# The use of T-PODs to identify echolocation behaviour in bottlenose dolphins (*Tursiops truncatus*) in New Quay Bay, Wales.

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Master of Science Thesis

Marine Mammal Science

2006

In association with



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Bottlenose dolphin (*Tursiops truncatus*) feeding on sea bass (*Dicentrarchos labrax*) in New Quay Bay on the morning of 11<sup>th</sup> September 2006. (Photograph courtesy of Lisa Morris/monstertrucks.co.uk).

#### Abstract

The odontocete echolocation system has evolved as a dynamic and specialised process for spatial orientation and the detection and localisation of prey, thus optimising the chances of survival in an aquatic environment. This study was carried out primarily to explore the possibility of using T-POD acoustic data as a means of identifying the echolocation behaviour of bottlenose dolphins (*Tursiops* truncatus) in New Quay Bay, Wales. Dolphins were monitored through landbased visual surveys from May to September 2006, and observations were compared to corresponding click train parameter data collected with two T-POD units deployed in the study area. It was found that click trains produced by foraging dolphins had both significantly lower mean inter-click intervals and train durations and a significantly higher number of clicks than those emitted by dolphins observed in the behavioural states of travelling and foraging/travelling. These findings were applied to T-POD data collected in the study area throughout the year, revealing both significant diel and monthly variation in the number of foraging click trains acoustically detected. The secondary aim of this investigation was to broadly determine the influence of directionality, group size, distance and behavioural state on T-POD detection rates. The collective evaluation of data obtained over the study period indicated that a combination of these variables had an effect on T-POD detection rates. However, further work is required to determine the extent to which each of these factors influences acoustic detection rates, and how environmental variables may also contribute to the detection of echolocating dolphins with T-PODs. It was concluded that if the limitations of using T-PODs are accepted, the methodology employed in this study has the potential to monitor long-term changes in dolphin behaviour. Consequently, such monitoring could provide a method for monitoring fine-scale temporal changes in habitat use.

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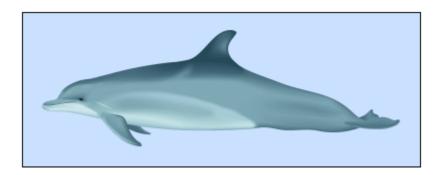
# 1. Introduction

#### 1. Introduction

# 1.1 The Bottlenose Dolphin

# 1.1.1 Species Description

The bottlenose dolphin (*Tursiops truncatus*) (Montagu, 1812) is a member of the family Delphinidae and is perhaps the most well studied of the odontocetes. A widely distributed species, bottlenose dolphins occur in most warm-temperate and tropical waters worldwide and can be found in both coastal and pelagic waters. Morphologically, bottlenose dolphins differ with geographical locality, a trait well demonstrated in the range of body lengths seen in this species, with dolphins measuring around 2 metres long typically found in warmer waters and larger individuals of up to 4 metres, usually found in cooler waters (Wells and Scott, 2002). The colouration of individuals also varies considerably with the region in which they are found, but bottlenose dolphins are usually identifiable by their light to dark grey dorsal colouration, a lighter coloured ventral area and a white belly (**Figure 1.1**).



**Figure 1.1** Illustration depicting the general appearance of the bottlenose dolphin *Tursiops truncatus*. (ACS online 2006)

#### 1.1.2 Distribution (European waters)

As mentioned, bottlenose dolphins can be found extensively worldwide and they are regularly observed in the waters of the North Atlantic (Reid *et al.*, 2003). In Northwest Europe, these dolphins are most frequently recorded in coastal waters,

particularly those around the Spanish and Portuguese coasts, the Bay of Biscay, Northeast Scotland, Western Ireland, and the Irish Sea (Reid *et al.*, 2003). Offshore populations have been sighted from as far as the Faeroe Islands to the eastern North Atlantic (de Boer and Simmonds, 2003), with sightings on and off the shelf edge peaking in July and August (Evans *et al.*, 2003).

In the Irish Sea, particularly high concentrations of bottlenose dolphins occur in the waters of Cardigan Bay, Wales. Cardigan Bay is internationally recognised as an area of significant importance, as habitat to one of the only two resident populations of bottlenose dolphin in UK waters, the other being in the Moray Firth, Eastern Scotland. The populations of dolphins inhabiting these locations are not closed and it is thought that there may be some movement between these populations at times (Evans *et al.*, 2003).

Coastal numbers of bottlenose dolphins in the UK are typically at their highest between May and September, with seasonal peaks also evident. In Cardigan Bay, young calves are usually observed at during this time, especially in July and August (Evans *et al.*, 2003). Using both distance sampling and photo identification data for the dolphins in this area, the population in these Welsh waters has recently been estimated to be in the region of 215 individuals (Baines *et al.*, 2002; Ugarte and Evans, 2006).

Both the distribution and movement patterns of studied bottlenose dolphin populations have been found to be generally non-uniform, although the local distribution appears to be dependent on several variables including environmental and oceanographic parameters, seasonality, anthropogenic influences and prey abundance, availability and distribution (Shane *et al.*, 1986; Baines *et al.*, 2005; Liret *et al.*, 2002). In coastal waters, these dolphins appear to show a preference for river estuaries, headlands or sandbanks (Evans *et al.*, 2003).

Areas that are particularly favoured by dolphins or 'hotspots' have also been identified, which seem to be closely linked with prey distribution and therefore foraging (Wilson *et al.*, 1997; Hastie *et al.*, 2004). In Cardigan Bay, areas such as Ynys Lochtyn, Mwnt, Pen Peles, Cemaes Head and New Quay Bay have all been identified as hotspot locations, with a high frequency of sightings (Evans and Lewis, 1993; Evans, 1995; Grellier *et al.*, 1995; Evans *et al.*, 2000; Baines *et al.*, 2005).

#### 1.1.3 Life History

Bottlenose dolphins have a relatively long life span, with males known to live over 40 years and females to over 50 years of age (Wells and Scott, 2002). The onset of sexual and physical maturity differs between the sexes, with females maturing between 5 and 13 years old and males considerably later, somewhere between 8 and 13 years of age (Reynolds *et al.*, 2000). As a result, sexual size dimorphism can be moderately pronounced in this species. As with all marine mammals, bottlenose dolphins typically give birth to a single calf and this is usually on a 2- to 3-yearly basis (Connor *et al.*, 2000). Maternal care is especially attentive and calves are dependent on their mothers far beyond weaning age (around 12-18 months), sometimes remaining in close maternal association until they are between 3 and 5 years of age (Wells and Scott, 2002).

#### 1.1.4 Behaviour and Social Structure

Bottlenose dolphins are highly gregarious delphinids and live in what is described as a fission-fusion society, where group formation changes regularly as individuals frequently join and leave, although long-term associations are also evident (Connor *et al.*, 2000). The composition of these groups seems to be determined by several factors, including age, sex, reproductive state and social and genetic associations (Connor *et al.*, 2000; Wells and Scott, 2002). A strongly cooperative nature exists amongst bottlenose dolphins, which is evident in this type of group living and well reflected in the various group foraging strategies seen in many of the studied populations of this species (Shane *et al.*, 1986).

Group size is highly variable, averaging between 2 to 25 individuals in coastal areas but is sometimes seen to be in the hundreds in deeper, offshore waters (Reid et al., 2003). It is thought that such variations in group size are likely to be linked to the differing environments that these dolphins inhabit. For instance, in coastal waters many prey species are sedentary and benthic and are mainly dispersed individually, thus individual foraging is more common. Equally, foraging efficiency may be increased with larger groups of dolphins in offshore waters, where pelagic midwater shoaling fish are more important. (Barros and Wells, 1998; Connor et al., 2000).

Activities such as feeding, travelling, socialising and resting appear to occur both diurnally and nocturnally in wild bottlenose dolphins (Shane *et al.*, 1986). Activity patterns and the intensity and frequency with which they occur appear to vary depending on both environmental determinants such as habitat, tidal state, time of day and season and on physiological factors, such as reproductive state, age and health condition of the animal (Bearzi *et al*, 1999; Wells and Scott, 2002).

Measuring such activity patterns and therefore the behavioural states of dolphins is inherently difficult, since such observations are usually only possible when the dolphin surfaces to breathe. Such surfacing events can be divided into several behavioural categories, such as competition, predator avoidance, social and sexual displays, movement and orientation, and foraging activities (Tyack, 2002).

#### 1.1.5 Sound Production and Echolocation

Whilst terrestrial mammals rely primarily on vision and smell in order to survive, the nature of the aquatic environment means that the use of these senses is limited, and sound is the most valuable sense to marine mammals. Burst-pulse sounds, tonal whistles and echolocation clicks are produced by many of the odontocetes and in dolphins, sound is essentially used for communication, orientation and foraging. The highly specialised nature of the odontocete auditory

system has been documented in great detail and echolocation has been studied intensively, particularly in captive bottlenose dolphins, where it has been demonstrated to be used in both target detection and discrimination (Au, 1993; Richardson *et al.*, 1995).

The short, high intensity sounds characteristic of dolphin echolocation clicks are produced in the upper part of the animal's head (see **Figure 1.2**). By forcing air past the phonic lips, which are associated with the dorsal bursae in the nasal complex, rapid, transient clicks are produced. The sound is then focused and propagated into the water by the melon, a complex fatty structure situated behind the rostrum, on top of the skull (Cranford, 1996). Sound travels at a speed of approximately 1,530m/s in seawater, which is approximately 4.5 times faster than the speed of sound in air (Ketten, 2000). The dolphin brain is well adapted to process such rapid information and the melon has acoustic properties similar to those of water, thus allowing sound to couple across the melon and into the water quickly and with little deflection.

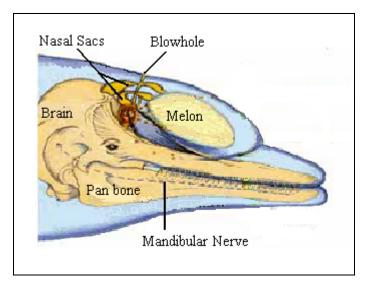


Figure 1.2 Diagram of a dolphin's head, highlighting the locations of the brain, melon, blowhole, nasal sacs, pan bone and mandibular nerve, all of which are involved in sound production.

Adapted from www.inkokomo.com/dolphin/echolocation.html

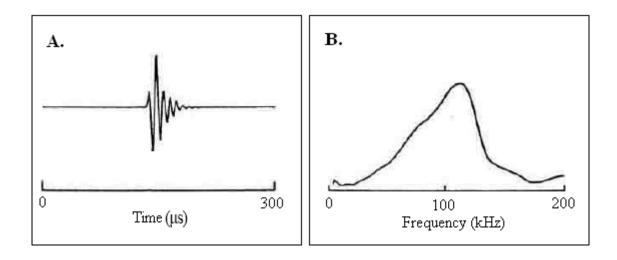
After emitting such clicks, it is thought that the pan bone in the dolphin's lower jaw receives the reflected echo from the target, possibly via the mandibular nerve, as the sound waves return. Fatty tissue located behind the pan bone then channels this information to the middle ear, where it is transmitted to the brain and the animal generates another click (Tyack and Miller, 2002). In this way, clicks are usually produced in a train and echolocation is utilised by the bottlenose dolphin for locating prey, navigation and predator avoidance.

The distances at which dolphins can discriminate targets using their echolocating capabilities have been studied extensively in captive animals and their performances in such experiments have been exceptional. As an example, a bottlenose dolphin can detect a 2.5cm target from approximately 72 metres away (Tyack and Miller, 2002). It is due to the high frequency of dolphin echolocation clicks that this type of high resolution detection and discrimination is possible.

The time between clicks emitted by the dolphin, known as the interclick interval (ICI), gradually decreases as the animal closes in on a target (Au, 1993). Dolphins can modulate the number and frequency of clicks they emit, relative to the information they require about their environment. Consequently, it has been found that echolocation click rates will vary depending on several factors, including the behavioural state of the dolphin, group size, habitat utilisation and geographic location (Jones and Sayigh, 2002). It is possible to measure several aspects of echolocation production, and it has been found that the distribution and rate of change of ICI, click train patterns and overall echolocation use may be used to quantify the influence of such variables (Leeney and Tregenza, 2006).

