoustical communication, which is can particularly impact upon reproduction success (Slabbekoorn *et al*., 2010). Supporting empirical evidence has also shown in mysticetes that the presence of two commercial shipping vessels results in an 84% loss of communication space in right whales (Clark *et al*., 2009). In addition, it has been calculated that vessels moving at a speed of 5 knots will reduce the communication range of bottlenose dolphins within 50m of the vessel by 26%, increasing with vessel speed and gear changes (Jenson *et al*., 2009). There is also increasing concern that proposed offshore wind farms may cause signal masking in the low frequency band, which in particular, will mask the low frequency communication propagated by mysticetes (Madsen *et al*., 2006).Furthermore, the construction of these by pile-driving also has masking potential over a relatively large distance (David, 2006).

1.5 Avoidance of Signal Masking

Where signal masking occurs, individuals, or individuals of a species collectively, can adapt by changing their own signalling method. For example, because many species of tree frogs tend to form dense aggregations to perform mating calls, some species have adapted to rely on optic, rather than acoustic, signalling due to signal masking by conspecifics and other sympatric species (Gerhardt and Klump, 1988). The tropical *Anolis* lizard uses visual environmental cues to time its displays to competing males and receptive females, so that it avoids displaying in a 'noisy environment' for example, when the wind is strong and vegetation may obscure the display, resulting in wasted energy (Ord *et al*., 2011).

Other methods of compensating for masking by noise include: elongating the time frame of a signal, waiting until the noise masking the signal has reduced, or by emitting louder signals themselves (Tyack, 2008). Alternating calls with conspecifics has also been documented: for example, in nightingales (Naguib, 1999). Another option involves a shift in frequency of the sound so that the inanimate noise is no longer overlapping the same band range. This has been documented in bats such as *Tadarida teniotis* which show a 'Jamming Avoidance Response' by altering the frequency of echolocation by varying amounts according to the distance between conspecifics whilst foraging (Ulanovsky, 2004).

However, avoidance of signal masking can also involve a more significant change of the signal entirely or stimulate a physical behavioural response. For

example, the individual may alter their behaviour to avoid 'noise polluted' areas. This has been shown in bottlenose dolphins that dolphins will move away from foraging areas when boat traffic becomes heavy (Allen, 2000) and head directly away from nearby boats (Mattson *et al*., 2005), although a neutral, rather than an avoidance response, has been found in the same species in Cardigan Bay (Gregory and Rowden, 2001). In dolphins off the Moray Firth in Scotland, it has been reported that heavy boat traffic is associated with increased breathing synchrony between pod members, although the function of this behavioural change is still unclear but it has been suggested that it is an anti-predatory response to the threat posed by boats (Hastie *et al*., 2003).

Evidence of increased whistle rate was found in bottlenose dolphins in Florida, where dolphins came into contact with passenger vessels very frequently (every 6 minutes), leading to an increased whistle rate upon vessel approach which may be in response to signal masking (Buckstaff, 2004). It has recently been suggested that mass strandings of cetaceans may be linked to military sonar, with this anthropogenic noise causing their navigation systems to fail, although it is difficult to confirm the exact cause (Fernandez *et al*., 2005). It may be that there is a particular threshold, where noise reduces the ability for the acoustic signals to be recognised so much that it is no longer advantageous to remain in a particular area, even if food is in high abundance. However, negative behavioural changes may be associated with the other dangers boats pose to cetaceans, such as damage by propellers caused by collisions with boats and entanglement in fishing gear (Garrod and Fennell, 2004).

It has recently been hypothesised that resting frequency divergence of echolocation in rhinolophid bats could be to determine members of their own species from other sympatric species (Siemers *et al*., 2005), and by calling at different species, overlap and interference is avoided (Russo *et al*., 2007) Alternatively, it has been argued that the difference in echolocation frequency of sympatric species could be to allow different sized prey to be captured (Houston *et al*., 2004 in Jones and Holderied, 2007).

It has been shown that signal masking of communication occurs within various cetacean species within the aquatic environment. For example, it has been shown that communication masking occurs in singing humpback whales which produce lower frequency songs when there is a higher ambient noise in the surrounding area (Clark, 2009). Further studies on the effects of boat noise on the vocalisations of the Pacific humpback dolphin (*Sousa Chinensis*) found that although click rate did not change, dolphins increased their whistling rate when coming in contact with boats (Van Parijs and Corkeron, 2001). Acoustical analysis of indo-pacific dolphins highlighted that in habitats with higher ambient noise, dolphins produced whistles with lower frequencies (Morisaka *et al*, 2005), illustrating that this is an adaptive response to signal masking that may also be applied to boat noise. The effect of boats on the acoustical behaviour has also been investigated in beluga whales (*Delphinapterus leucas*) where calling rate decreased as boats approached, as well as a shift in frequency bands to a higher frequency when the vessels were close, although this shift only lasted up to one minute (Lesage *et al*., 1999).

The depth of water also has the capacity to affect acoustic signalling). Only signals above a certain 'cut-off' frequency will propagate without much attenuation in shallow waters due to there being sound constraints by the boundary conditions between substrates (Rodgers and Cox 1988 *In* Atema *et al*.,1988). However, little research has been done in this area of aquatic acoustics to date. As Cardigan Bay is a relatively shallow area with depths only reaching up to 55m at its' deepest, (Ceredigion County Council *et al*., 2008) it may be that noise propagates more readily and is therefore a good area to study the effects of depth on possible frequency shift in echolocation to reduce signal masking.

1.6 Cardigan Bay and bottlenose dolphins

Cardigan Bay has the highest abundance of bottlenose dolphins, *Tursiops truncatus,* (Gervais, 1855) in the U.K (Pesante *et al*., 2008 *In* Pierpoint *et al*, 2009) and is one of only two regions in the United Kingdom where there is a resident population; the other being the Moray Firth in Scotland (Wilson *et al*. 1997). Recent estimates from photo Identification studies suggest that there are currently over 200 individuals that are regularly sighted in the area (Grellier *et al*., 1995). There is a seasonal distribution of bottlenose dolphins within Cardigan Bay with significantly more sightings between April and October since 1990, which is thought to be associated with the migration of shoals of prey such as mackerel (Grellier *et al*, 1995).

Part of the Cardigan Bay coastline was designated a Special Area of Conservation (SAC) under the European Habitats Directive, in 2004, with the aim of

addressing the conservation needs of the bottlenose dolphin (Grellier *et al*. 1995). This area encompasses the Southern part of Cardigan Bay, and reaches approximately 12 miles offshore (See Figure 1). As well as bottlenose dolphins being of prevalence in this area, another cetacean; the more elusive Harbour porpoise, *Phocoena phocoena,* (Linaeus, 1758) is also relatively abundant, as well as the pinniped: Atlantic grey seals, *Halichoerus grypus* (Fabricius, 1791). Boat users within Cardigan Bay are required to adhere to a strict Code of Conduct within the SAC; particularly when coming into contact with cetaceans, Atlantic grey seals (*Halichoerus grypus)* and bird colonies.

Land observations are conducted throughout the Summer months at various points down the coast of Cardigan Bay (See Figure 1) where the number of marine mammals as well as boat activity is recorded. The 2008-2009 report has further substantiated the findings of previous surveys which show that Mwnt has the highest sightings rate of bottlenose dolphins, compared to the other observation points (Ceredigion County Council *et al*., 2008). There is a thriving tourist and fishing industry in Cardigan Bay, and the focal area for this hive of activity is New Quay, with the highest number of boats being recorded at New Quay Harbour in the years 2004-2009 consecutively. However, it has also been found from compiled data from 1994-2007 that site use of the New Quay Harbour area by bottlenose dolphins is suppressed by heavy boat traffic, compounded by the observation of significantly more dolphins in 2007 when boat traffic levels were low because of poor weather during the tourist season (Pierpoint *et al.,* 2009). Previous research conducted in this area, and

abundance of bottlenose dolphins indicates that it is a good location to continue the study of the affects of boat noise on their acoustical behaviour.
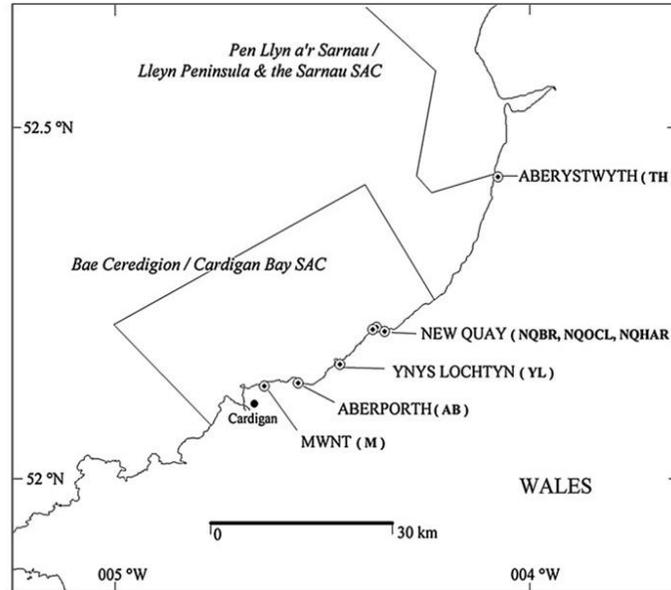

Figure 1: Map illustrating the area designated as Cardigan Bay SAC (Pierpoint *et al*., 2009)

1.7 This Study

The aims of this research are to investigate the following questions:

- Does boat presence affect the frequency of bottlenose dolphin echolocation?
- Does boat presence affect the rate of echolocation clicks?
- Does distance to harbour influence the frequency of dolphin echolocation?
- Does distance to harbor influence the rate of echolocation clicks?
- Does depth of water influence the frequency of dolphin echolocation clicks

2.0 METHODS

All sound recordings and observational data were collected during Summer 2010 from 22nd July to the 5th September onboard The Sulaire: a 33 foot long dolphin survey vessel (Figure 3), operating trips from New Quay Harbour. The data was obtained at various locations during two hour trips along the West Coast of Wales from New Quay (52°21N, 004°35W), Ceredigion to Ynys Lochtyn (52°16N, 004°46W) though the specific routes of different trips varied (Figure 2).
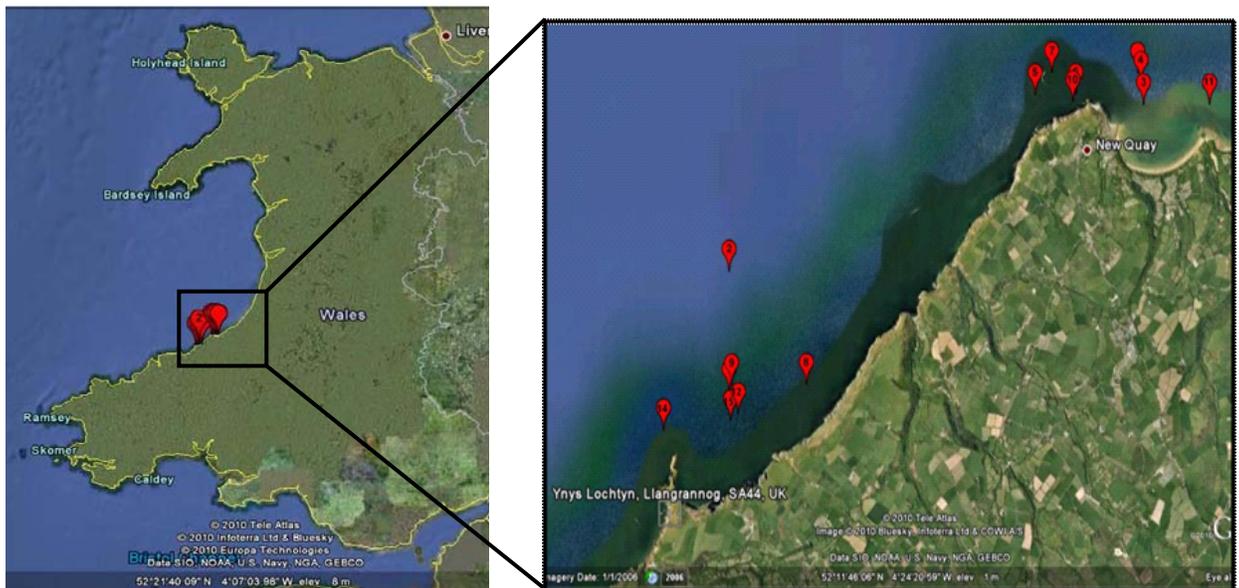

Figure 2: Left: Map image with red markers illustrating the location of sound recordings made in relation to a Map of Wales. Right: A closer view of the Ceredigion Coast illustrating where the recordings were made. Two clusters of recordings are observable: one near New Quay Harbour and the other near Ynys Lochtyn (Image from Google Earth© Version 6.0.2)

In 1997, commercial passenger boat operators agreed to a universal Code of Conduct for their behaviour around the marine Wildlife of the SAC. According to this Code of Conduct, the main points to consider when coming into contact with cetaceans are : not to approach an individual head on, throttle back when within

300m, remain stationary or cruise by when within 100m from any group and let them come to you and avoid deviating from agreed routes to see the animals (Ceredigion County Council, 2009). The Code of Conduct was adhered to by the Sulaire throughout the duration of the trips when data was collected.

Volunteers, including myself, from the Cardigan Bay Marine Wildlife Centre, recorded Environmental (Effort) data continuously throughout each trip. This data included: the position of the boat (location, speed, course) environmental conditions (precipitation, sea state, swell, wind direction, wind force) and details of cetacean and seal sightings (numbers, behaviours, angle and distance from boat) as well as details of other boats in the area. All volunteers received training at the start of the project to ensure data was recorded consistently.

Location, speed and Course Over Ground (COG) were established using a hand-held Global Positioning Satellite (GPS). Sea state was recorded according to the universal Beaufort Scale sea surface criteria (Table 1). All recordings were made in a Sea State of 1 or 2, minimising any effects of differing ambient noise due to water movement. Observers recorded a new effort line of environmental data every time the following survey conditions changed: speed, boat course, precipitation, sea state, wind direction, wind force, or if there was no change; a new line was recorded every 15 minutes. On encountering marine mammals, each sighting was allocated a number which was recorded next to the last effort line made and this number corresponded to the data subsequently recorded on the sightings form.

Table 1: The Beaufort Scale of Sea State (as used by Cardigan Bay Marine Wildlife Centre on every survey)

Sea State	
0	Calm, glassy, mirror sea
1	Calm, rippled surface
2	Wavelets, glassy crests that do not break
3	Small Waves (<1m) occasional whitecaps
4	Longer Waves (1-1.5m) frequent whitecaps
5	Many white horses, waves (2m)
6+	Rough, white foam crests everywhere, waves >2.5m high

Sound recordings were opportunistic, dependant on bottlenose dolphin sightings, and obtained by lowering a hydrophone (Standard Cetacean Monitoring Hydrophone from Seiche Measurements Ltd.) overboard into the sea when coming within 300 metres of bottlenose dolphins. The hydrophone acts as a pressure transducer; converting the acoustic signals into an electronic sound wave that can be recorded and viewed on a spectrogram. The hydrophone was connected to a bat detector (Magenta Bat4 Precision), connected to a sound card, connected via USB to a laptop. Underwater sounds were then recorded to the Sound Card using the dolphin acoustic programme PAMGUARD (Passive Acoustic Monitoring Guardianship: Version 1.9.01 Beta).

A separate form for recording data specific to the hydrophone recordings was made in order to relate particular recordings to the corresponding Effort and Sightings data. The depth of water was also recorded in order to explore the second hypothesis of whether water depth affects the frequency of bottlenose dolphin echolocation. This data was collected by the OLEX system: a bathymetric sounder that measures the

time delay of the seabed echo to create a 3D image of the sea floor (Lurton, 2002).

The distance to the harbour from each recording point was measured by using the

latitude and longitude of where the recordings were made (as was recorded during

data collection) to plot the locations onto a map using Google Earth © (Version 6.0.2.).

The ruler tool on this software was then used to calculate the distance from the

position of the boat at the time of each recording to New Quay Harbour suing a

straight line, avoiding land if the path crossed a headland.

Observer position – high up to enable accurate observations

Figure 2: The boat (The Sulaire) from which hydrophone recordings were taken and observations of bottlenose dolphins made

The information recorded about other boats in the area was recorded and

included the type of boat in abbreviated form as well as the estimated distance to the

boat. The type of boat may influence the type and level of noise created, therefore

having different impacts on the vocal impacts of bottlenose dolphins.

Prior to each hydrophone recording, the Sulaires' engine was turned off, and

electrical equipment, including the radio and inverter was also switched off to

minimise interference, though it was difficult to totally eliminate all interference. Each sound recording is identifiable by its automatically saved filename which corresponds to the date and time the recording was made. For example the filename SUL_20100722_115850 shows that the recording was made on the 22nd July 2010 at 11.58. Recordings vary in length and contain a varying number of click trains, which have been separated into new files for analysis using the programme Wave Pad© Sound Editor (Version 4.0; Canberra, Australia). All together, a total of 242 separated click trains have been identified from 15 different recordings, for frequency analysis.

Only pulsed sounds (clicks) were audible and visible on the spectrogram. This may have been because the dolphins were not communicating using non-pulsed sounds (whistles) at the time of the recordings. Therefore, only the frequencies of echolocation clicks were analysed in relation to boat noise, depth of water and distance to the harbour. Recordings were separated into 'click trains' which were defined as having a two second gap before the first and following the last click in a sequence.

In order to analyse the differences in echolocation when boats were and were not present, Mann-Whitney-U tests were conducted to compare the peak frequencies (Hz) of echolocation clicks and also the number of clicks per second in each sound clip. To analyse the effects of depth of water and distance from harbour, a Pearson's correlational test was conducted to test if there is a relationship between these two factors with peak frequency of echolocation clicks and number of clicks per second.

Frequency analysis and calculation of number of clicks per second were made 'blind' to the knowledge of the distance to the harbour, depth of water or presence of boats so as not to inadvertently bias the results.

3.0 RESULTS

13 out of 15 hydrophone recordings contained cetacean echolocation clicks. These are presumed to originate from bottlenose dolphins, rather than the other commonly present cetacean in Cardigan Bay: the harbour porpoise, as all recordings were taken at a time when bottlenose dolphin presence was recorded. From the recordings containing clicks, three were when one adult was present, five were when there were two adults present, two were when three adults were present and three were when four adults were present (Figure 4). There were calves present for three of the recordings and juveniles for two of the recordings. It was difficult to observe the sex of dolphins from the boat so distinctions between sexes were not made. Specific activities were observed and recorded at the time the recordings were made; the most common behaviour exhibited and observed was foraging (Figure 5).
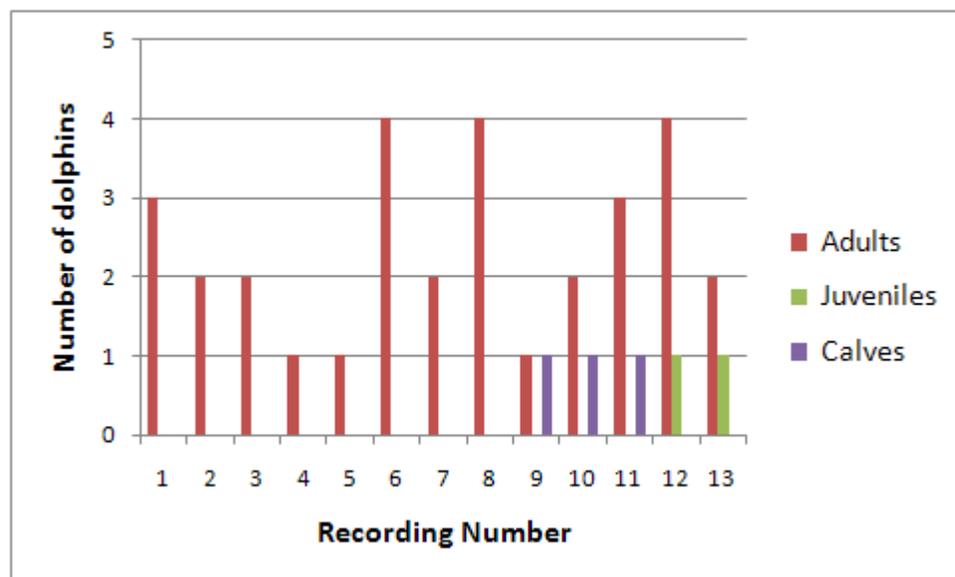