Species-specific variation is seen in the characteristics of the echolocation clicks produced by odontocetes, both in the duration, bandwidth and amplitude. It has been demonstrated that bottlenose dolphins are able to adapt the peak energies of their echolocation clicks, in order to maximise returning echoes and to counteract the masking effects of background noise; a trait which has also been demonstrated

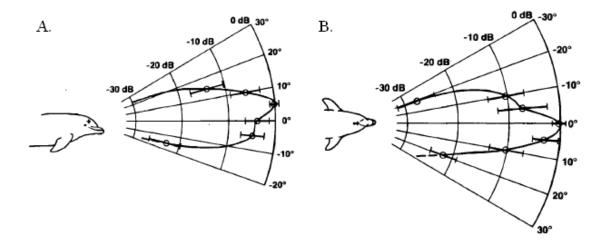
in the beluga whale, *Delphinapterus leucas*, (Au *et al.*, 1985). The echolocation signal of the bottlenose dolphin is characterised by a short duration, typically 50 to 200µsec (Au, 2003), peak frequencies from 60 to 140kHz and a relatively broad bandwidth of 38 to 46kHz (**Figure 1.3**). A variety of source levels have been recorded in this species, with peak-to-peak amplitudes of 150 to 228dB (*re* 1µPa at 1m) recorded in echolocating animals (Au, 1993), demonstrating the highly dynamic nature of the dolphin echolocation system.



**Figure 1.3** Example of the average waveform (A) and spectra (B) of the bottlenose dolphin echolocation click. Adapted from Tyack (1987).

It is thought that echolocation clicks are focused by the melon, producing a highly directional transmission beam from the dolphin's head (Au, 1993). Within this echolocation beam, the intensity of sound measured decreases at increasing angles from the source, resulting in variation in the spectral content of clicks. The beamwidth can be measured using the major axis of the beam as a reference point and calculating the angle that is within 3dB of this point (Richardson *et al.*, 1995). In the bottlenose dolphin, the 3-dB beamwidth is 10-11.7° at an upward angle of approximately 5° (Au *et al.*, 1986); this is shown in **Figure 1.4**. As a result of this directionality, the measurement of echolocation clicks in the wild is very

challenging as the signal becomes more distorted at increasing distances from the centre of beam (Au, 2002).



**Figure 1.4** Bottlenose dolphin transmission beam pattern in the vertical (A) and horizontal (B) planes. From Au *et al.*, 1986.

# 1.2 Acoustic Monitoring of Cetaceans

It is inherently difficult to study cetaceans using visual survey techniques alone, as these animals spend large amounts of time underwater. This, in addition to the fact that visual techniques are only practical in favourable weather conditions and during the hours of daylight, means that the use of passive acoustic monitoring techniques in the field of cetacean research has become increasingly popular. Acoustic surveying of cetaceans also has advantages over visual techniques in that they are less labour intensive (at least in the field), they provide a way of surveying submerged marine mammals and of collecting objective data, and they can be conducted continuously, regardless of season, daylight, and in most weather conditions. However, acoustic monitoring does also have limitations, for instance, it relies upon vocalising animals, group size and behaviour can have an effect on detection rates, and it is currently not possible to extrapolate data to measure absolute abundance.

It has been suggested that an integrated approach, incorporating both visual and acoustic methods, will improve the efficiency of marine mammal surveys (Lewis et al., 1998; Weir et al., 2001) Many studies in cetacean research incorporate acoustic survey techniques into the data collection, in order to complement the visual element of the research (e.g. Bearzi et al., 1999). However, the use of acoustic methods as the primary, or sole, methodology in marine mammal research is less common. As acoustic surveying is reliant on animals producing vocalisations and visual surveying is only useful when an animal surfaces, it seems that such techniques are not mutually exclusive and should be used to complement one another.

#### 1.2.1 **The T-POD**

The T-POD is an acoustic measuring device that has been developed for the echolocation monitoring of odontocetes. These acoustic data loggers are self-contained ultrasound monitors that record the time and duration of tonal clicks to a 10µsec resolution. Originally developed for the detection and monitoring of harbour porpoises (*Phocoena phocoena*), the T-POD has now been improved and is capable of detecting a wider range of species, including bottlenose, common (*Delphis delphinus*) and Risso's (*Grampus griseus*) dolphins and short-finned pilot whales (*Globicephala macrorhynchus*) amongst others (Tregenza, 2001).

Functionally, the T-POD works as an omni-directional hydrophone system consisting of an analogue click detector, a digital timer, duration logger and a ceramic transducer, all of which are housed inside a 50-70cm PVC tube (**Figure 1.5**). The T-POD detects clicks by running a series of 6 successive scans, each with a 9.3 second duration. The settings for these scans can be selected by the user for the appropriate target species (dolphin or porpoise) then, by comparison of two bandpass filters, the T-POD assesses the bandwidth of the signal to determine the probability of it being of cetacean origin. The sensitivity settings required can also be adjusted, depending on the environmental conditions of the location selected and the length of the study (Tregenza, 2001).

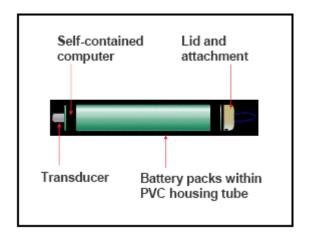


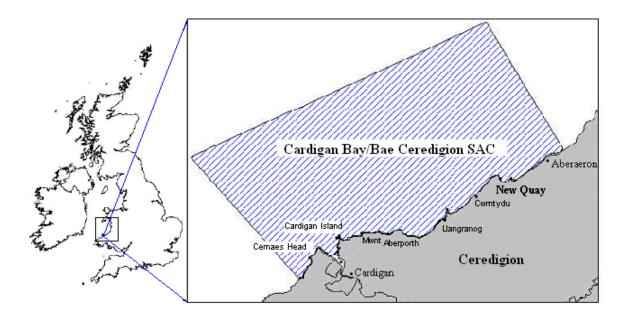
Figure 1.5 Diagram of a T-POD unit, indicating the positions of the major components and the PVC housing tube (www.chelonia.co.uk).

T-PODs have been used successfully in several aspects of cetacean monitoring, particularly with harbour porpoises. Such studies have investigated anthropogenic noise disturbance (e.g. the Horns Reef offshore wind farm development (Skov *et al.*, 2002)), habitat use (e.g. Verfuß *et al.*, 2006), the effects of acoustic pingers (e.g. Cox *et al.*, 2003), activity patterns (e.g. Carlström, 2005), and echolocation behaviour (e.g. Verfuß *et al.*, 2005). Studies with bottlenose dolphins are more limited in number, although T-PODs are considered to be a valuable tool in the monitoring of this species. The majority of investigations with bottlenose dolphins have examined the performance and detection ranges of T-PODs (e.g. Ingram *et al.*, 2004; Reyes Zamudio, 2005; Philpott *et al.*, 2006). More recently, studies have focused on more detailed aspects, such as the determination of ranging patterns and habitat use (Senior, 2006; Simon *et al.*, 2006) and echolocation behaviour (e.g. Reyes Zamudio, 2005; Leeney and Tregenza, 2006) in bottlenose dolphins.

# 1.3 Cardigan Bay, West Wales

# 1.3.1 Location Description

Cardigan Bay is a large, shallow embayment located off the west coast of Wales (**Figure 1.6**), which covers an area of approximately 5500km<sup>2</sup> and is topographically characterised by a gentle shelf, typically less than 50 metres deep (Barne *et al.*, 1995). The sediment characteristics of the bay are variable, with gravel and cobbles predominantly found offshore and finer silt and sand found near shore (Evans *et al.*, 2000). Although influenced by the Irish Sea, Cardigan Bay experiences weak tidal currents for the most part, as it is relatively sheltered.



**Figure 1.6** Map of the United Kingdom mainland. The box highlights the location of Cardigan Bay and the inset box shows the location and extent of the Cardigan Bay SAC.

Bottlenose dolphins are sighted year round in Cardigan Bay, and as this species is identified in Annex II of the EU Habitats and Species Directive, this was the primary reason that an area of Cardigan Bay was established as a candidate Special Area of Conservation (cSAC) in 1996 (JNCC, 2006). The Cardigan Bay SAC became a fully managed conservation area in 2004, and extends 12 miles

offshore from Aberarth in the north, to the Teifi Estuary in the south (see **Figure 1.6**). As a designated SAC, the site is considered as a high-quality conservation site and as a result, the dolphins here are afforded a level of protection from both 'significant disturbance' and habitat deterioration (Cardigan Bay SAC Management Plan, 2001).

In addition to the presence of the resident group of bottlenose dolphins, other cetacean species have been reported in Cardigan Bay waters, ranging from the common and widespread harbour porpoise (*Phocoena phocoena*) to the occasional minke whale (*Balaenoptera acutorostrata*) (Evans, 1995).

A wide variety of fish species are abundant in Cardigan Bay, particularly during the warmer months, including dab (*Limanda limanda*), grey mullet (*Chelon labrosus*), sea bass (*Dicentrarchos labrax*), mackerel (*Scomber scombrus*) and herring (*Clupea harengus*) (Evans *et al*, 2000). Locally and seasonally abundant prey species form the large majority of the bottlenose dolphin diet, reflecting the opportunistic feeding habits of this species. Both pelagic and benthic species are frequently consumed and the dolphins have been observed to regularly feed on clupeids, mullids, scombrids, serranids and salmonids (Grellier *et al.*, 1995; Sanots *et al.*, 2001).

Ceredigion County Council (CCC) conducts visual surveys of bottlenose dolphin site use and interactions with boat traffic at six land-based study sites across the SAC. The Sea Watch Foundation (SWF) coordinates one of these, on New Quay pier. Additionally, passive acoustic monitoring of bottlenose dolphins and harbour porpoises has been in place since 2005, with ten T-PODs deployed at coastal locations throughout the SAC, to monitor the occurrence and movements of these animals (Simon *et al.*, 2006). In 2005, a study was carried out at Mwnt and New Quay Bay using visual observations and theodolite tracking to investigate T-POD performance and the possibility of using T-POD data to identify bottlenose dolphin feeding behaviour (Reyes-Zamudio, 2005). It was concluded that

detection probabilities are influenced by both dolphin behaviour and distance from the T-POD, and that it may be possible to use T-PODs in the investigation of spatio-temporal feeding patterns.

# 1.3.2 Study Site: New Quay Bay

New Quay Bay (52° 13'N, 004° 21'W) is a small, sheltered embayment situated in the southern region of the Cardigan Bay SAC (see **Figure 1.6**). This small fishing port is characterised by a rocky outcrop at New Quay Head to the west and Llanina Reef extending offshore to the east of the bay (**Figure 1.7**). Bottlenose dolphins are seen regularly in New Quay Bay and anecdotal evidence suggests that they have frequented the area from at least the 1920's (Bristow, 2004). It is thought that the bay provides an important foraging and breeding habitat to these dolphins and a long-term land-based study, conducted for over 14 years, has confirmed, amongst other observations, a high degree of site fidelity for a number of individuals (Bristow and Rees, 2001; Bristow, 2004).

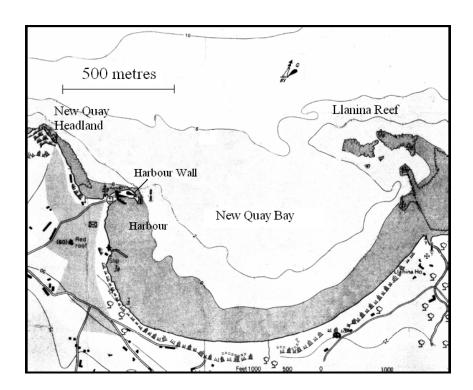


Figure 1.7 Map of the study location: New Quay Bay, West Wales.

Since 2004, the SWF has operated a seasonal, land-based monitoring program of dolphin presence, behaviour and boat interactions in New Quay Bay. This was in recognition of the fact that in order to conserve the bottlenose dolphin population in this area, it is necessary to develop a thorough understanding of the importance of these waters as a habitat, and of the dolphins sighted in this area. In addition to the visual monitoring of the bay, T-POD units were also deployed by SWF to acoustically monitor for dolphin (and porpoise) presence throughout the year.

#### 1.4 Study Aims

The aforementioned investigation by Reyes Zamudio (2005) in Cardigan Bay found that both T-POD detection rates and the number of detected echolocation clicks were significantly higher in foraging bottlenose dolphins than in those that were simply travelling. Additionally, ICI's were significantly lower in click trains from dolphins engaged in feeding activities than those travelling. Philpott and colleagues (2006) also reported comparable findings for bottlenose dolphins in the Shannon Estuary, Ireland. Both studies concluded that it may be possible to identify the behavioural state of echolocating bottlenose dolphins by examining the acoustic characteristics of T-POD data.

The primary aim of this project is to study the surface behaviour of the dolphins in New Quay Bay and compare those data to the corresponding click train parameter data collected from the two T-PODs in the bay. The present study aims to use land-based observations from the New Quay pier. Any significant patterns found from this will be applied to existing T-POD data from the last 12 months, in order to determine whether any seasonal or diel variations in dolphin habitat use of the bay exist.