Figure 4: The relative abundance of numbers of adults, juveniles and calves observed when each recording was made
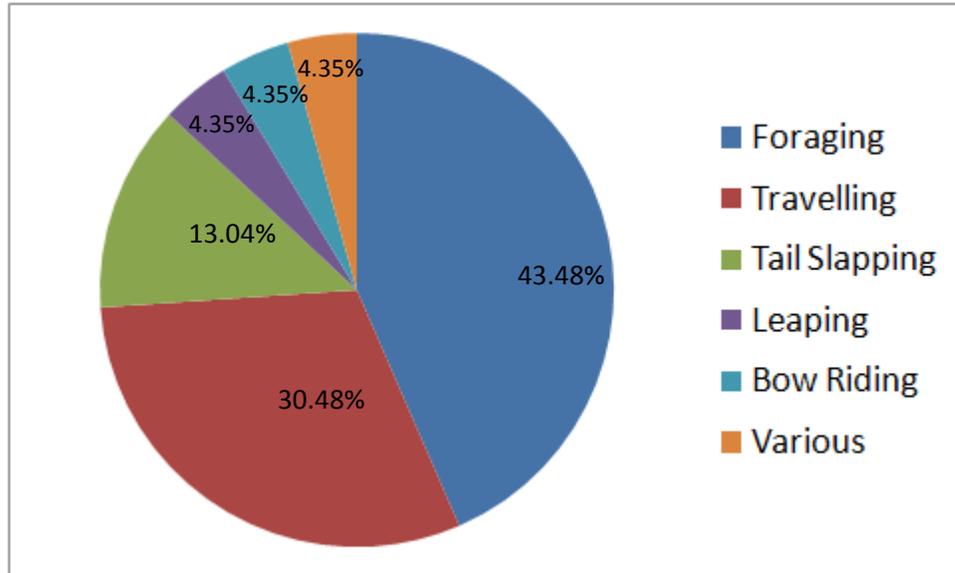
Figure 5: Pie Chart illustrating the percentage of recordings, dolphins were observed engaged in various activities

A Fast Fourier transform (FFT) was calculated and displayed using Wavepad© Sound Editor (Version 4.0; Canberra, Australia) software, enabling each recording to be separated into identifiable click trains (Figure 6). A click train was defined as a group of three or more clicks separated from other groups of clicks by at least a two second gap from the first and last click. Overall, between the 13 recordings, a total of 242 separated click trains were identified for analysis. There were a varying number of distinguishable click trains between the different recordings, with the least being one and the greatest being 55.
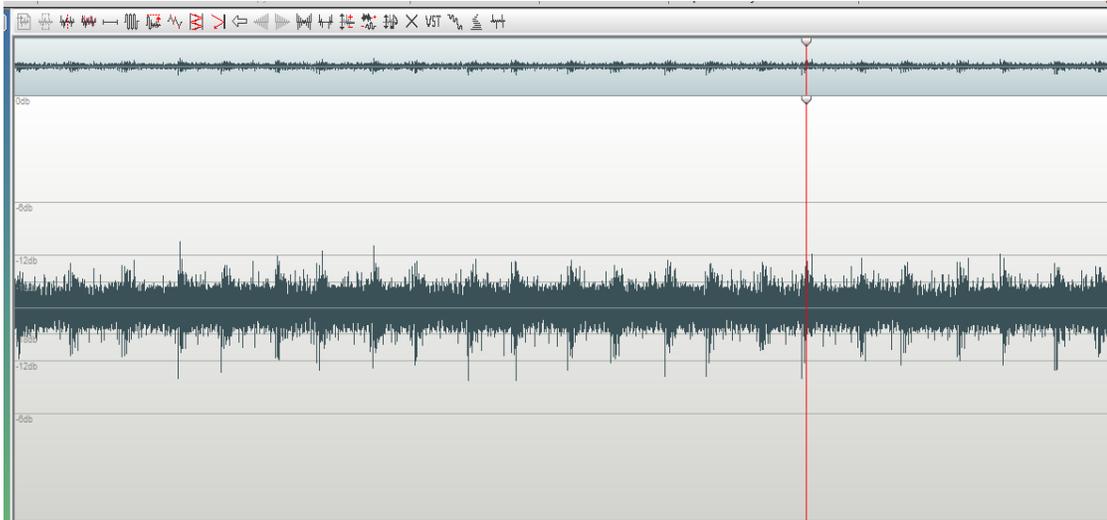
Figure 6: A screenshot of an FFT produced by Wavepad© of the sound recording SUL_20100725_090914-A showing 23 identifiable peaks that correspond to echolocation clicks

Frequency analysis was conducted on the first clear distinguishable click train of each recording using Raven Pro© Interactive Sound Analysis software (version 1.4; New York, U.S.A.) which created a sonogram (Figure 7). The peak frequency of each click (measured in Hz) was analysed at the point where the amplitude was greatest (measured in Db). A mean peak frequency for that click train was then calculated.
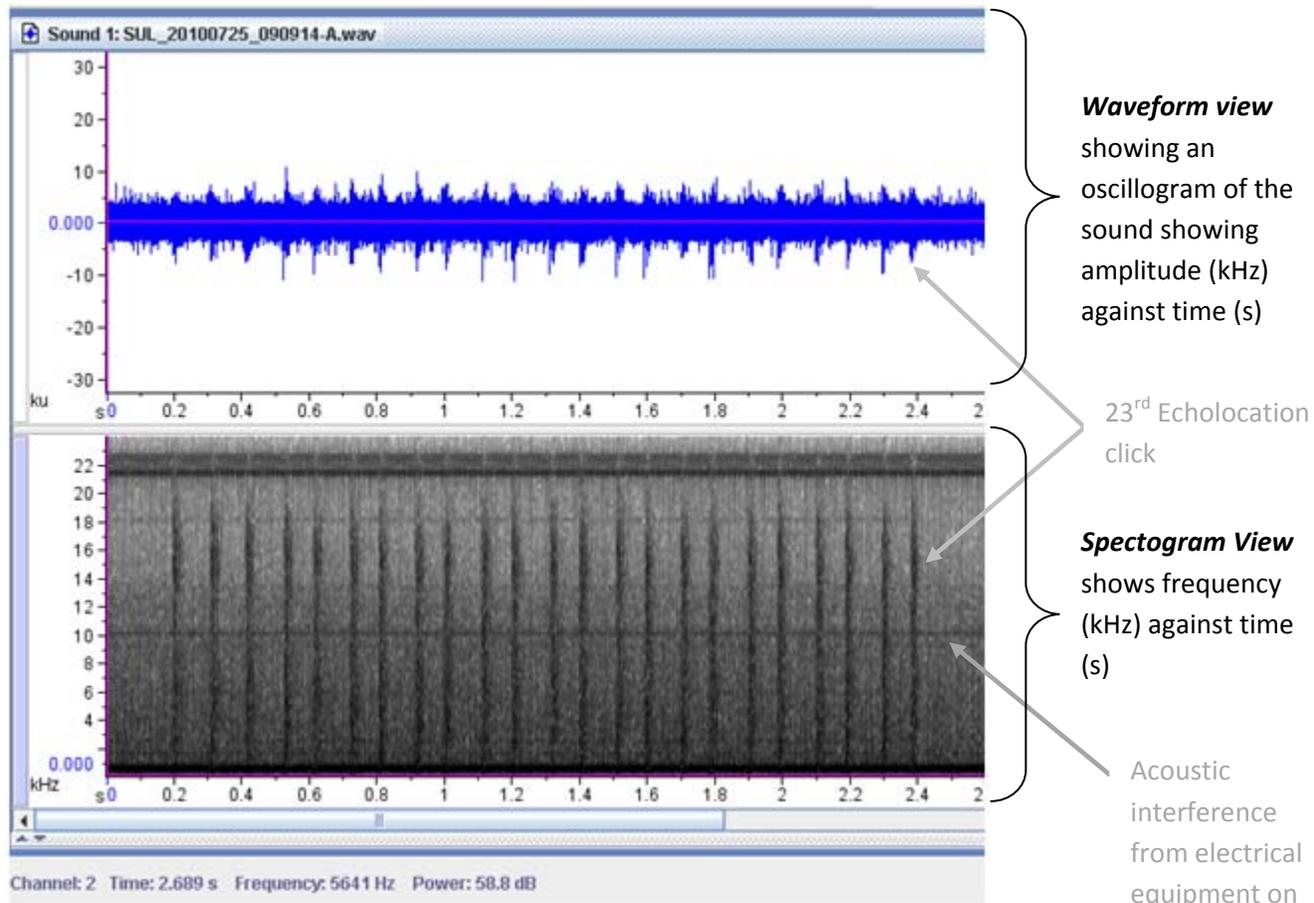
Figure 7: Image of a sonogram produced by Raven© of the sound clip SUL_20100725_090914-A from the recording made on 25/07/10 at N52°13075'W004°21454 with both waveform (upper) and sonogram (lower) view

All boats recorded in this study were Motor Boats, (MB) Visitor Passenger Boats (VPB) or Rigid Inflatable Boats (RIB) meaning they all produce engine noise that propagates through the water. The mean peak frequency of echolocation clicks was significantly higher when no boats were present than when boats were present (W=6597, n=264, P=0.0488; Figure 8)
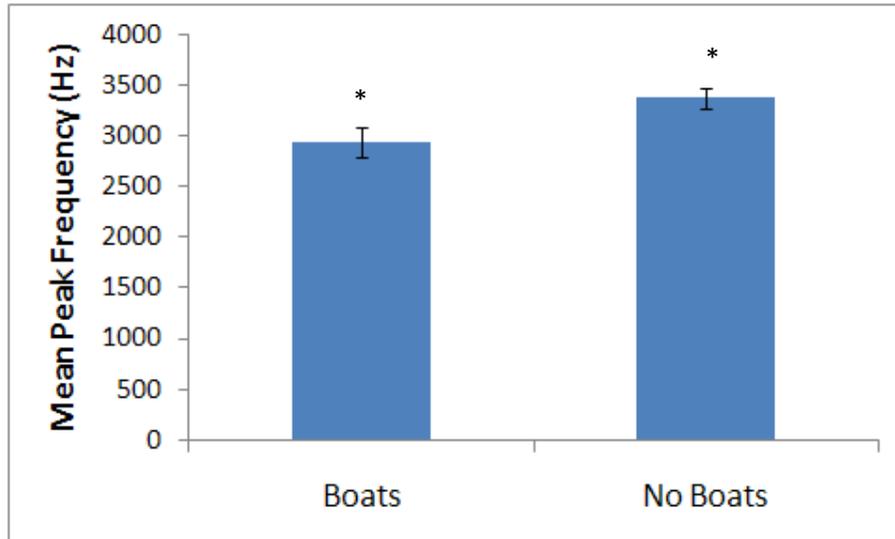
Figure 8: Illustrates the Mean Peak Frequency (Hz) of echolocation clicks from bottlenose dolphins when other boats were present (n=62) and when boats were not present (n=180). Standard error bars are also shown. Asterix indicates statistically significant difference

There was a statistically significant negative correlation between the distance to harbour and the mean peak frequency of dolphin echolocation clicks (r = -0.149, p =0.021; Figure 9).
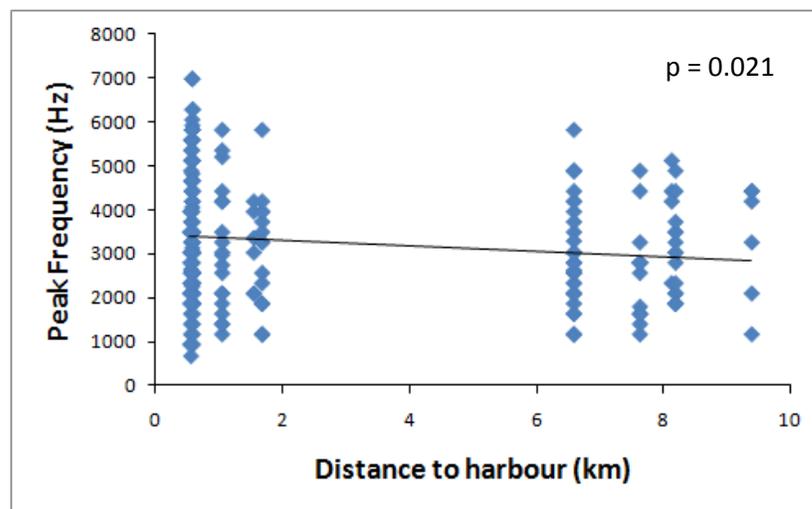

Figure 9: Scattergram showing the correlational relationship between the distance to New Quay Harbour (km) and the peak frequency of echolocation clicks

Distance from the points of recordings to the nearest shoreline was also measured and a Pearsons Correlation Coefficient was conducted to establish if there was a relationship between distance to the shore and peak frequency of echolocation (Hz) and the number of echolocation clicks per second. There was no significant correlation between distance to shore and either peak frequency ($r = -0.107$, $p = 0.097$; Figure 10) or number of clicks per second ($r = 0.019$, $p = 0.768$; Figure 11). This indicates that it is distance to the harbour, which has a high level of boat activity, rather than just distance to the shore that affects the peak frequency of bottlenose dolphin echolocation in this study.
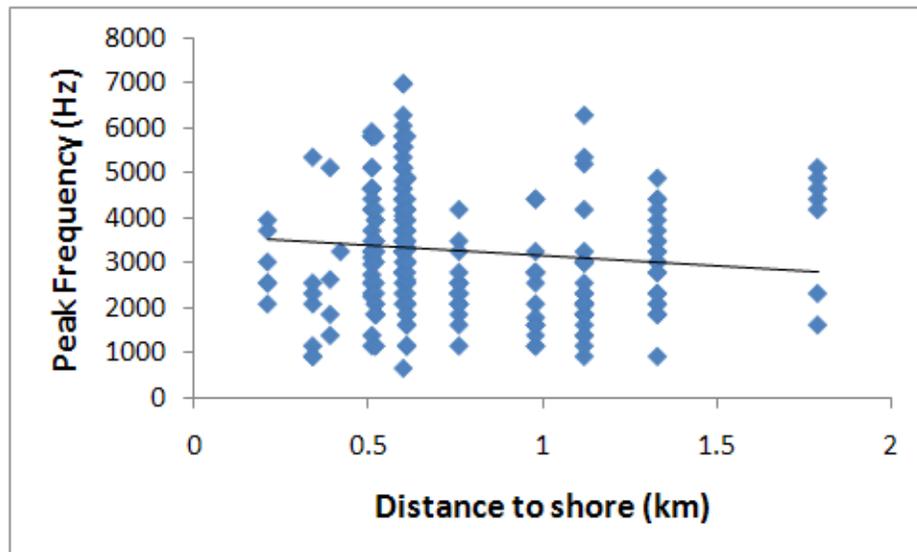

Figure 10: Scattergraph illustrating the correlational relationship between distance to the shore (km) and the Peak Frequency (Hz) of echolocation clicks
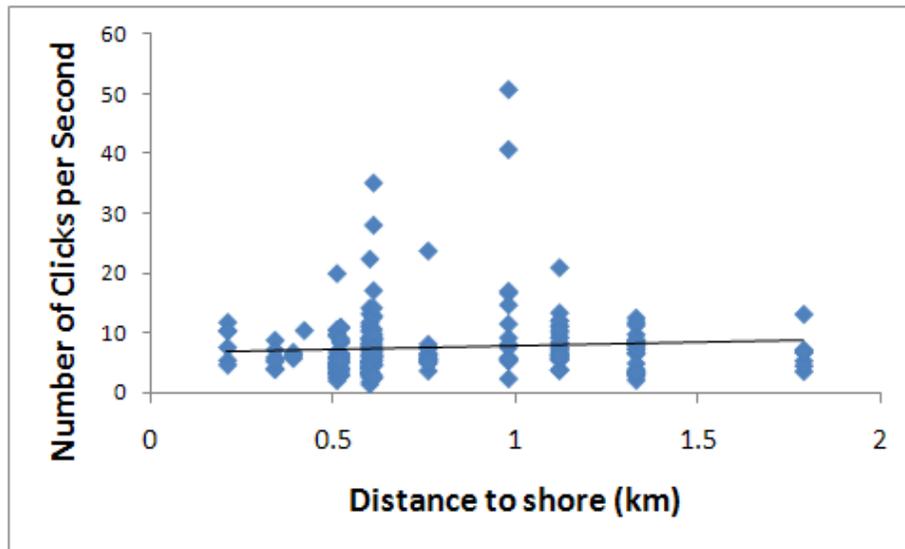
Figure 11: Scattergraph illustrating the relationship between the distance to the shore (km) and the number of echolocation clicks per second

The effect of depth of water on the peak frequency of echolocation clicks was tested by using a Pearsons Correlation Coefficient to establish if there was a relationship between depth of water and mean peak frequency of echolocation. The results show a statistically significant negative correlation of with peak frequency decreasing as water depth increases (r = -0.290, p= <0.01; Figure 12).

Figure 12: Scattergraph illustrating the correlational relationship between water depth (m) and the peak frequency of echolocation clicks

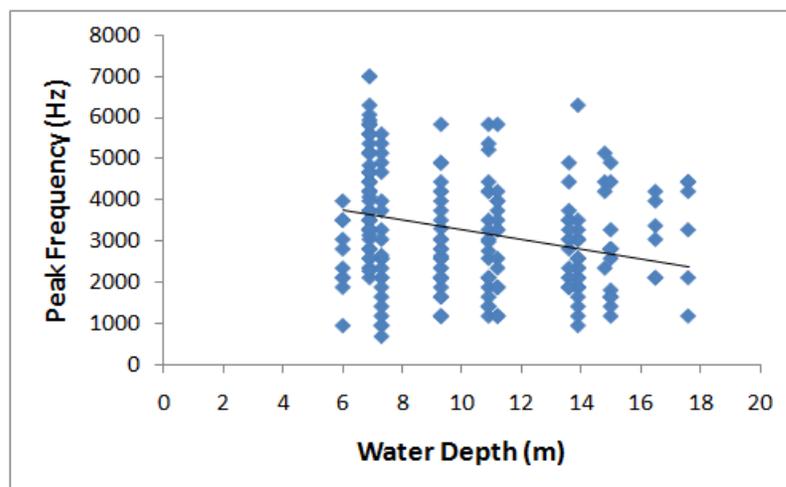In addition to peak frequency, the number of clicks per second was calculated for each of the 242 separated click trains, by counting the number of clicks and dividing by the total time from the first to last click. A Mann-Whitney-U test conducted found a statistically significant difference between the mean number of clicks per second when boats were (n = 92) or were not present (n = 172; W = 10250.5, p = 0.001; Figure 13).
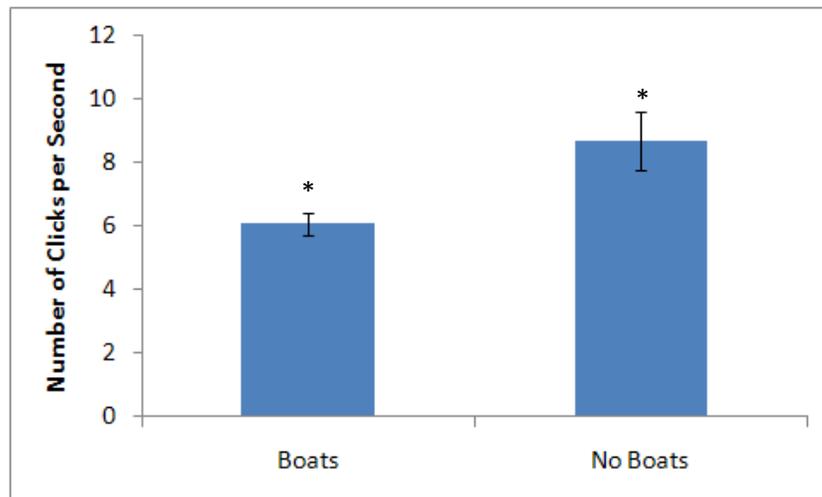
Figure 13: Bar chart demonstrating the Mean number of clicks per second when other boats were present (n=92) and when boats were not present (n=172). Standard Error bars are included. Asterix indicates significant difference

The relationship between the number of clicks per second and water depth and distance to the harbour was calculated using Pearson's correlations. There was no statistically significant relationship between distance from the harbour (km) and number of clicks per second (r = -0.003, p =0.9650; Figure 14). However, there was a statistically significant positive correlation between the depth of water and number of clicks per second (r = 0.215, p = 0.001; Figure 15).