As echolocation clicks are highly directional, this project will also aim to examine the effects of dolphin directionality on T-POD detection. This will be done opportunistically from a vantage point in the bay, when dolphins are clearly observed in the vicinity of the T-POD and the bearing of these animals can be assessed with a corresponding time. This directionality data will then be compared to the corresponding acoustic data from the T-PODs.

Additionally, reference buoys will be used to determine the approximate distances of animals in relation to the T-POD locations, whilst behavioural data are being collected. The number of dolphins observed will also be recorded as a measure of group size. This information will be used to determine the influence that distance and group size may have on T-POD detection rates in the study area.

Thus, the aims of the current investigation are:

- To investigate whether T-POD-detected acoustic characteristics are related to behavioural observations of bottlenose dolphins in New Quay Bay.
- To apply any findings from the above to determine if seasonal or diel variation in dolphin habitat use exists, using past T-POD data.
- To examine the importance of directionality when dolphins are travelling, and any effects this may have on T-POD detection rates.
- To investigate whether distance and group size of dolphins has any effect on T-POD detection rates.

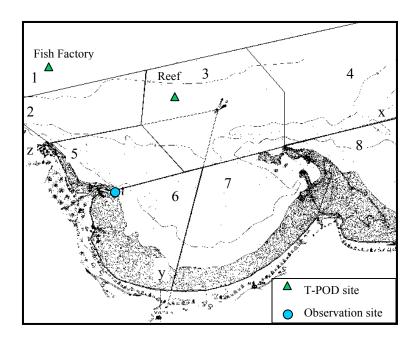
# 2. Methods

#### 2. Materials and Methods

# 2.1 Acoustic Survey Methods

#### 2.1.1 **T-PODs**

Passive acoustic monitoring of bottlenose dolphins was carried out using two Version 4 (v4) T-POD units, both of which were statically moored at selected sites in New Quay Bay. The first T-POD was moored in the proximity of the fish factory and the second near Llanina reef (GPS positions N 52°13.314 W 4°21.620 and N 52°13.29 W 4°21.11 respectively)(**Figure 2.1**). Reference buoys were attached to both T-PODs in order to aid with visual positioning of the units.



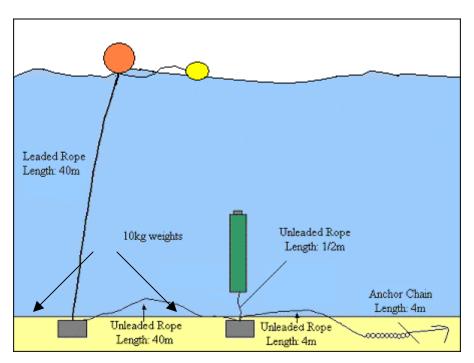
**Figure 2.1.** Map of the New Quay Bay study area, illustrating the locations of the T-POD units and the visual observation site.

The T-POD is powered by 12 alkaline D-cell batteries and it is possible to collect data on T-POD units continuously at sea, until the batteries expire, or the computer memory is full, which can take up to 8 weeks. However, it was decided, to be safe, that retrieval would take place every 4-6 weeks.

#### 2.1.2 Deployment and Mooring

Prior to the original deployment of the T-PODs, echo sounders were used to investigate the seabed within a 100m radius of the T-POD deployment locations, to ensure the area was free of obstacles, which could possibly reflect or scatter dolphin echolocation clicks. The T-PODs were both deployed and retrieved with the help of local fishermen (Winston Evans and Karl Steans). The locations selected for the T-PODs were inshore and relatively sheltered, and this was taken into account when the mooring system used to stabilise the equipment was developed.

Since v4 T-PODs are positively buoyant, both were statically deployed on a mooring system, in order to keep the unit situated above the seabed. The mooring system was developed prior to this investigation in collaboration with professional fishermen and allowed the T-POD hydrophone to float approximately 1.5m above the seabed (**Figure 2.2**).



**Figure 2.2** The T-POD mooring system, highlighting the T-POD and reference buoy positions and the weights and lengths of ropes used.

# 2.1.3 Calibration and Settings

Although newer T-POD versions, such as the v4 type used in this study, have been found to have less threshold variation between units than earlier models (v3 or less) (Dähne *et al.*, 2006), calibration of T-PODs is nevertheless essential, for both sensitivity measurements, and comparability of data between sites and studies. The T-PODs used in this study were calibrated under controlled laboratory conditions at the German Oceanographic Museum (Stralsund, Germany) (**Appendix A**). The T-POD hydrophones were calibrated to an absolute sensitivity of  $\pm 2 dB$  *re*  $1 \mu Pa$  between one another. A field calibration was also performed in order to validate the settings (Simon *et al.*, 2006).

The appropriate settings for the detection of bottlenose dolphin clicks (filter A: 50kHz; filter B: 70kHz) were selected for channels 1,3 and 5 in both units and the remaining three channels were set to detect harbour porpoises (filter A: 130kHz; filter B: 92kHz).

## 2.1.4 Processing T-POD Data

Data were downloaded from the T-PODs on the day they were retrieved and the T-POD was then redeployed as soon as possible. Communication is established between the T-POD and the PC via a parallel printer port, the T-POD data is then read onto the PC. This is facilitated by the specialised TPOD.exe software, which creates a .pdc file for each continuous period of data logging. When the download is complete, it is necessary to process the .pdc files, during which TPOD.exe uses a train detection algorithm to identify click trains characteristic of dolphins and porpoises and of boat sonar.

The algorithm uses a probability model and various statistics to classify trains according to the likelihood of them being of cetacean origin. The following classifications are used:

- Cet Hi: Click trains with a high probability of coming from cetaceans
- Cet Lo: Low probability cetacean click trains when logged alone, but assumed to be correctly classified when associated with Cet Hi trains
- ? (Doubtful): Not classified as coming from cetaceans as these click trains are sometimes unreliable. However, these trains can be used if examined carefully as they are often from non-feeding animals.
- **??** (Very Doubtful): These are usually click trains from boat sonar or random non-train producing sources.

Tregenza (2001) has suggested that doubtful click trains should be included in T-POD data analysis when attempting to study cetacean behaviour. This is to ensure both a more valid data set and the inclusion of short click trains, which may otherwise be excluded. As the aim of this study was to investigate the possibility of identifying bottlenose dolphin behaviour from T-POD acoustic data, Cet Hi, Cet Lo and doubtful click trains were examined. These train classifications were also used when investigating the effects of dolphin directionality on T-POD detection, as these data involved observations exclusively from travelling animals (this will be discussed further below).

Click train detections were viewed using TPOD.exe, where the data are presented graphically. Here, the channels set for dolphin detection were selected (scans 1,3 and 5) and the train classifications required were activated, which it is necessary to do before exporting data for analysis. In TPOD.exe, the date and time of each train is displayed and the duration, pulse repetition frequency (PRF) and ICIs of clicks can be inspected individually.

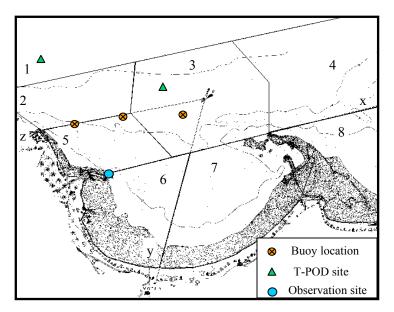
In order to view these data numerically, the data were exported to Microsoft Excel as a .txt file for analysis. For the purposes of this investigation, the 'click times' option was selected in option A of the 'Export' menu, which exports click detection times (in the format of minutes in the year) and the duration of logged trains. Details of individual train characteristics were also exported by selecting

'train detail data' in option B of the 'Export' menu. Details such as the total duration of trains, minimum and maximum ICIs, and the number of clicks in each train can be analysed by exporting these data.

# 2.2 Visual Survey Methods

#### 2.2.1. Pilot Study

An initial pilot study was carried out for 5 days, in order to assess the suitability of the data collection forms used by the Sea Watch Foundation for the CCC study. It was decided that the original format of both the effort and sightings forms (**Appendices B & C**) needed to be altered, to ensure that the data collected was appropriate for this study.



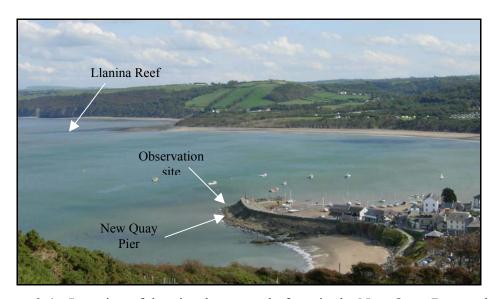
**Figure 2.3** Map of the New Quay Bay study area, illustrating the locations of the marker buoys, the T-POD units and the visual observation site.

Modifications included removing the general weather and wind direction parameters from the effort form and altering the boat tally to include changes in boat presence every 15 minutes, instead of the standard 2-hourly recording. Alterations were made to the sightings form, so that it was possible to record

dolphin presence and behaviour to the nearest minute. Additionally, three buoys were deployed across the study area as reference markers, in order to allow for more accurate estimations of dolphin positions in the bay (**Figure 2.3**).

#### 2.2.2 Visual Data Collection

Land-based visual surveys were conducted from May to September 2006 from a vantage point at the end of the New Quay pier (52° 13'80"N, 004° 21'05"W), which overlooks the study area and allows for an observation height of between 6 to 10 metres, depending on tidal height (**Figure 2.4**).



**Figure 2.4** Location of the visual survey platform in the New Quay Bay study area. (Photograph courtesy of Eleanor Stone, UWB)

Data were collected on days with good light conditions and no precipitation and in sea states less than 3 on the Beaufort scale, in order to ensure that all dolphin behaviours were visible to the observers. Watches were carried out in randomised time blocks between 7am and 9pm, depending on conditions, in an attempt to reduce bias. Typically, two trained observers were present for visual data collection and 10x25 binoculars were used to assist with observations.

#### 2.2.3 Effort Data

Throughout each visual survey, effort data were continually collected at 15-minute intervals, which included recordings of time, an associated effort index, the tidal and sea state, and a tally of boat activity (Form 1; **Appendix D**). The effort index was recorded as a sequentially increasing 4-digit number, which could be used for cross-referencing purposes. The tide was categorised as one of four states; flood, high (defined as 45 minutes either side of high water), ebb or low (defined as 45 minutes either side of low water). Sea state was recorded applying the Beaufort scale, with observations being terminated if conditions increased beyond sea state 2. Boat presence was tallied throughout each 15-minute interval, using the categorisations displayed in **Table 2.1**.

**Table 2.1** Boat type descriptions used on the effort form throughout the study.

<b>Boat Type</b>	Description
MOTOR	Recreational motor boats, dinghies with outboard motors and visitor passenger boats
SPEED	Speed boat or RIB
FISHING	Commercial fishing boat
SAIL	Any boat under sail, including windsurfer
CANOE	Any boat being paddled

#### 2.2.4 Sightings Data

Data collected during dolphin sightings were recorded on Form 2 (**Appendix E**), on which both the date and corresponding effort indices were also recorded for cross-referencing purposes. Once an individual or group of dolphins was sighted, the initial position of the dolphin/s was recorded with a dot and labelled with an identification letter on the map. In the notes section of the form, a corresponding

record was made of the number of animals present (including the calves), and the time and behavioural state of the dolphin/s alongside the identification letter. The behaviour of individuals and groups of dolphins was classified into one of five behavioural categories, based on definitions made by Viddi and Lescrauwaet (2005)(**Table 2.2**).

**Table 2.2** Definitions of individual and group behaviour of dolphins applied during sightings data collection.

Behaviour	Description
Foraging	Regular dives in approximately the same area, surfacing in various directions
Travelling	Consistent movement in one direction, regular surfacing
Foraging/Travelling	Long dives whilst travelling in a consistent direction, surfacing at irregular intervals
Resting	Lying motionless at or milling around the water's surface
'Quick'	Fast moving, energetic activities causing splashes (classified as behavioural events)

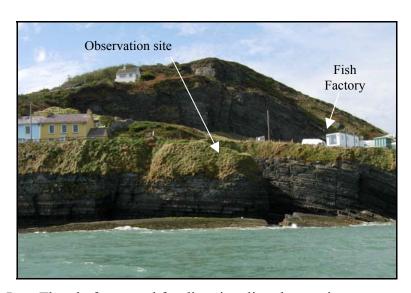
A group of dolphins was defined as two or more individuals, which were within 100 metres of one another and behaving in a similar manner or if travelling, moving in the same direction, a definition described by Wells and colleagues (1987; cited in Mendes *et al.*, 2002). The distance of 100 metres was chosen as it was found that when dolphins were within this distance of one another, individual identification often became problematic. If dolphins were seen to form new groups or separate into individuals, a new dot and identification letter was assigned and corresponding notes made on times and new behaviours.