Figure 14: Scattergraph illustrating the correlational relationship between distance to harbour (km) and the number of echolocation clicks per second including anomalous result

Figure 15: Scattergraph illustrating the correlational relationship between The depth of water (m) and the number of echolocation clicks per second including anomalous result
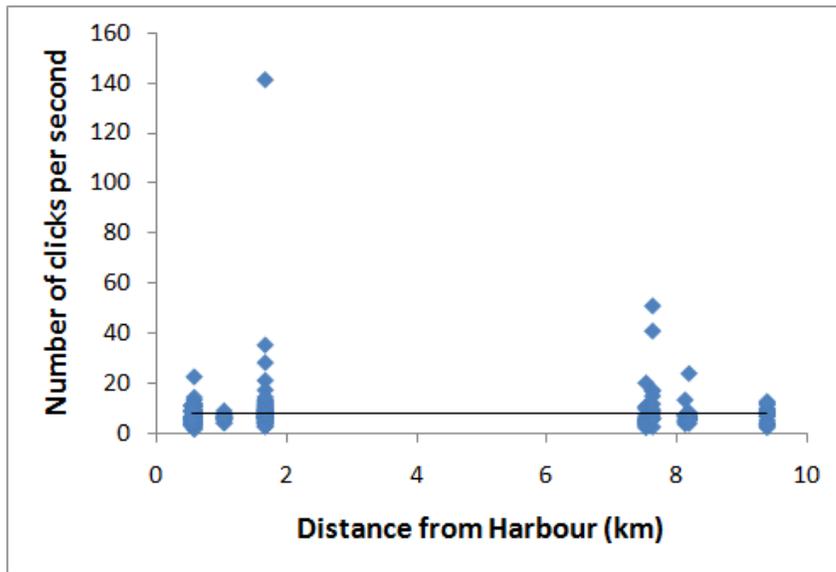
However, it was observed that there was an obvious anomalous result of 141 clicks per second that may have skewed the results that may have caused the

statistically significant correlation. Therefore, further Pearson's Correlation's were conducted without including the anomaly. There was a slight change in the strength of the correlation between depth of water and number of clicks per second when the anomaly was omitted from analysis but there was a replication of a significant positive correlation nonetheless (r = 0.207 p = 0.001, Figure 16). The correlation between distance to harbour (km) and number of clicks per second, when replicated without the anomaly was also found not to be statistically significant, (r = 0.052, p = 0.427, Figure 17).

Figure 16: Scattergraph showing the correlational relationship between the distance from New Quay Harbour (km) and the number of echolocation clicks per second not including the anomalous result
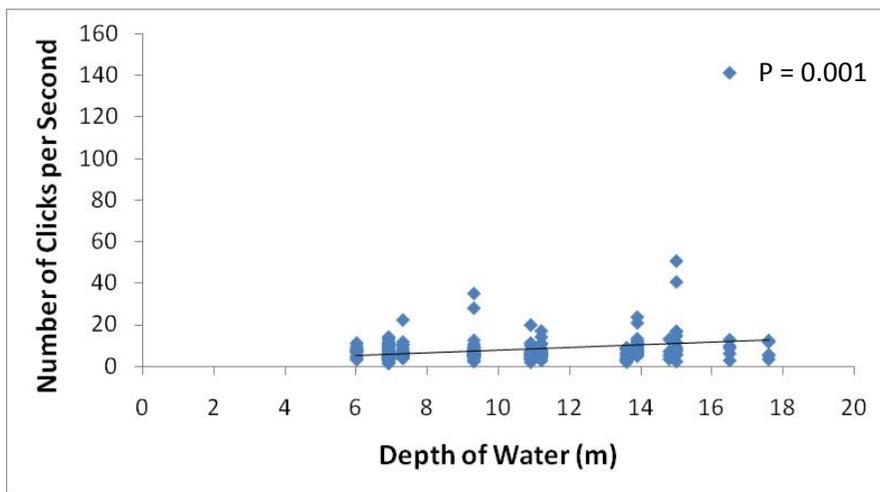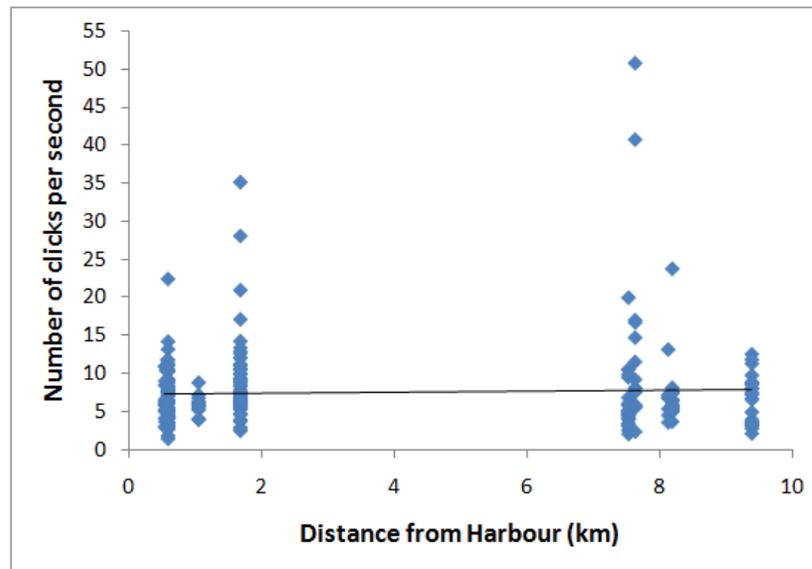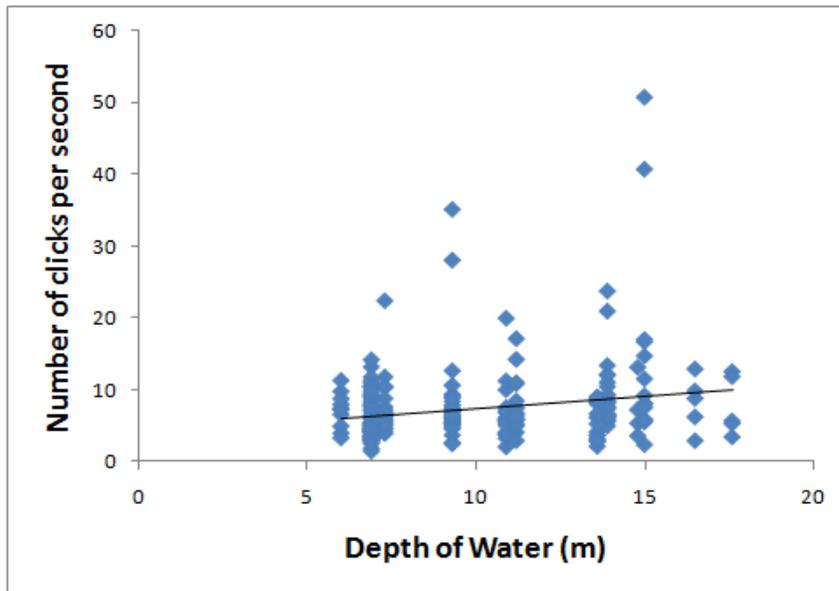
Figure 17: Scattergraph showing the correlational relationship between depth of water (m) and number of echolocation clicks per second not including the anomalous result

4.0 DISCUSSION

4.1: The effect of boat presence on echolocation

The results indicate that the bottlenose dolphins of Cardigan Bay alter the frequency of echolocation clicks when boats are present and that there is a negative correlation between distance to harbour and peak frequency. As there was no statistically significant difference between distance to shore and peak frequency of echolocation, this indicates that it is boat noise from the harbour that may be influencing the change in frequency, rather than other sources of anthropogenic or biological noise, particularly as boat traffic is reported to be highest within the SAC at New Quay Harbour (Allan *et al.*, 2010). However, it is important to take into consideration that boat noise may affect individuals differently, based on their age and sex as well as species, and therefore it is unwise to extrapolate the findings shown in this study (Weilgart, 2007).

Furthermore, the number of clicks per second decreased significantly when boats were present, but not with distance to harbour. This may indicate that the rate of echolocation clicks is only affected when at close range with boats. However, there is a gap in echolocation frequency analysis between 2km and 6km (See Figures 9, 14 and 16). This was unintentional and the reason this occurred was due to the location of the dolphins when recording took place. Mwnt and New Quay Harbour are where bottlenose dolphins are most commonly observed along Cardigan Bay (Allan *et al.*, 2010), explaining why there are two clusters of data points.

4.2: Acoustic Communication and echolocation of bottlenose dolphins

Bottlenose dolphins are known to make two different sound: clicks at peak frequencies at a range of 110-130 kHz (Au, 1993), and whistles with a peak frequency range of 5-20 kHz (Sayigh *et al.*, 1990). Most anthropogenic noise from boats ranges from 20-200 kHz which propagate well at this low frequency (Tyack, 2008). During this study, the hydrophone only recorded echolocation clicks, but no whistle sounds. This may be because the dolphins were not whistling at the time of recording. Whistling is thought to be used for communication purposes in a social context (Reiss *et al.*, 1997) so it would be expected that in recordings made when two or more dolphins were present whistling would be heard, so this was unexpected. In light of this, the effect of boat noise on the frequency of echolocation alone was investigated. As clicks are broad spectrum noises covering broad, continuous range of frequencies, only the peak frequency of each click was measured and compared.

However, there are many problems associated with collecting acoustical data on dolphins in the wild as the echolocation beam emitted is narrow and if it is not measured close to its axis, the signal can become distorted during the hydrophone recording which will impact upon the quality of the sound recorded (Au and Herzing, 2003). Some studies overcome this by studying acoustic reactions of captive dolphins to artificial noises (e.g. Caldwell and Caldwell, 1968). However, the findings of such studies cannot be extrapolated to free-ranging dolphins as the acoustics in a tank environment are very different to those under open water and there is evidence to

show geographical variations between the vocal activity and echolocation patterns of bottlenose dolphins (Jones and Sayigh, 2002). This was not taken into account in this study, so the frequencies analysed may not have been accurate. In order to reduce the impact of this in future experiments, an array of hydrophones could be used to determine the distance of the dolphin (Au, 2003).

The change in peak echolocation frequency in response to boat noise supports the findings of previous studies investigating the effect of boats e.g. in right whales (Parks *et al*., 2007) and beluga whales (Lesage *et al*., 1999). However, it was proposed by Au *et al*., (1974) that bottlenose dolphins can hear more efficiently at higher peak frequencies rather than lower ones, unlike mysticetes which communicate at lower frequencies (Tyack, 2008). Therefore, it would be expected, that rather than lowering their peak frequency, they would increase it, in order to distinguish echolocation clicks more efficiently when signal masking occurs caused by boat noise, for example. Sounds with higher frequencies also propagate through shorter distances, due to more rapid absorption through sea water (Urick,1972), therefore meaning it may be an advantage to lower the frequency of echolocation in the presence of boats.

It has been suggested that the frequency of acoustic signals emitted by bottlenose dolphins is linked to the intensity of the sound (Au and Nachtigall, 1997). A comparison can be made to the results of this study as when boats were absent, both the peak frequency of echolocation and the number of clicks per second were

statistically significantly higher. Further research could be conducted to analyse the connection between frequency of echolocation and intensity of echolocation clicks.

Different types of boat and engine produce noises of different frequency with ferries having the greatest affect on the vocal behaviour of belugas (Lesage *et al*. (1999). In this study the boats present when recordings were made were all recreational motor boats and small commercial visitor passenger vessels, meaning there was not too much variation in the volume of boat noise made between different recordings.

As there are only 33 moorings within New Quay Harbour (Ceredigion County Council *et al*., 2008), and there are regular trips that follow the same route daily, it could be likely that the dolphins could become habituated to their presence over time. However, as bottlenose dolphins live in a fission-fusion society (Mann *et al*., 2000) and some groups of individuals show stronger site fidelity than others (Bristow and Rees, 2001), the plasticity of being able to alter the frequency of echolocation sounds may still be of importance. Furthermore, bottlenose dolphins are relatively long lived: both males and females can live for up to 40-50 years with a slight sex bias as males tend not to survive as long as females, on average (Wells and Scott, 1990). Therefore, within an individual's lifetime, and with increasing boat traffic, an individual may have had to make alteration to avoid signal masking within its lifetime. However, the length that cetaceans live for may not be able to adapt genetically, quick enough to the pace of

change in anthropogenic noise and habitat that may occur during an individuals' lifetime (Rabin and Greene, 2002).

4.3: The effects of boats on bottlenose dolphins in Cardigan Bay

The Code of Conduct within the Cardigan Bay SAC Management Plan has only recently been established in 2001 (Ceredigion County Council *et al*., 2008), in response to increasing tourism and increasing research on the effect of boats on the behaviour of these cetaceans. This voluntary Code of Conduct has already proved successful as in 2008 and 2009, 87% of boat users complied with this voluntary Code of Conduct (Allan *et al*., 2010). The speed restrictions and distance regulations to maintain between the boats and dolphins are likely to have had a positive effect as the number of negative behavioural responses by dolphins to boat which comply with the Code is much lower than with those who go against the regulations. It has previously been shown that increased boat speed increases the volume of noise produced, and therefore increases the distance the sound travels through the water (Arveson and Vendittus, 2000).

This study only investigated the effects of boat noise on bottlenose dolphins. However, there is another commonly occurring cetacean within the Cardigan Bay SAC: the harbour porpoise (Ceredigion County Council *et al*., 2008). These cetaceans are more elusive and thus harder to observe and study but with the use of TPOD's which enable species-specific and long-term acoustic behaviour (Simon et al, 2010) the effects on the frequency of echolocation clicks by boat noise in this species could also be studied, to find whether boat noise has a universal effect on all cetacean species.

Although harbour porpoise do not use whistles to communicate, unlike bottlenose dolphins, they are able to communicate acoustically using a specific pattern of clicks, similar to those used for echolocation. This requires that they have less distance between individuals, when compared to other cetacean species in order to communicate effectively (Clausen et al, 2010). Therefore, the effects of boat noise could have a more severe masking effect on harbour porpoise communication and further study using T-POD's could be conducted to investigate whether they change the frequency of their acoustical projections.

However, of possible future concern is the impact of scallop dredging as although it is currently banned, there is the potential for scallop dredgers from Scotland and Spain to dredge on the border or even within the SAC as there is limited law enforcement (Bianchessi, 2008). As well as affecting food availability for foraging dolphins (Eleftheriou and Robertson, 1992), this method creates increased ambient noise volumes which may contribute to signal masking, although due to the low frequency of the noise produced it is less likely to affect odontocetes which communicate at a relatively high frequency (Thompson *et al*., 2009). Further research should be conducted to monitor levels of noise created by scallop dredging, and the possible acoustical impacts on local cetaceans.

4.4: The effect of water depth on echolocation

The effect of depth of water on echolocation frequency was also investigated in this study and it was found that bottlenose dolphins have a higher peak frequency of

echolocation at lower depths, with a negative correlation between increasing water depth and peak frequency of echolocation. Cardigan Bay is a relatively shallow area, with an average depth of 40m and reaching depths of no more than 50m, in comparison to an average sea depth of around 40km (Evans, 1995). Although this means that data could only be collected over a narrow range of depths, a clear pattern is apparent. However, there is little scientific study in this area at current.

Number of clicks per second also increased significantly with increasing depth of water. However, there are many factors which could have affected this other than water depth; for example, different behaviours may have been conducted by individuals at the time of each recordings. It is likely that foraging activity will cause click rate to increase when compared to behaviours such as travelling (Au, 1993), regardless of water depth. In this study, the most common behaviour recording at the time of acoustical recordings was foraging (43.48%) meaning this could be a contributing factor to the change in click rate. However it has been found that as pressure increases at greater water depth, that although the whistle response of two white whales (*Delphinapterus leucas*) changed at depth causing higher peak frequencies of sounds emitted as greater depths, they had unchanged hearing sensitivity (Ridgway *et al*, 2001). This has consequences for the study of anthropogenic noise on cetaceans, as it seems that noise can propagate and possibly cause signal masking of the same level of impact both at depth as at the surface. However, in contrast, peak frequency of the social calls of short-finned pilot whales (*Globicephala macrorhynchus*) were unaffected by increasing depths up to 800m, although the

length of calls was shorter at depth (Jenson *et al.*, 2011) meaning it is unclear whether all odontocetes have the same response to water depth.

4.5: Evidence and Implications of Signal Masking

The results in this study indicate that boat noise may have a negative impact by causing signal masking so that bottlenose dolphins have to adjust the frequency of their echolocation clicks to compensate for it. However, anthropogenic noise is not the only source of noise in the marine environment that may have a similar effect. For example, snapping shrimp (family Alpheidae), which were heard by the hydrophone during this study, are known to create high levels of ambient noise by the rapid closure of its enlarged claw which creates a bubble cavitation which upon collapse, creates a sound up to 220 dB (Versluis *et al.*, 2000). They can produce sound over a wide range of frequencies from two Hz to >200 KHz (Au and Banks, 1998). Large congregations of snapping shrimp, can therefore increase the ambient noise level greatly. Furthermore, as these are bottom dwelling animals, and Cardigan Bay is relatively shallow, attenuation of this noise would be expected to be high, particularly at times of low sea state, where noise transmitted from snapping shrimp can travel up to 1 mile, with highest abundance of shrimp found at depths up to 40 fathoms, or 55 metres (Johnson *et al.*, 1947). Therefore, this shows that dolphins in Cardigan Bay are already subject to loud ambient noise from biological sources as well as anthropogenic ones. It is therefore hard to establish the direct source causing an effect of frequency change as it may be that varying levels of snapping shrimp noise in localised areas may cause

signal interference and may be a contributing factor to the change in echolocation frequency.

Although much of the recent research on the effect of boat noise on cetacean communication and echolocation shows the short term effects of signal masking e.g. in mysticetes (Clark *et al.,* 2009) and in bottlenose dolphins (Jenson *et al.,* 2009), further research is required to determine long term impacts of anthropogenic noise in particular, to see if it has behavioural effects which in turn, could reduce reproductive success. Possible long term effects suggested include: a reduction in foraging or mating opportunities, although mysticetes with long distance communication calls may be affected more than odontocetes, or physiological consequences such as increased stress levels (Weilgart, 2007). Further behavioural changes such as displacement from important habitats may occur, although whether this has a positive or negative effect will depend on the relative quality of the original habitat and the habitat cetaceans move to when displaced (Nowacek *et al.,* 2007). However Nowacek *et al.,* 2007 also discuss that anthropogenic noise may have a positive effect in the context of acoustical deterrents which can reduce the number of cetaceans caught as by-catch.

In comparison with other areas where bottlenose dolphins inhabit, the number of boats and therefore boat noise is relatively low with 133 boat moorings in New Quay Harbour, 80 at Aberaeron and 300 at Cardigan (Ceredigion County Council *et al.,* 2008). Perhaps this is one of the reasons it is a popular habitat for bottlenose dolphins, although they are known to occur globally in areas with heavy boat usage. It would be

interesting to conduct further research to compare the acoustics of the echolocation of dolphins in Cardigan Bay to those in a much noisier area, such as the English Channel as it would be expected that the dolphins in a noisier environment would have to change their frequency to avoid signal masking to a much greater degree.