Any changes observed in the behavioural state of individuals or groups present were noted with a new dot on the map, and the time and new behaviour was recorded in the notes section. Additionally, arrows were drawn on the map to represent movement of the dolphins present, in order to aid the analysis of distance from the T-PODs and for calculating detection rates.

Maps were used until sufficient data were recorded on them to fill the sheet, at which point a new map was started to avoid confusion during the data input stage. Dolphins were regarded as having left the study area or lost from view when they could no longer be seen from the observation point. To indicate such events, the time of the last observation was noted and an 'X' plotted on the map to signify the last position of the dolphin/s sighted.

# 2.2.5 Directionality Observations

It was decided during the pilot study that it would not be possible to accurately collect the data required for dolphin directionality from the observation point on the pier, due to its low height in relation to the T-POD buoys. For this reason, directionality data was collected from a vantage point of approximately 15m high, overlooking the fish factory T-POD (**Figure 2.5**), which provided a 360° view in the region of the T-POD. Since an equally elevated observation platform does not exist in the vicinity of the reef T-POD, the effects of directionality on T-POD detection rates were examined in this study using only one of the two T-PODs.

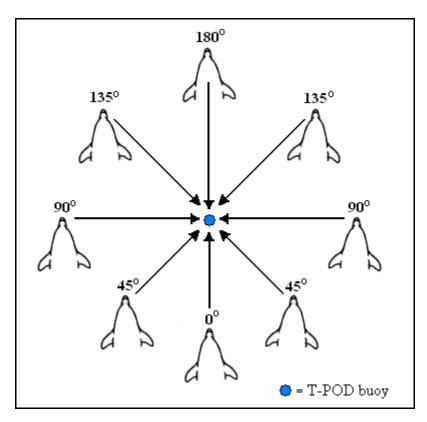


**Figure 2.5** The platform used for directionality observations.

Furthermore, it was found that determining directionality of feeding dolphins would not be possible, due to the inconsistencies which are likely to exist between the direction in which the dolphin surfaces when feeding and the direction it may be echolocating when searching for prey or hunting. Conversely, the more consistent surfacing nature of travelling dolphins makes this behaviour more feasible to study for this directionality investigation.

Directionality data were recorded on Form 3 (**Appendix F**) and were collected opportunistically, when a dolphin was clearly sighted in the vicinity of the T-POD. As with the sightings data collection, 10x25 binoculars were used to assist with observations. Directionality recordings were only taken when one dolphin was present, as it would not be possible to determine the source of the click trains logged in the presence of several dolphins. Each time the dolphin surfaced, both the relative bearing from the cross section of the animal's head in relation to the T-POD buoy (0°, 45°, 90°, 135°, or 180°) (**Figure 2.6**) and the time of the surfacing were recorded. Additionally, the date, associated effort index, and tidal state were also recorded.

In order to determine the importance of distance in addition to directionality, the approximate distance of the animal from the T-POD buoy (either 0-100m or 100-500m) was also recorded. Dolphins further than 500m away from the T-POD buoy were not included in this part of the study, as it has been found that detection probability sharply declines when dolphins are at these distances (Reyes Zamudio, 2005).



**Figure 2.6** Diagrammatic representation of the relative bearing (0°, 45°, 90°, 135°, or 180°) from the cross section of the dolphin's head in relation to the T-POD buoy for the directionality observations in this study.

# 2.3 Data Analysis

Visual data and acoustic data were matched to the nearest minute and where more than one dolphin was present, it was assumed that the dolphin closest to the T-POD produced the detected click train. Since dates are stored in Excel as the number of days since 01/01/1900 and the time as a fraction of one day, it was necessary to use the following equation to calculate the date and time of click detections:

# Number of days since 01/01/1900 + (minute in the year) / 1440

The number of days for the year was obtained from the T-POD help file (Tregenza, 2001), which in 2006 was 38718 days and in 2005 was 38353 days.

The values obtained were then formatted to provide the date and time (to the nearest minute) for the start of each click train detected by the T-POD.

# 2.3.1 Behaviour and ICI Analysis

Where corresponding visual data were collected, the behaviour of the dolphins detected by the T-POD was matched with the appropriate click trains. The exported 'click times' data were examined and the ICIs for each click train calculated by subtracting the time of each click from the time of the preceding click. Data such as the number of clicks and the total duration of each train were obtained from the 'train details' export. The mean ICI of each click train was also calculated from the train details export, using the following equation:

Mean ICI (
$$\mu$$
s) = (Train Duration /(No of Clicks – 1)) / 100

Mean ICIs were analysed in this investigation, as opposed to minimum or maximum values, as it has been found that they are more stable over time than minimum and maximum ICIs. Also, the T-POD train detection algorithm can sometimes include non-cetacean clicks at the extreme ends of click trains, which can then lead to ambiguous minimum and maximum ICIs in some cases (Nick Tregenza, *pers.comm*.).

## 2.3.2 Detection Distance

In order to broadly investigate whether distance from the T-POD influences detection probabilities, each dolphin or group of dolphins sighted was categorised as being 0-100m, 101-500m or greater than 500m away from the T-POD. This was achieved by preparing a transparency with 100m and 500m radial contours depicting these zones, as seen in **Figure 2.7**. By placing this transparency over each completed map, the approximate distance of each dolphin sighting was calculated.

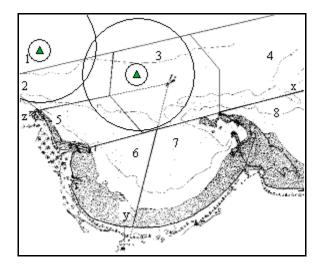


Figure 2.7 Demonstration of the radial contours used to approximate the distance of each dolphin sighting from the T-POD during the study. The smaller circles represent the 100m contours and larger circles the 500m contours.

# 2.3.3 Directionality

Since the bearings of the dolphins observed in this study were actually in relation to the reference buoy on the waters surface, it was necessary to correct these data to allow for discrepancies between the position of the reference buoys and the T-POD. Aberystwyth tidal data (www.tourism.ceredigion.gov.uk) was used to calculate the mean high (4.4m) and low (1.3m) tidal heights for the study period. Using this information, a right-angle triangle was created and the shortest distance between the buoy and its weight at high and low tides was calculated using the Pythagorean theorem (**Figure 2.8**). The position of the buoy at each tidal state (high, flood, ebb and low tide) was then calculated, where the flood buoy position was considered to be 25% and the ebb buoy position as 75% of the difference between the high and low tide buoy positions.

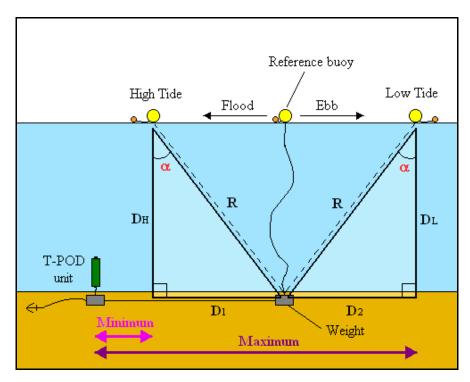


Figure 2.8 The method used to calculate the minimum (high tide) and maximum distances (low tide) of the reference buoy from the T-POD unit. Where:

**D**H = adjacent = mean water depth at high tide

**D**L = adjacent = mean water depth at low tide

 $\mathbf{R}$  = hypotenuse = length of rope connected to buoy (40 m)

 $\alpha$  = opposite angle of the right-angled triangle

**D**<sub>1</sub> = shortest distance between buoy and weight at high tide

**D2** = shortest distance between buoy and weight at low tide

The following measures were calculated for the approximate distance between the reference buoy and the T-POD unit in each tidal state:

**High tide:** 0.24m

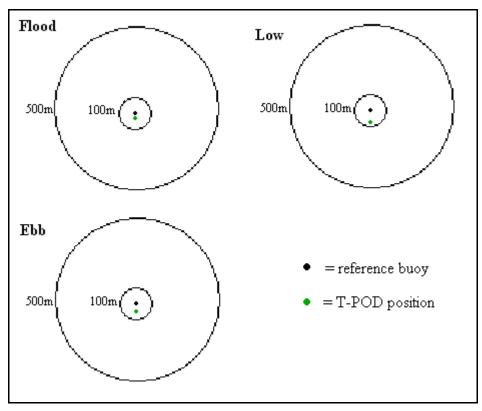
**Flood:** 19.935m

**Ebb:** 59.805m

**Low Tide:** 79.98m

These calculated buoy positions were used to prepare transparencies for each tidal state, incorporating the correct T-POD position, which were then placed over the maps (**Figure 2.9**). Each completed map from the directionality observations was then examined and the bearings corrected accordingly where necessary.

Corrections were not made for observations at high tide, due to the negligible difference between the buoy and the T-POD position at this tidal state.



Examples of the transparencies used to correct the bearing of the dolphins observed during the directionality measurements. Flood, ebb and low tide corrections are shown. Dolphin directionality observed at high tide was not corrected due to the small discrepancy between the buoy and T-POD position at this tidal state (0.24m).

# 3. Results

#### 3. Results

# 3.1 Survey Effort

Visual survey data were collected on 78 days from 9th May to 18th September 2006, resulting in the collection of 410 hours (24,570mins) of effort data (**Appendix 1**). Over this study period, bottlenose dolphins were observed on 51 days and a total of 362 dolphin sightings were recorded (**Appendix 2**). The duration of these sightings was 110 hours (6,622mins), which accounted for 27% of the total effort time.

It was not possible to continuously collect acoustic data throughout the study period, due to either delays in re-deployment, as a result of adverse weather conditions, or technical problems with the T-POD units. As a result, data were collected on the fish factory T-POD for 93.6% (73 days) of the visual observation time and on the reef T-POD for 84.6% (66 days) of the visual survey time. The acoustic data from both T-PODs were combined for comparison with the sightings data.

#### 3.2 Dolphin Behaviour

## 3.2.1 Visual Data

Sightings data was separated into the amount of time that each dolphin or group of dolphins was observed individually. This resulted in a total of 190 hours (11,380mins) of behavioural data for analysis (**Appendix 2**).

By far the most common behavioural state observed was 'foraging', which was recorded for 136 hours. Travelling behaviour accounted for 24 hours of observations, foraging/travelling for 30 hours and resting dolphins were observed for 10 minutes of the total dolphin duration (**Figure 3.1**). Since resting behaviour was observed for less than 0.01% of the observation period, it was not included in further analysis for this investigation. As the duration of 'quick' behaviours was

highly variable (ranging between 1 second and 7 minutes), each 'quick' occurrence was considered as an event, of which 312 were observed over the study period.

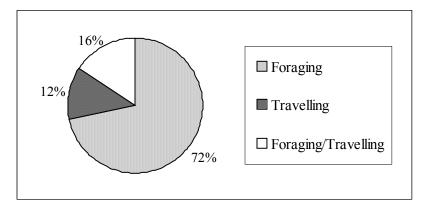


Figure 3.1 Percentage of time dolphins were recorded foraging, travelling and foraging/travelling during visual observations. Resting is not included, as this behaviour was observed for less than 0.01% of the observation period.

#### 3.2.2 Acoustic Data

#### 3.2.2.1 Click Train Variables and Behavioural State

A total of 377 detected click trains (Cet Hi, Cet Lo and Doubtful) were matched to visual observations of dolphin behaviour (**Appendix 4**). Of these, 221 trains were classified as foraging, 81 as travelling and 75 as foraging/travelling. Several echolocation variables were analysed to investigate whether T-POD-detected acoustic characteristics could be related to dolphin behavioural state.

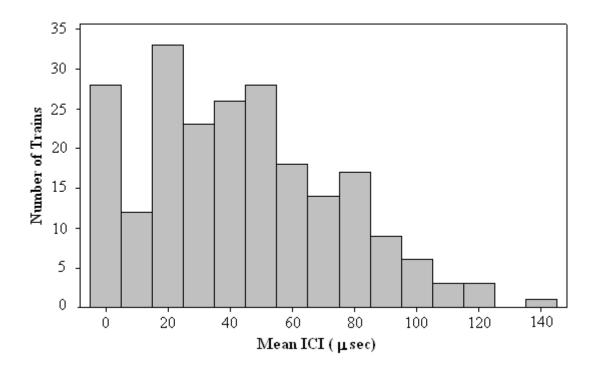
### i) Inter-click Intervals

The results of the Kruskal-Wallis test suggested that mean ICI varied significantly amongst the behavioural states (H = 89.31, df = 2, p = <0.001). The ranges of mean ICI values for each behavioural category are shown in **Table 3.1** (**Appendix 4**) and the distributions displayed in **Figure 3.2**. *Post-hoc* Mann-Whitney U tests indicated that the mean ICIs of click trains produced by echolocating dolphins were significantly lower in the behavioural state of

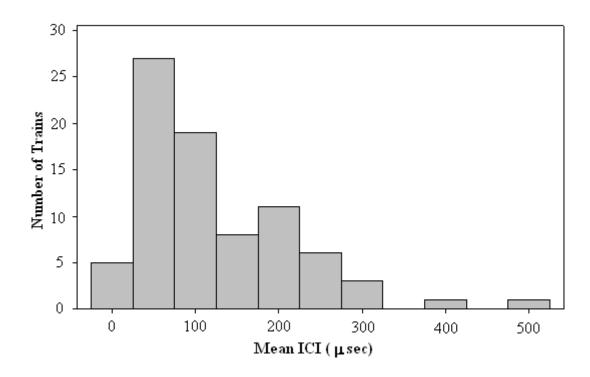
'foraging' than those produced by both travelling and foraging/travelling dolphins, which were not significantly different from each other (**Appendix G**). The dispersion of mean ICIs for each behavioural state is presented for comparison in **Figure 3.3**.

Table 3.1 The mean inter-click interval ranges (μs) of click trains detected by the T-PODs and matched to the three behavioural states of dolphins observed during the study period.

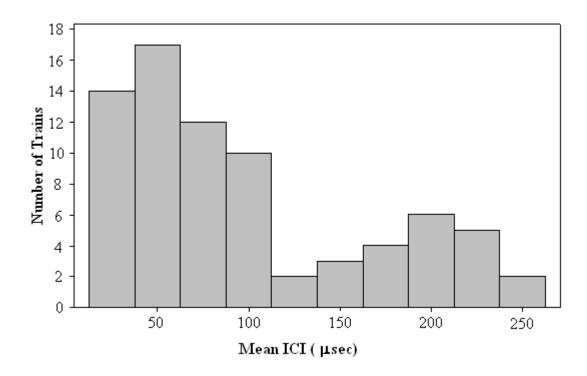
Behavioural State	Mean ICI range (μs)		
Foraging	1.53 – 137.38		
Travelling	15.15 – 490.21		
Foraging/Travelling	12.78 – 245.15		



**Figure 3.2a)** Frequency distribution of mean inter-click intervals in clicks trains produced by dolphins in the 'foraging' behavioural state.



**Figure 3.2b)** Frequency distribution of mean inter-click intervals in clicks trains produced by dolphins in the 'travelling' behavioural state.



**Figure 3.2c)** Frequency distribution of mean inter-click intervals in clicks trains produced by dolphins in the 'foraging/travelling' behavioural state.

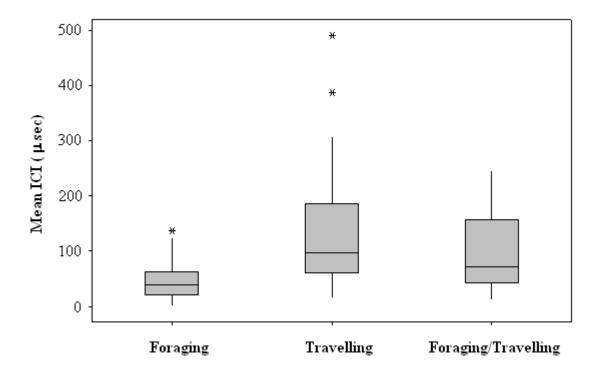


Figure 3.3 Box plot comparing the mean inter-click interval values (μs) for click trains produced by dolphins observed in the three behavioural states. Asterisks represent outliers.

# ii) Total Duration of Click Train

Significant variation was found in the total duration of click trains produced by dolphins in different behavioural states. The minimum, maximum and mean click train durations for each behavioural state can be seen in **Table 3.2** (**Appendix 4**). A Kruskal-Wallis test indicated highly significant variation in the duration of click trains produced by dolphins in different behavioural states (H = 44.53, df = 2, p = <0.001). *Post-hoc* Mann-Whitney U tests suggested that click train durations were significantly higher in the behavioural states of travelling and foraging/travelling than in foraging (**Appendix G**). These results are displayed for comparison in **Figure 3.4**.

**Table 3.2** Minimum, maximum and mean values for the total duration of click trains produced by dolphins observed in each of the behavioural states.

	Total Train Duration (ms)			
Behavioural State	Minimum	Maximum	Mean	
Foraging	0.62	331.5	70.4	
Travelling	10.6	499.8	141.1	
Foraging/Travelling	11.5	439.1	108.6	

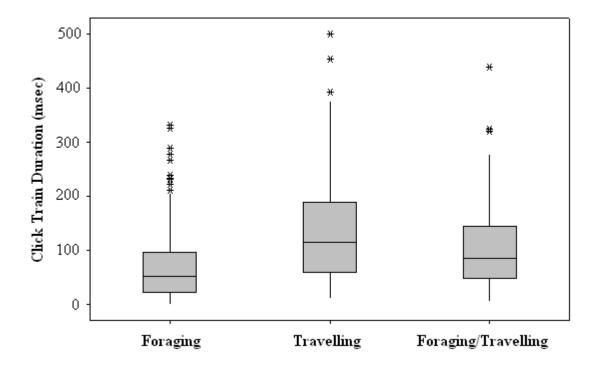


Figure 3.4 Box plot comparing the total duration of click trains (ms) produced by dolphins observed in foraging, travelling and foraging/travelling behaviours. Asterisks represent outliers.

# iii) Number of Clicks

It was found that the number of clicks in click trains emitted by dolphins in different behavioural states varied significantly. The minimum, maximum and mean number of clicks for each behavioural state can be seen in **Table 3.3** (**Appendix 4**) and these data are presented for comparison in **Figure 3.5**. A Kruskal-Wallis test suggested significant variation in the number of clicks produced by dolphins in different behavioural states (H = 10.89, df = 2, p = 0.004; adjusted for ties).

**Table 3.3** Minimum, maximum and mean number of clicks produced by dolphins observed in each of the behavioural states.

	Number of Clicks				
Behavioural State	Minimum Maximum Mean				
Foraging	5	113	17.3		
Travelling	5	42	13.4		
Foraging/Travelling	5	75	14.3		

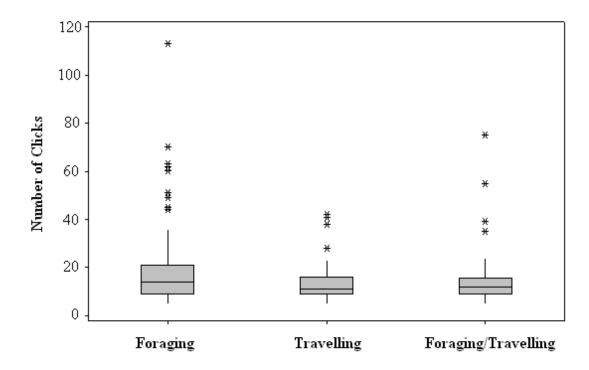


Figure 3.5 Box plot comparing the number of clicks produced by dolphins observed in foraging, travelling and foraging/travelling behaviours.

Asterisks represent outliers.

Post-hoc Mann-Whitney U tests revealed that the number of clicks emitted by foraging dolphins were significantly higher than those produced by both travelling and foraging/travelling dolphins. No significant difference was found between the number of clicks emitted by travelling and foraging/travelling dolphins (**Appendix G**).

# 3.2.2.2 Echolocation Acoustic Characteristics

All echolocation variables investigated differed significantly in relation to the behavioural state of the dolphins. Specifically, it was found that foraging dolphins produced click trains with significantly different values for mean ICI, click train duration and number of clicks when compared to those produced by both travelling and foraging/travelling dolphins. Analysis of these echolocation variables for click trains emitted by travelling and foraging/travelling dolphins suggested that these behavioural states were similar in their acoustic characteristics.

Thus, it may be possible to determine the behavioural state of echolocating dolphins by examining the echolocation variables of click trains recorded on T-PODs. Through the results of this investigation, the values appropriate for each of these echolocation variables and the corresponding behavioural classifications are displayed in **Table 3.4**.

Table 3.4 Applicable values for click train variables (mean ICI, train duration and number of clicks) for the classification of dolphin behavioural state. Travelling and foraging/travelling behaviours are pooled due to similarities in their acoustic characteristics.

Behavioural State	Mean ICI	Train Duration	No of Clicks	
Foraging	$1.5 - 12.9 \mu s$ and $< 137 \mu s$	0.6 – 10ms and < 332ms	5 -113	
Travelling or Foraging/Travelling	140 - 491μs	335 – 500ms	5 - 75	

Data logged on the two T-PODs in the study area from the 6<sup>th</sup> October 2005 to 30<sup>th</sup> September 2006 were analysed, and click trains classified as foraging or nonforaging (which encompassed travelling and foraging/travelling trains) for analytical purposes, using the values described in **Table 3.4**. In addition, click trains previously classified during the study were included. A total of 13,410 click trains were classified as high, low and doubtful probability of being of bottlenose dolphin origin. Of these data, 9,631 click trains could be classified as 'foraging' and 219 click trains as 'non-foraging'.

# i) Diel Variation in Echolocation Behaviour

In order to determine whether any significant diel variation existed in the number of foraging click trains detected during the day and the night, the diel cycle was divided into two phases: hours after sunrise (day) and hours after sunset (night). The sunrise phase also included the hour before sunrise, as a certain amount of natural light is reflected towards the Earth's surface by the upper atmosphere during this time interval, which is also the case during the hour after sunset. Sunrise and set tables and definitions were obtained from the U.S. Naval Observatory website (2006) and were defined as the times when the upper edge of the Sun was on the horizon.

During the day phase, 5,434 click trains were classified as 'foraging' and 202 as 'non-foraging', and in the night phase, 4,128 foraging trains and 17 non-foraging click trains were detected. The number of foraging click trains detected during each hour of the diel phases was calculated (**Figures 3.6** and **3.7**)(**Appendix 6**). An unpaired *t*-test indicated that there was no significant variation in the number of foraging click trains detected between the two diel phases (t = 0.72, df = 32, p = 0.475).

Analyses were conducted in order to determine whether any differences existed in the number of foraging click trains detected in each hour within each diel phase. This data is displayed in **Figure 3.6**. The results of a G-test indicated that the frequency of foraging click trains deviated significantly from a truncated Poisson distribution during the day phase (G = 4438.41, df = 16, p = <0.001). For the purposes of this test it was necessary to amalgamate the number of detections in hour 14 and above (**Appendix G**).

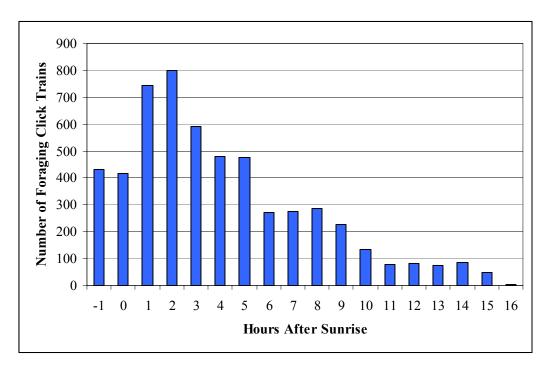


Figure 3.6 Number of foraging click trains detected on the T-PODs in the study area during the hour before and each hour after sunrise from October 2005 to September 2006.

A G-test also indicated significant deviation in the number of foraging click trains detected in each hour of the night phase (G = 3745, df =15, p = <0.001) (**Appendix G**). It can be seen that the highest number of foraging trains occurs in the 1<sup>st</sup> hour after the hour of sunset, a decrease is then evident for the next three hours, followed by a moderately high number of foraging click trains in hour 5. A relatively regular decrease is then apparent throughout the night phase until hour 10 (**Figure 3.7**).

The relatively high latitude of Britain means that day length and therefore hours of daylight and darkness are highly variable throughout the seasons of the year. Thus, it should be noted that the number of hours after sunrise and set are not constant throughout the year and this will affect comparisons in the number of foraging clicks detected during certain hours, particularly those in the later hours of each phase.

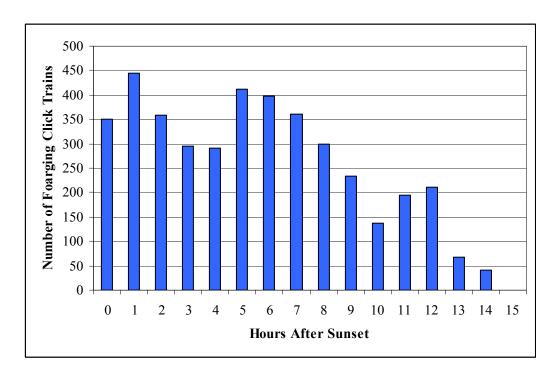


Figure 3.7 Number of foraging click trains detected on the T-PODs in the study area during the hour before and each hour after sunset from October 2005 to September 2006.