4.6: Conclusion

Overall, the results shown here indicate that boat noise impacts upon the acoustic behaviour of bottlenose dolphins as they significantly lower the peak frequency (Hz) of their echolocation clicks when boats are present. Distance to the harbour also has a significant positive correlation to the peak frequency of bottlenose dolphin echolocation. Therefore, although boat noise may cause signal masking, the dolphins of Cardigan Bay are able to compensate to overcome this anthropogenic source of masking. There was also a significant positive correlation between water depth and the frequency of echolocation, further illustrating the plasticity of echolocation clicks of bottlenose dolphins in response to environmental conditions. Further investigations need to be conducted in order to determine the long-term impacts of boat noise on acoustic echolocation and communication as well as study the wider impacts that boat noise may have on bottlenose dolphin behaviour overall.

References

ALLAN, L., GREEN, M. & KELSALL, J. 2010. Bottlenose dolphins & boat traffic on the Ceredigion Coast, West Wales 2008 & 2009. Ceredigion County Council.

ALLEN, M. C. 2000. Habitat selection of foraging bottlenose dolphins in relation to boat density near Clearwater, Florida. *Marine Mammal Science,* 16**,** 815-824.

ARVESON, P. T. & VENDITTIS, D. J. 2000. Radiated noise characteristics of a modern cargo ship. *Journal of the Acoustical Society of America,* 107**,** 118-129.

ATEMA, J., FAY, R. R., POPPER, A. N. & TAVOLGA, W. N. 1988. *Sensory biology of aquatic animals,* New York, Springer-Verlag.

AU, W. W. L. 1993. *The Sonar of Dolphins,* New York, Springer-Verlag.

AU, W. W. L. 2004. Echolocation signals of wild dolphins. *Acoustical Physics,* 50**,** 454-462.

AU, W. W. L. & BANKS, K. 1998. The acoustics of the snapping shrimp Synalpheus parneomeris in Kaneohe Bay. *Journal of the Acoustical Society of America,* 103**,** 41-47.

AU, W. W. L., FLOYD, R. W., PENNER, R. H. & MURCHISO.AE 1974. Measurement of echolocation signals of atlantic bottlenose dolphin, Tursiops truncatus Montagu, in open waters. *Journal of the Acoustical Society of America,* 56**,** 1280-1290.

AU, W. W. L. & HERZING, D. L. 2003. Echolocation signals of wild Atlantic spotted dolphin (Stenella frontalis). *Journal of the Acoustical Society of America,* 113**,** 598-604.

AU, W. W. L. & NACHTIGALL, P. E. 1997. Acoustics of echolocating dolphins and small whales. *Marine and Freshwater Behaviour and Physiology,* 29**,** 127-162.

BERGLUND, A., BISAZZA, A. & PILASTRO, A. 1996. Armaments and ornaments: An evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society,* 58**,** 385-399.

BERMUDEZ-CUAMATZIN, E., RIOS-CHELEN, A. A., GIL, D. & GARCIA, C. M. 2011. Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird. *Biology Letters,* 7**,** 36-38.

BIANCHESSI, A. Managing Marine SACs: What can be learnt from the Cardigan Bay Experience? *In:* EVANS, P. G. H., ed. Selection Criteria for Marine Protected Areas for Cetaceans, 2008 The Aquarium, San Sebastien, Spain. 72-77.

BRISTOW, T. & REES, E. I. S. 2001. Site fidelity and behaviour of bottlenose dolphins (Tursiops truncatus) in Cardigan Bay, Wales. *Aquatic Mammals,* 27**,** 1-10.

BRUMM, H. 2006. Signalling through acoustic windows: nightingales avoid interspecific competition by short-term adjustment of song timing. *Journal of Comparative Physiology A Neuroethology Sensory Neural and Behavioral Physiology,* 192**,** 1279-1285.

BUCKSTAFF, K. C. 2004. Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, Tursiops truncatus, in Sarasota Bay, Florida. *Marine Mammal Science,* 20**,** 709-725.

CALDWELL, M. C. & CALDWELL, D. K. 1965. Individualized whistle contours in bottlenose dolphins (Tursiops truncatus). *Nature,* 207**,** 434-435.

CALDWELL, M. C. & CALDWELL, D. K. 1968. Vocalisation of naive captive dolphins in small groups. *Science,* 159**,** 1121-1126.

CAVALLISFORZA, L. L. & FELDMAN, M. W. 1983. Paradox of the evolution of communication and social interactivity. *Proceedings of the National Academy of Sciences of the United States of America-Biological Sciences,* 80**,** 2017-2021.

CLARK, C. W., ELLISON, W. T., SOUTHALL, B. L., HATCH, L., VAN PARIJS, S. M., FRANKEL, A. & PONIRAKIS, D. 2009. Acoustic masking in marine ecosystems: intuitions, analysis, and implication. *Marine Ecology-Progress Series,* 395**,** 201-222.

CLAUSEN, K. T., WAHLBERG, M., BEEDHOLM, K., DERUITER, S. & MADSEN, P. T. 2010. Click communication in harbour porpoises Phocoena phocoena. *Bioacoustics-the International Journal of Animal Sound and Its Recording,* 20**,** 1-28.

CEREDIGION COUNTY COUNCIL, WALES, C. C. F., WALES, E. A. F., COMMITTEE, N. W. A. N. W. S. F., AUTHORITY, P. C. N. P., COUNCIL, P. C., COMMITTEE, S. W. S. F. & WATER, D. C. W. 2008. Cardigan Bay Special Area of Conservation (SAC) Management Scheme.

CRANFORD, T. W., AMUNDIN, M. & NORRIS, K. S. 1996. Functional morphology and homology in the odontocete nasal complex: Implications for sound generation. *Journal of Morphology,* 228**,** 223-285.

DAVID, J. A. 2006. Likely sensitivity of bottlenose dolphins to pile-driving noise. *Water and Environment Journal,* 20**,** 48-54.

EHRET, G. & GERHARDT, H. C. 1980. Auditory masking and effects of noise on responses of the green tree frog (Hyla cinerea) to synthetic mating calls. *Journal of Comparative Physiology,* 141**,** 13-18.

ELEFTHERIOU, A. & ROBERTSON, M. R. 1992. The effects of experimental scallop dredging on the fauna and physical environment of a shallow sandy community. *Netherlands Journal of Sea Research,* 30**,** 289-299.

ENDLER, J. A. 1993. Some general comments on the evolution and design of animal communication systems. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences,* 340**,** 215-225.

EVANS, C. D. R. 1995. Offshore environment.

EVANS, W. E. & MADERSON, P. F. 1973. Mechanisms of sound production in delphinid cetaceans - review and some anatomical considerations. *American Zoologist,* 13**,** 1205-1213.

FENTON, M. B., PORTFORS, C. V., RAUTENBACH, I. L. & WATERMAN, J. M. 1998. Compromises: sound frequencies used in echolocation by aerial-feeding bats. *Canadian Journal of Zoology-Revue Canadienne De Zoologie,* 76**,** 1174-1182.

FERNANDEZ, A., EDWARDS, J. F., RODRIGUEZ, F., DE LOS MONTEROS, A. E., HERRAEZ, P., CASTRO, P., JABER, J. R., MARTIN, V. & ARBELO, M. 2005. "Gas and fat embolic syndrome" involving a mass stranding of beaked whales (Family Ziphiidae) exposed to anthropogenic sonar signals. *Veterinary Pathology,* 42**,** 446-457.

FORDYCE, R. E. 1980. WHALE EVOLUTION AND OLIGOCENE SOUTHERN-OCEAN ENVIRONMENTS. *Palaeogeography Palaeoclimatology Palaeoecology,* 31**,** 319-336.

FORREST, T. G. 1994. From sender to receiver - propagation and environmental effects on acoustic signals. *American Zoologist,* 34**,** 644-654.

GARROD, B. & FENNELL, D. A. 2004. An analysis of whalewatching codes of conduct. *Annals of Tourism Research,* 31**,** 334-352.

GAZDA, S. K., CONNOR, R. C., EDGAR, R. K. & COX, F. 2005. A division of labour with role specialization in group-hunting bottlenose dolphins (Tursiops truncatus) off Cedar Key, Florida. *Proceedings of the Royal Society B-Biological Sciences,* 272**,** 135-140.

GELFAND, S. A. 2004. *Hearing - an introduction to psychological and physiological acoustics.,* New York, Marcell Dekker.

GERHARDT, H. C. & KLUMP, G. M. 1988. Masking of acoustic signals by the chorus background noise in the green tree frog - a limitation on mate choice. *Animal Behaviour,* 36**,** 1247-1249.

GINGERICH, P. D. 2006. Environment and evolution through the Paleocene-Eocene thermal maximum. *Trends in Ecology & Evolution,* 21**,** 246-253.

GREGORY, P. R. & ROWDEN, A. A. 2001. Behaviour patterns of bottlenose dolphins (Tursiops truncatus) relative to tidal state, time-of-day, and boat traffic in Cardigan Bay, West Wales. *Aquatic Mammals,* 27**,** 105-113.

GRELLIER, K., ARNOLD, H., THOMPSON, P., WILSON, B. & CURRAN, S. 1995. Management recommendations for the Cardigan Bay bottlenose dolphin population. Aberdeen: Countryside Council for Wales.

HALFWERK, W., HOLLEMAN, L. J. M., LESSELLS, C. M. & SLABBEKOORN, H. 2011. Negative impact of traffic noise on avian reproductive success. *Journal of Applied Ecology,* 48**,** 210-219.

HASTIE, G. D., WILSON, B., TUFFT, L. H. & THOMPSON, P. M. 2003. Bottlenose dolphins increase breathing synchrony in response to boat traffic. *Marine Mammal Science,* 19**,** 74-84.

JANIK, V. M., SAYIGH, L. S. & WELLS, R. S. 2006. Signature whistle shape conveys identity information to bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America,* 103**,** 8293-8297.

JENSEN, F. H., BEJDER, L., WAHLBERG, M., SOTO, N. A., JOHNSON, M. & MADSEN, P. T. 2009. Vessel noise effects on delphinid communication. *Marine Ecology-Progress Series,* 395**,** 161-175.

JOHNSON, M. W., EVEREST, F. A. & YOUNG, R. W. 1947. The role of snapping shrimp (Crangon and Synalpheus) in the production of underwater noise in the sea. *Biological Bulletin,* 93**,** 122-138.

JONES, G. & HOLDERIED, M. W. 2007. Bat echolocation calls: adaptation and convergent evolution. *Proceedings of the Royal Society B-Biological Sciences,* 274**,** 905-912.

JONES, G. J. & SAYIGH, L. S. 2002. Geographic variation in rates of vocal production of free-ranging bottlenose dolphins. *Marine Mammal Science,* 18**,** 374-393.

LESAGE, V., BARRETTE, C., KINGSLEY, M. C. S. & SJARE, B. 1999. The effect of vessel noise on the vocal behavior of Belugas in the St. Lawrence River estuary, Canada. *Marine Mammal Science,* 15**,** 65-84.

LINDBERG, D. R. & PYENSON, N. D. 2007. Things that go bump in the night: evolutionary interactions between cephalopods and cetaceans in the tertiary. *Lethaia,* 40**,** 335-343.

LURTON, X. 2002. *An Introduction to Underwater Acoustics: Principles and Applications,* Chichester, UK., Praxis Publishing Ltd.

MADSEN, P. T., WAHLBERG, M., TOUGAARD, J., LUCKE, K. & TYACK, P. 2006. Wind turbine underwater noise and marine mammals: implications of current knowledge and data needs. *Marine Ecology-Progress Series,* 309**,** 279-295.

MANN, J., CONNOR, R. C., BARRE, L. M. & HEITHAUS, M. R. 2000. Female reproductive success in bottlenose dolphins (Tursiops sp.): life history, habitat, provisioning, and group-size effects. *Behavioral Ecology,* 11**,** 210-219.

MARLER, P. 1967. ANIMAL COMMUNICATION SIGNALS. *Science,* 157**,** 769-774.

MARTIN, G. 1990. *Birds by Night*, A & C Black Publishers Ltd.

MATTSON, M. C., THOMAS, J. A. & ST. AUBIN, D. 2005. Effects of Boat Activity on the Behavior of Bottlenose Dolphins (*Tursiops truncatus*) in Waters Surrounding Hilton Head Island, South Carolina. *Aquatic Mammals,* 31**,** 133-140.

MOCKFORD, E. J. & MARSHALL, R. C. 2009. Effects of urban noise on song and response behaviour in great tits. *Proceedings of the Royal Society B-Biological Sciences,* 276**,** 2979-2985.

MORISAKA, T., SHINOHARA, M., NAKAHARA, F. & AKAMATSU, T. 2005. Effects of ambient noise on the whistles of Indo-Pacific bottlenose dolphin populations. *Journal of Mammalogy,* 86**,** 541-546.

NAGUIB, M. 1999. Effects of song overlapping and alternating on nocturnally singing nightingales. *Animal Behaviour,* 58**,** 1061-1067.

NORRIS, K. S. 1968. The evolution of acoustic mechanisms in odontocete cetaceans. *Evolution and Environment***,** 297-324.

NOWACEK, D. P., THORNE, L. H., JOHNSTON, D. W. & TYACK, P. L. 2007. Responses of cetaceans to anthropogenic noise. *Mammal Review,* 37**,** 81-115.

ORD, T. J., CHARLES, G. K. & HOFER, R. K. 2011. The Evolution of Alternative Adaptive Strategies for Effective Communication in Noisy Environments. *American Naturalist,* 177**,** 54-64.

PARKS, S. E., CLARK, C. W. & TYACK, P. L. 2007. Short- and long-term changes in right whale calling behavior: The potential effects of noise on acoustic communication. *Journal of the Acoustical Society of America,* 122**,** 3725-3731.

PAYNE, R. S. 1971. Acoustic location of prey by barn owls (Tyto alba). *Journal of Experimental Biology,* 54**,** 535-&.

PESANTE, G., EVANS, P. G. H., ANDERWALD, P., POWELL, D. & MCMATH, M. 2008. Connectivity of bottlenose dolphins in Wales:North Wales Photo-Monitoring Interim Report. *CCW Marine Monitoring Report 62.* Bangor: Countryside Council for Wales.

PIERPOINT, C., ALLAN, L., ARNOLD, H., EVANS, P., PERRY, S., WILBERFORCE, L. & BAXTER, J. 2009. Monitoring important coastal sites for bottlenose dolphin in Cardigan Bay, UK. *Journal of the Marine Biological Association of the United Kingdom,* 89**,** 1033-1043.

POTTER, J. R. & TAYLOR, E. A. 2001. On novel reception models for bottlenose dolphin echolocation. *Proceedings-Institute of Acoustics,* 23**,** 103-112.

PYE, J. D. 1960. A theory of echolocation by bats. *J Laryngol Otol,* 74**,** 718-29.

RABIN, L. A. & GREENE, C. M. 2002. Changes to acoustic communication systems in human-altered environments. *Journal of Comparative Psychology,* 116**,** 137-141.

REISS, D., MCCOWAN, B. & MARINO, L. 1997. Communicative and other cognitive characteristics of bottlenose dolphins. *Trends in Cognitive Sciences,* 1**,** 140-145.

RICE, W. R. 1982. Acoustical location of prey by the marsh hawk - adaptation to concealed prey. *Auk,* 99**,** 403-413.

RIDGWAY, S. H., CARDER, D. A., KAMOLNICK, T., SMITH, R. R., SCHLUNDT, C. E. & ELSBERRY, W. R. 2001. Hearing and whistling in the deep sea: depth influences whistle spectra but does not attenuate hearing by white whales (Delphinapterus leucas) (Odontoceti, Cetacea). *Journal of Experimental Biology,* 204**,** 3829-3841.

RUSSO, D., MUCEDDA, M., BELLO, M., BISCARDI, S., PIDINCHEDDA, E. & JONES, G. 2007. Divergent echolocation call frequencies in insular rhinolophids (Chiroptera): a case of character displacement? *Journal of Biogeography,* 34**,** 2129-2138.

SAYIGH, L. S., TYACK, P. L., WELLS, R. S. & SCOTT, M. D. 1990. Signature whistles of free-ranging bottlenose dolphins Tursiops truncatus - stability and mother offspring comparisons. *Behavioral Ecology and Sociobiology,* 26**,** 247-260.

SCHUSTERMAN, R. J., KASTAK, D., LEVENSON, D. H., REICHMUTH, C. J. & SOUTHALL, B. L. 2000. Why pinnipeds don't echolocate. *Journal of the Acoustical Society of America,* 107**,** 2256-2264.

SIEMERS, B. M., BEEDHOLM, K., DIETZ, C., DIETZ, I. & IVANOVA, T. 2005. Is species identity, sex, age or individual quality conveyed by echolocation call frequency in European horseshoe bats? *Acta Chiropterologica,* 7**,** 259-274.

SIMON, M., NUUTTILA, H., REYES-ZAMUDIO, M. M., UGARTE, F., VERFUB, U. & EVANS, P. G. H. 2010. Passive acoustic monitoring of bottlenose dolphin and harbour porpoise, in Cardigan Bay, Wales, with implications for habitat use and partitioning. *Journal of the Marine Biological Association of the United Kingdom,* 90**,** 1539-1545.

SLABBEKOORN, H., BOUTON, N., VAN OPZEELAND, I., COERS, A., TEN CATE, C. & POPPER, A. N. 2010. A noisy spring: the impact of globally rising underwater sound levels on fish. *Trends in Ecology & Evolution,* 25**,** 419-427.

SLABBEKOORN, H. & RIPMEESTER, E. A. P. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. *Molecular Ecology,* 17**,** 72-83.

THOMPSON, F., MCCULLY, S., WOOD, D., PACE, F. & WHITE, P. 2009. A generic investigation into noise profiles of marine dredging in relation to the acoustic sensitivity of the marine fauna in UK waters with particular emphasis on aggregate dredging. Marine Aggregate Levy Sustainability Fund.

TYACK, P. L. 2008. Implications for marine mammals of large-scale changes in the marine acoustic environment. *Journal of Mammalogy,* 89**,** 549-558.

ULANOVSKY, N., FENTON, M. B., TSOAR, A. & KORINE, C. 2004. Dynamics of jamming avoidance in echolocating bats. *Proceedings of the Royal Society of London Series B-Biological Sciences,* 271**,** 1467-1475.

URICK, R. J. 1972. Sound transmission from deep to shallow water. *Journal of the Acoustical Society of America,* 52**,** 172-172.

VAN PARIJS, S. M. & CORKERON, P. J. 2001. Boat traffic affects the acoustic behaviour of Pacific Humpback dolphins, Sousa chinensis. *Journal of Marine Biological Association of the United Kingdom,* 81**,** 533-538.

VERSLUIS, M., SCHMITZ, B., VON DER HEYDT, A. & LOHSE, D. 2000. How snapping shrimp snap: Through cavitating bubbles. *Science,* 289**,** 2114-2117.

WEILGART, L. S. 2007. The impacts of anthropogenic ocean noise on cetaceans and implications for management. *Canadian Journal of Zoology-Revue Canadienne De Zoologie,* 85**,** 1091-1116.

WELLS, R. S. & SCOTT, M. D. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. *Hammond, P. S., S. a. Mizroch and G. P. Donovan (Ed.). Report of the International Whaling Commission Special Issue, No. 12. Individual Recognition of Cetaceans: Use of Photo-Identification and Other Techniques to Estimate Population Parameters; Proceedings of the Us National Marine Fisheries Service Symposium and Workshop on Individual Recognition and the Estimation of Cetacean Population Parameters, La Jolla, California, USA, April 1988. Viii+440p. International Whaling Commission: Cambridge, England, Uk. Illus. Maps***,** 407-416.

WILEY, R. H. & RICHARDS, D. G. 1978. Physical constraint on acoustic communication in atmosphere - implications for evolution of animal vocalizations. *Behavioral Ecology and Sociobiology,* 3**,** 69-94.

WILKINSON, G. S. & BOUGHMAN, J. W. 1998. Social calls coordinate foraging in greater spear-nosed bats. *Animal Behaviour,* 55**,** 337-350.

WILSON, B., THOMPSON, P. M. & HAMMOND, P. S. 1997. Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology,* 34**,** 1365-1374.