# ii) Seasonal Variation in Echolocation Behaviour

The analysed T-POD data were divided into the number of foraging click trains detected during each month of the year, in order to determine whether any significant seasonal variation existed. The number of foraging click trains detected in each month can be seen in **Figure 3.8 (Appendix 6)**. An increase in the number of foraging click trains was evident from April to July, followed by a noticeable decline in August and then a marked increase in October. The number

of foraging click trains then declined in the winter months and was especially low in January and March. Overall, it can be seen that the highest number of foraging click trains was detected in October and the lowest number between January and March.

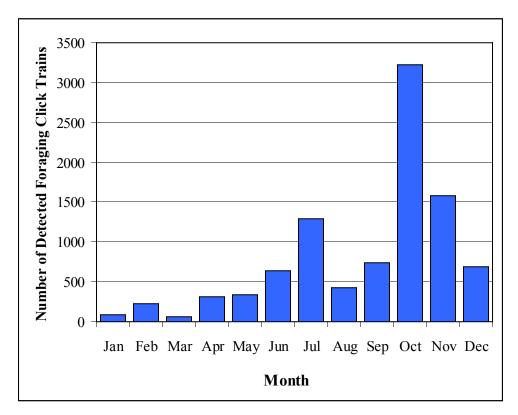


Figure 3.8 Number of foraging click trains detected on the T-PODs during each month in the study area from October 2005 to September 2006.

These monthly data were then corrected to account for the total number of click trains detected by the T-PODs during each month, thus the number of foraging click trains was expressed as representative proportions of the total number of click trains for statistical analysis (**Figure 3.9**). An angular transformation was then applied to this percentage data. The results of a G-test indicated that the proportion of foraging click trains detected between the months of the year did not exhibit significant variation (G = 6.292, df = 11, p = 0.853).

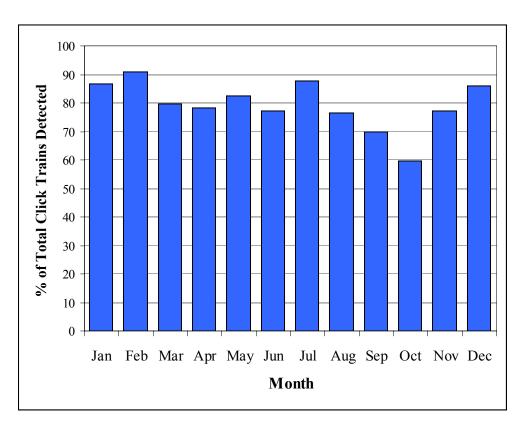


Figure 3.9 Percentage of the total number of click trains classified as 'foraging' for each month of the year from October 2005 to September 2006.

The numbers of foraging click trains detected during the day phase and night phase of each month were calculated to determine whether any diel variation in foraging activity existed over the year (**Figure 3.10**). All foraging click train quantities were then converted to percentage values for the appropriate phase or season, and angular transformations applied to these data for statistical analysis.

Comparisons were made between the proportions of foraging click trains detected in the day phase for each month. Peak proportions of foraging click trains were evident during the day phase of the summer months of June, July and August and also in September. A lower proportion of foraging click trains were detected during the day phase in October, November and December (see **Figure 3.10**). Although, a G-test indicated that there was no significant seasonal variation in the number of foraging click trains detected in the day phases of each month (G =

16.311, df = 11, p = 0.130), analysis of the proportion of foraging click trains detected in the night phase of each month indicated significant seasonal variation (G = 21.842, df = 11, p = 0.026). Here, a significantly higher proportion of foraging click trains was detected in December than in the summer months of June, July and August (see **Figure 3.10**).

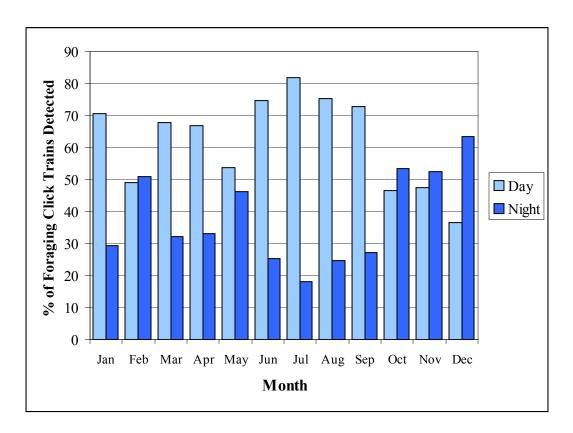


Figure 3.10 Number of foraging click trains detected on the T-PODs during the day and night phases throughout each month in the study area from October 2005 to September 2006.

Within-month analyses were performed for each of the diel phases, in order to determine whether any seasonal variation in the number of foraging click trains detected during the day and night was evident. The results from these analyses are displayed in **Table 3.5**. The results suggested highly significant variation in the number of foraging click trains between the diel phases in the months of June, July August and September, where considerably higher numbers of foraging click trains were detected during the day than in the night. This was also the case

during January, March and April. During late autumn and early winter, the majority of foraging click trains were detected during the night, although the difference was not statistically significant.

**Table 3.5** Summary of the *G*-test results, comparing the number of foraging click trains detected during the day and night phases throughout each month. Results in bold are significantly different at the 95% level.

Month	G value	d.f	p-value
January	6.660	11	0.010
February	0.018	11	0.894
March	4.877	11	0.027
April	4.372	11	0.037
May	0.211	11	0.646
June	9.832	11	0.002
July	17.935	11	<0.001
August	10.472	11	0.001
September	8.306	11	0.004
October	0.189	11	0.663
November	0.099	11	0.753
December	2.657	11	0.103

# **3.2.2.3 Directionality**

Directionality data were analysed to determine whether the relative bearing of the dolphin's head during surfacing (referred to as bearing hereafter) had any influence on T-POD detection rates. The data were separated into bearings recorded for visually detected dolphins and the number of such sightings that were detected on the T-POD (**Figure 3.11**)(**Appendix 3**). Acoustic detections were made for dolphins observed with bearings of  $0^{\circ}$ ,  $45^{\circ}$  and  $90^{\circ}$  to the T-POD. No acoustic detections were made for dolphins with bearings of  $135^{\circ}$  and  $180^{\circ}$ ,

although this was likely to be due to very small sample sizes (n = 1 for each bearing) for these bearings.

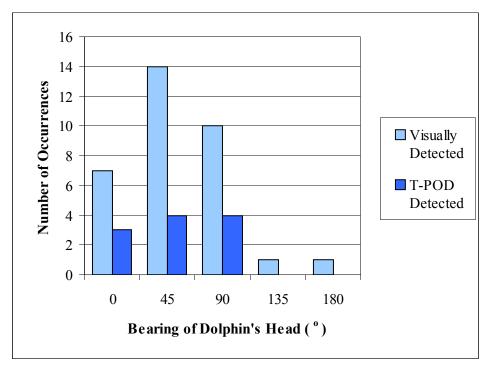
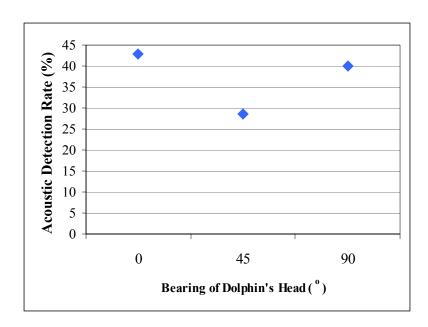


Figure 3.11 Number of dolphins detected visually and the number of those detected acoustically in relation to the relative bearing from the cross section of the dolphin's head (°) to the T-POD.

The acoustic detection rates at the  $0^{\circ}$ ,  $45^{\circ}$  and  $90^{\circ}$  bearings were calculated (**Figure 3.12**), and an angular transformation applied to the percentage values for the statistical analysis. A *G*-test indicated that there was no significant variation in the detection rates for dolphins observed with the cross section of the head at the bearings of  $0^{\circ}$ ,  $45^{\circ}$  and  $90^{\circ}$  (G = 1.129, df = 2, p = 0.569)(**Appendix G**).

The distances of each dolphin from the T-POD during the directionality recordings were analysed to broadly determine if this had any influence on detection rates. The number of visually detected dolphins that were acoustically detected by the T-POD in relation to the distance and bearing of the dolphin are displayed in **Figure 3.13**.



**Figure 3.12** Percentage of visually observed dolphins acoustically detected on the T-POD in relation to the relative bearing from the cross section of the dolphin's head (°) to the T-POD.

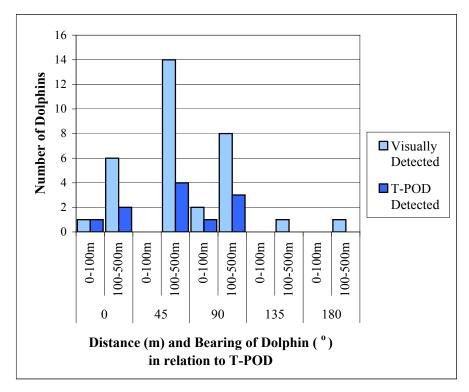
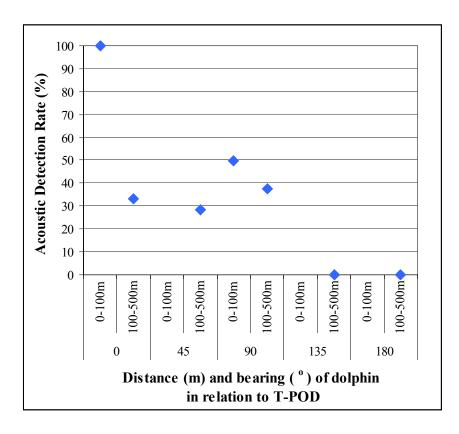


Figure 3.13 Number of dolphins detected visually and the number of those detected acoustically in relation to the distance (m) of the dolphin and the relative bearing from the cross section of the dolphin's head (°) to the T-POD.

The majority of dolphins were sighted within the 100-500m range of the T-POD, and no dolphins were observed in the 0-100m range of the T-POD with bearings of  $45^{\circ}$ ,  $135^{\circ}$  or  $180^{\circ}$ . Detection rates for dolphins observed with  $0^{\circ}$  (n = 1) and  $90^{\circ}$  (n=2) bearings in the 0-100m range were 100% and 50% respectively. Dolphins sighted at 100-500m from the T-POD, with bearings of  $135^{\circ}$  and  $180^{\circ}$  (total number = 2), were not acoustically detected (**Figure 3.14**).

Acoustic detection rates for dolphins sighted in the 100-500m range of the T-POD with bearings of  $0^{\circ}$ ,  $45^{\circ}$  and  $90^{\circ}$ , were compared with a *G*-test. The results indicated that there was no significant variation between the acoustic detection rates for dolphins observed at these bearings within 100-500m of the T-POD (G = 0.422, df = 2, p = 0.810).



**Figure 3.14** Percentage of visually observed dolphins acoustically detected on the T-POD in relation to the distance (m) of the dolphin and the relative bearing from the cross section of the dolphin's head (°) to the T-POD.

#### 3.2.2.4 T-POD Detection Rates

In addition to dolphin directionality, the distance that dolphins were observed from the T-POD, their group size and behaviour were also investigated in order to determine whether these factors had any influence on T-POD detection rates. Acoustic data recorded on the T-PODs were matched to visual data obtained throughout the study period (**Appendix 5**). Analysed data were then separated into 'visual' data (which included all visual detections of dolphins) and 'acoustic' data (where dolphins detected visually were also detected acoustically). Of the 860 dolphin sightings (groups and individuals), 23% (200 groups) were detected by the T-PODs.

# i) Distance from T-POD

The majority of dolphins sighted (77%; 662 groups) were within 100-500m of the T-PODs and of these, 27% (179 observations) were detected acoustically. Groups of dolphins sighted over 500m away from the T-POD accounted for 21% (178 groups) of visual data, of which 10% were detected by the T-PODs. Only 2% of the dolphins observed (20 groups) were 100m or less from the T-PODs, 15% (3 groups) of which were acoustically detected (**Figures 3.15 and 3.16**).

The highest rates of acoustic detection occurred for dolphin groups observed in the 100-500m range of the T-POD. However, this was the largest of the three ranges. The lowest acoustic detection rates were for dolphins over 500m away from the T-PODs. This is shown in **Figure 3.16**. With these distance categories, a regression analysis indicated that no significant relationship existed between detection rates and the distance at which dolphins were observed from the T-POD (F = 0.09, p = 0.815) (**Appendix G**).

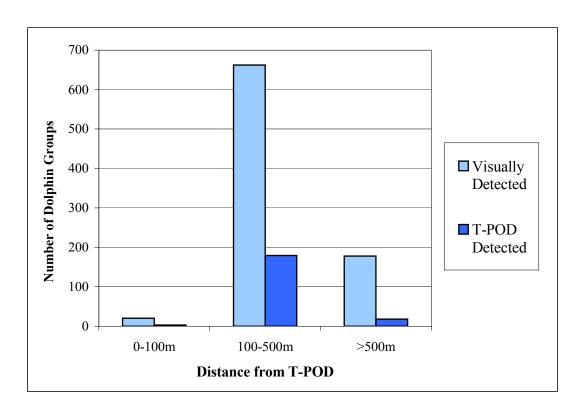


Figure 3.15 Number of dolphins detected visually and the number of those detected acoustically in relation to the distance at which dolphins were sighted from the T-PODs.

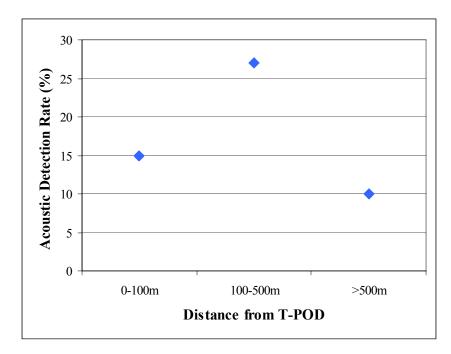


Figure 3.16 Percentage of visually observed dolphins that were acoustically detected in relation to the distance at which dolphins were sighted from the T-PODs.

# ii) Group Size

In order to determine whether group size had an effect on T-POD detection rates, the number of dolphins present during each sighting was analysed and matched to the corresponding acoustic data from the T-PODs (**Figure 3.17**). Single dolphins were the most commonly observed, accounting for 53% of all sightings. Groups of 4 and above were the least frequently sighted. The highest rate of acoustic detection was for groups consisting of six dolphins, and the lowest detection rate was for single dolphins. All group size data are summarised in **Table 3.6**.

Generally, an increase in detection rate was observed with increasing group size (**Figure 3.18**). However, the results of a linear regression analysis indicated that the relationship between group size and detection rates was not significant (F = 2.19, p = 0.199) (**Appendix G**).

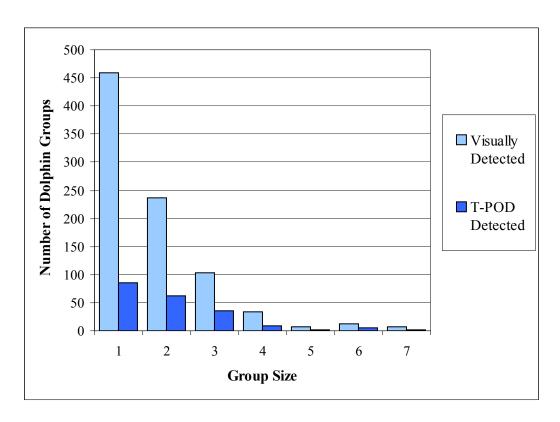
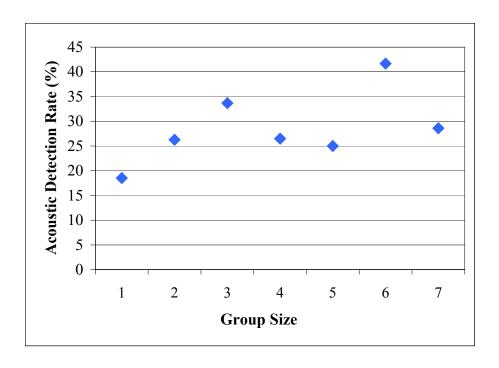


Figure 3.17 Number of dolphins detected visually and the number of those detected acoustically in relation to the observed group size.



**Figure 3.18** Percentage of visually observed dolphins that were acoustically detected in relation to observed group size.

Table 3.6 The number of visual observations and acoustic detections for each group size. Visual detections are also presented as a percentage of the total number of sightings. The percentage of acoustic detections for each of the visual detections for the appropriate group size is also shown.

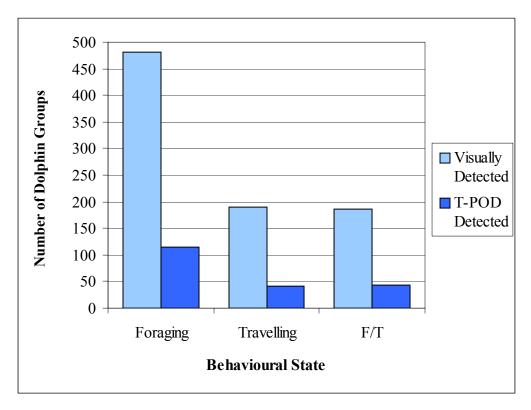
	Visual Detections		<b>Acoustic Detections</b>	
<b>Group Size</b>	Number % of Total		Number	% of Visual
1	459	53.4	85	18.5
2	236	27.4	62	26.3
3	104	12.1	35	33.7
4	34	4	9	26.5
5	8	0.9	2	25
6	12	1.4	5	41.7
7	7	0.8	2	28.6

# iii) Behavioural State

The visual behavioural data collected throughout the study were analysed and matched to the T-POD data, in order to determine whether the observed

behavioural state of dolphins had any influence on T-POD detection rates. The number of dolphin groups visually detected was compared to the number detected acoustically (**Figure 3.19**). The majority of the dolphin groups observed during the study period were considered to be foraging (55.9%; 481 occurrences) and of these, 24% (n = 114) were acoustically detected on the T-PODs (**Figure 3.20**).

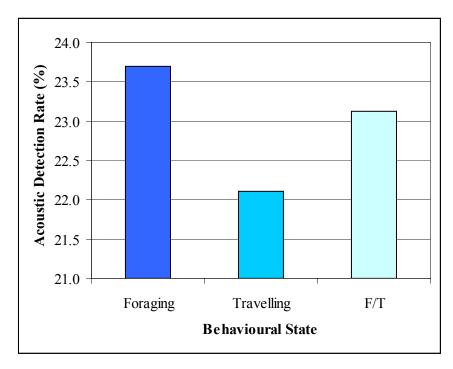
Approximately equal numbers of travelling and foraging/travelling dolphins were visually recorded, accounting for 22.1% (n = 190) and 21.6% (n = 186) of behavioural observations respectively. Of the dolphins in a travelling behavioural state, 22.1% (n = 42) were detected by the T-PODs and 23.1% (n = 43) of observed foraging/travelling dolphins were acoustically detected (**Figure 3.20**).



**Figure 3.19** Number of dolphins detected visually and the number of those detected acoustically in relation to the observed behavioural state of the dolphins.

Detection rates were broadly similar between the behavioural categories. An angular transformation was applied to the detection rate percentage values for

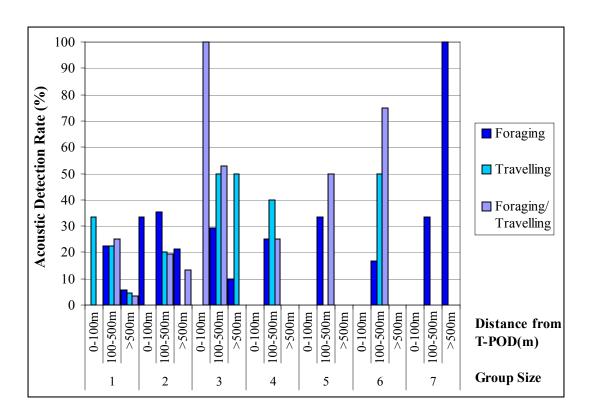
statistical analysis. The results of a G-test indicated that there was no significant variation between the acoustic detection rates for foraging, travelling, and foraging/travelling dolphins (G = 0.021, df = 2, p = 0.989) (**Appendix G**).



**Figure 3.20** Percentage of observed dolphins groups acoustically detected on the T-PODs in relation to behavioural state.

## iv) Distance, Group Size and Behavioural State

Analyses indicated that T-POD detection rates did not vary significantly with dolphin behavioural state and were not significantly related to either dolphin distance from the T-POD or group size. However, these variables have been examined independently and, since they are not mutually exclusive, must be collectively evaluated. The number of visual detections and the corresponding acoustic detections for each combination of these variables were assessed (**Appendix 5**), and the T-POD detection rates (%) calculated (see **Figure 3.21**). Where sufficient data were obtained for all variables, detection rates were compared using the *G*-test. Angular transformations were applied to all percentage values prior to this statistical analysis.



**Figure 3.21** Percentage of visually observed dolphins acoustically detected on the T-PODs in relation to behavioural state, group size and distance from the T-POD.

Analyses revealed highly variable results and this was probably due to variable and sometimes small sample sizes. Nonetheless, results indicated significant variation in detection rates in all behavioural states observed at all distance ranges from the T-PODs in groups of 1 and 3 dolphins. Detection rates were broadly similar for foraging groups of 2 dolphins sighted in all distance categories. These results are displayed in **Table 3.7** (**Appendix G**).

No significant variation was evident in the detection rates for foraging or foraging/travelling dolphins sighted 100-500m from the T-POD, regardless of group size. However, travelling dolphins were detected at higher rates in this distance category when in groups of 3 and 6 dolphins, compared to groups of 1, 2 and 4 animals. However, visually detected groups of 5 and 7 dolphins were not acoustically detected when travelling (**Table 3.8**) (**Appendix G**).

**Table 3.7** Summary of the *G*-test results, comparing acoustic detection rates in relation to dolphin group size, behavioural state and distance from the T-POD. Detection rates for distance categories in bold are significantly higher than those for other distances. p-values in bold are significantly different at the 95% level.

<b>Group Size</b>	Behaviour	Distance	G	p-value
		0-100m		
1	Foraging	100-500m	39.050	< 0.001
		>500m		
		0-100m		
1	Travelling	100-500m	12.059	0.002
		>500m		
	Foraging/	0-100m		
1	Travelling	100-500m	42.534	< 0.001
	Travelling	>500m		
	Foraging	0-100m		0.474
2		100-500m	1.494	
		>500m		
	Travelling	0-100m	58.369	<0.001
2		100-500m		
		>500m		
		0-100m	45.484	<0.001
3	Foraging	100-500m		
		>500m		
		0-100m		<0.001
3	Travelling	100-500m	36.492	
		>500m		
3	Foraging/ Travelling	0-100m	124.808	<0.001
		100-500m		
	Travelling	>500m		

**Table 3.8** Summary of the *G*-test results, comparing acoustic detection rates in relation to dolphins observed 100-500m from the T-POD for all group sizes and behavioural states. p-values in bold are significantly different at the 95% level.

<b>Group Size</b>	Behaviour	Distance	G	p-value
All (1 to 7)	Foraging	100-500m	5.469	0.485
All (1 to 7)	Travelling	100-500m	52.968	<0.001
All (1 to 7)	Foraging/Travelling	100-500m	8.559	0.200

**Table 3.9** Summary of the *G*-test results, comparing acoustic detection rates in relation to dolphin group size, distance from the T-POD and behavioural state. Detection rates for behavioural states in bold are significantly higher than those for other behaviours; p-values in bold are significantly different at the 95% level.

Group Size	Behaviour	Distance	G	p value
	Foraging			
1	Travelling	100-500m	0.073	0.964
	Foraging/Travelling			
	Foraging			
1	Travelling	>500m	0.447	0.800
	Foraging/Travelling			
	Foraging			
2	Travelling	100-500m	2.195	0.334
	Foraging/Travelling			
	Foraging			<0.001
2	Travelling	>500m	40.323	
	Foraging/Travelling			
	Foraging	100-500m	4.466	0.107
3	Travelling			
	Foraging/Travelling			
	Foraging	>500m	62.917	<0.001
3	Travelling			
	Foraging/Travelling			
	Foraging		1.671	
4	Travelling	100-500m		0.434
	Foraging/Travelling			
	Foraging		66.261	
5	Travelling	100-500m		< 0.001
	Foraging/Travelling			
6	Foraging	100-500m	16.027	
	Travelling			< 0.001
	Foraging/Travelling			

No significant variation was found in the acoustic detection rates between foraging, travelling and foraging/travelling dolphins with a group size of 1, 2, 3 or 4 at 100-500m. However, when comparing these behavioural states in this distance category for group sizes of 5 and 6, it was found that detection rates were significantly higher for foraging/travelling dolphins. Highly variable results were

revealed for dolphins sighted over 500m from the T-PODs. No significant variation in detection rates was found between solitary dolphins observed in the three behavioural states at this distance. For groups of two dolphins, foraging animals were acoustically detected at rates significantly higher than those observed both travelling and foraging/travelling. However, when analysing detection rates for groups of three dolphins at this distance, it was found that travelling animals were detected at a significantly higher rate than both foraging and foraging/travelling dolphins (**Table 3.9**) (**Appendix G**).

# 3.3 Summary

A number of the results from this investigation have been found to be significant and the following is a summary of these findings:

- All investigated click train variables from the T-POD acoustic data varied significantly with the behavioural state of the dolphins observed.
   Specifically, foraging dolphins produced echolocation click train characteristics that varied significantly from those produced by both travelling and foraging/travelling dolphins.
- Applying these findings, diel variation in foraging echolocation behaviour was evident throughout both the day and night phases in New Quay Bay.
- Significant seasonal variation was found in the number of foraging click trains detected during the night phase throughout the year.
- Analyses indicated significant differences between the diel phases for several of the months of the year, particularly during the summer.
- When considered collectively, dolphin behavioural state, group size and distance from the T-POD all influenced acoustic detection rates, although these results were highly variable.

# 4. Discussion

### 4. Discussion

## 4.1 Interpretations and Evaluation of Results

The mechanisms involved in dolphin echolocation are highly complex and this has been well demonstrated in the current investigation. Previous studies have found that bottlenose dolphin echolocation rates vary depending on several factors, including group size, geographical location and behavioural state (e.g. Jones and Sayigh, 2002; Acevedo-Gutiérrez and Stienessen, 2004). During the study period, the bottlenose dolphins acoustically detected on the T-PODs in New Quay Bay produced echolocation click trains with click train parameters that varied significantly with observed behavioural state.

Comparison of the investigated echolocation variables of click trains produced by dolphins in the behavioural states of foraging, travelling and foraging/travelling revealed significant differences between those click trains emitted by foraging dolphins and those produced by travelling and foraging/travelling dolphins. The click trains produced by foraging dolphins were characterised by significantly lower mean inter-click intervals (ICIs) than those of both travelling and foraging/travelling dolphins. In addition, these click trains were also significantly shorter in duration and contained a significantly higher number of clicks than those emitted by travelling and travelling/foraging dolphins.

Similarities were evident in all of the echolocation variables studied for the click trains produced by dolphins in the travelling and foraging/travelling behavioural states. These results would suggest that the echolocation behaviour of dolphins in the foraging/travelling behavioural state, which represents travelling behaviour with opportunistic scanning and searching for prey (cf. Viddi and Lescrauwaet, 2005), is more comparable acoustically to the behavioural state of 'travelling' than to that of 'foraging' in this study area.

Generally, the results of this study concur with those of Reyes Zamudio (2005), who found that minimum and maximum ICIs were significantly lower in click trains produced by foraging bottlenose dolphins than by those observed travelling. Similarly, when comparing the activity states of bottlenose dolphins acoustically detected by T-PODs in the Shannon Estuary, Ireland, Philpott *et al* (2006) reported that the most rapid clicks were recorded for foraging dolphins. Reyes Zamudio (2005) also found that the number of clicks in trains emitted by foraging dolphins were significantly higher than the number recorded in click trains from travelling dolphins. However, no differences were found in train duration between these two behaviours, as was the case in the current investigation.

Thus, it would appear that the values for such click train variables can be related to the functional significance of echolocation clicks, and similar findings have been reported with other species of odontocete. During investigations into the clicks emitted by foraging narwhals (*Monodon monoceros*), Miller *et al* (1995) deduced that rapidly reducing ICIs were likely to be associated with whales closing in on detected prey. Additionally, whilst acoustically monitoring foraging Blainville's beaked whales (*Mesoplodon densirostris*), Madsen *et al* (2005) found distinct variation in the ICIs of emitted click trains. Their results indicated that several phases of echolocation exist during foraging in this species, with regular ICIs recorded during the search for prey and a rapid reduction in ICIs when a prey target was at close range.

The higher mean ICIs in click trains and lower number of clicks emitted by travelling and foraging/travelling dolphins in this study are representative of a slower rate of click production whilst dolphins are in these behavioural states. In his investigations of the vocalisations of bottlenose dolphins in Fiordland, New Zealand, Boisseau (2005) found that significantly higher echolocation click rates were recorded during highly 'active' behaviours, such as diving and socialising, when compared to dolphins that were observed travelling. Likewise, when studying bottlenose dolphins at four study areas in the United States, Jones and

Sayigh (2002) noted that at all study sites, echolocation occurred significantly less whilst dolphins were travelling than in any other behavioural state.

It has been suggested that during travel, odontocetes emit echolocation clicks that have a spatial orientation and navigational function (Richardson *et al.*, 1995). Such clicks have been described as 'scanning' clicks, and these have a slower, less variable rate of production than those utilised during foraging activities. As an example, the echolocation clicks emitted by travelling resident killer whales (*Orcinus orca*) have been described as being more constant than those emitted during foraging activities, which Barrett-Lennard and colleagues (1996) interpreted as evidence of such scanning behaviour.

Further evidence for the role of echolocation in odontocete spatial orientation has been described by Verfuß *et al* (2005) in a study with captive harbour porpoises. The results indicated that even when performing familiar tasks, these porpoises used echolocation to lock onto places in the background whilst orientating themselves in their enclosure. Furthermore, it was suggested that ICI values depended on the degree of navigation necessary to complete the spatial orientation task. Boisseau (2005) also suggested that familiarity of habitat could influence echolocation rates, particularly in resident populations of bottlenose dolphins. Here, reduced rates of echolocation may be the result of travelling dolphins having to scan less often than 'transient' or offshore populations that are unfamiliar with their environment.

It would therefore appear that there is a link between the characteristics of emitted echolocation click trains and odontocete behavioural state. The possibility of making such distinctions with echolocating bottlenose dolphins from acoustic data collected on T-PODs has been explored in the current investigation. The significant differences between foraging dolphins and those travelling or foraging/travelling for all investigated echolocation variables meant that it was

possible to quantify the characteristics of click trains emitted by dolphins in these behavioural states.

As discussed, evidence suggests that wild bottlenose dolphins engage in activities such as feeding, travelling, socialising and resting both diurnally and nocturnally (Shane *et al.*, 1986). However, the extent to which these activities occur is dependant on many variables, including habitat, prey availability, time of day and season (Bearzi *et al.*, 1999; Wells and Scott, 2002). Determining how these animals use certain habitats within the diel cycle and throughout the year can provide important insights necessary for conservation and management of populations.

When analysing acoustic data collected over the year, this study found significant variation in the number of foraging click trains detected by the T-PODs throughout the phases of day and night. In the day phase, a peak in the number of detected foraging click trains was evident during the first two hours after the hour of sunrise (744 and 799 trains, respectively). During these hours, the number of foraging click trains was more than double the amount detected during each hour from the 6<sup>th</sup> hour after sunrise onwards. Throughout the night phase, there was also significant variation in the number of these click trains detected. Here, two peaks were apparent, the initial one during the first hour after sunset (445 trains) and the subsequent one during the 5<sup>th</sup> hour (412 trains).

Examining the pattern of detected foraging click trains in each of the diel phases, it would appear that the level of variation in the day phase was more pronounced than during the night phase. The day phase was characterised by a high level of foraging activity in the hour prior to and during the hours after sunrise, followed by a rapid decline in the number of foraging click trains detected throughout the remainder of the day. By contrast, foraging click trains were detected more steadily during each hour after sunset, with a slight decrease in hours 3 and 4 after sunset and a further decline in numbers nearing the end of the night phase.

However, comparisons revealed no significant variation between the number of foraging click trains detected in the day and night phases.

Diurnal variation in the activity patterns of wild bottlenose dolphins has been documented in several inshore populations, and behavioural budgets of this dolphin species appear to vary greatly with geographical location (Shane *et al*, 1986). For instance, Bräger (1993) noted that feeding activities of dolphins observed off the Texan coast appeared to increase in the morning hours and around dusk. Yet in Croatian waters, Bearzi *et al* (1999) found no obvious trends in the diurnal behaviour of the bottlenose dolphins studied. The results of the current study also suggested strong diurnal patterns in feeding activity in New Quay Bay, where peaks in detected foraging click trains were evident in the hours around sunrise and those prior to and during sunset.

The nocturnal activity patterns of bottlenose dolphins are less well documented and most available literature is based on the observations of captive animals (e.g. McBride and Hebb, 1948). Whilst noteworthy, it is not usually feasible to compare the behaviour of dolphins kept in a contained environment with that of free-ranging animals. Shane *et al* (1986) noted that direct observations of the night-time activities of bottlenose dolphins are much needed, as the majority of evidence has been based on auditory cues of dolphin presence and satellite-monitored movement patterns. Acoustic monitoring provides a method of studying dolphins at night, and when analysing T-POD data for bottlenose dolphins in New Quay Bay in 2004, Lamb found a significant increase in the number of echolocation clicks at midnight and suggested that this could be evidence of increased foraging or navigational activity at night.

As stated previously, day length and therefore hours of daylight and darkness are highly variable in Britain through the seasons of the year. Consequently, the patterns of suspected foraging behaviour seen in the two diel phases will reflect the fact that the number of hours after sunrise and sunset are not constant throughout the year. Further analysis was undertaken, and when examining the number of foraging click trains detected during each month, several seasonal patterns in dolphin foraging activity were revealed.

The highest number of foraging click trains, a total of 3,230, were detected in October and the lowest number during March (59 trains). However, when these data were corrected to account for the total number of click trains detected in each month, it was found that, overall, there was no significant seasonal variation in the proportions of foraging click trains detected. Therefore, assuming a decrease in total detected click trains in New Quay Bay was indicative of a decrease in bottlenose dolphin presence, these results would suggest that whilst dolphins are frequenting this habitat less often in the winter months (December to February) and early spring (March and April), the level of foraging activity remains fairly regular throughout the year.

The year-round presence of dolphins in New Quay Bay is well documented and peak numbers are often observed in the summer months, particularly during August (Evans, 1995; Baines *et al.*, 2000; Gregory and Rowden, 2001). In addition, it has been suggested that the preference which bottlenose dolphins have for this site appears to be associated with calf rearing (Bristow and Rees, 2001) and prey availability (Evans *et al.*, 2000). Hastie and colleagues (2004) reported similar findings in the inner Moray Firth, concluding that bottlenose dolphin distribution and habitat preference was related to foraging behaviour. The results of the current study suggest that seasonal and diel fluctuations in habitat use of the Bay by bottlenose dolphins are strongly linked to foraging and hence, the availability and movements of prey species.

Detailed knowledge of the bottlenose dolphin diet in Cardigan Bay is limited, as is information about the distribution and seasonal variation of potential prey species. However, of the species these dolphins are thought to regularly feed on, peak numbers of sea bass (*Dicentrarchus labrax*), sand eel (Family

Ammodytidae), grey mullet (Chelon labrosus), sprat (Sprattus sprattus) and mackerel (Scomber scombrus) are known to occur during the summer months in this area, and herring (Clupea harengus) are known to spawn in southern Cardigan Bay between October and November (Evans et al, 2000). Such patterns in prey abundance appear to correlate with the seasonal peaks in the number of foraging click trains found in this study.

Therefore, it is possible that the intensity of bottlenose dolphin habitat use in Cardigan Bay is associated with prey abundance and availability. Furthermore, the seasonal occurrence and movements of certain fish species, such as bass, mackerel and herring, may influence the movements of bottlenose dolphins both around the Bay and into habitats further offshore (Evans *et al.*, 2000). Thus, in addition to monthly and seasonal changes in the intensity of dolphin foraging activity, it would also be expected that any seasonal diel patterns in foraging would be influenced by the diel behaviour of favoured prey species.

Whilst no significant variation was found in the proportions of foraging click trains detected between the months of the year during the day phase, night-time foraging activity showed significant variation throughout the year. The proportion of nocturnally detected foraging click trains exhibited an increase in late autumn, and peaked in December. In the summer months, the proportion of foraging click trains detected during the night markedly declined. It should be noted that some variation was evident in the proportion of foraging click trains detected diurnally, with peak activity in the summer months and early autumn, and a decrease in the late autumn and winter months.

The results indicated highly significant variation in the amount of foraging activity detected between the diel phases during several of the months. This difference was most pronounced in the summer months and during September, where proportions of foraging click trains detected during the day were approximately three times that detected during the night. Comparatively high

levels of diurnal foraging were also evident in January, March and April. However, during the rest of the year, approximately equal quantities of foraging click trains were detected between the two diel phases, with the exception of December, where night-time foraging activity dominated the diel cycle.

As stated, the diurnal and nocturnal activities of bottlenose dolphins appear to show marked variability with geographical locality. However, when studying the diel activities of the bottlenose dolphin prey species in Sarasota Bay, Florida, Barros and Wells (1998) suggested that this population of dolphins was probably feeding both diurnally and nocturnally. Similar inferences have been made for other odontocete species, for instance, the diving behaviour of tagged killer whales showed significant yearly variation between the day and night, with less deep dives and a slower swimming speed apparent at night (Baird *et al*, 2005).

Such diel patterns in foraging activities may be influenced by the vertical migration of prey species. Both herring and sprat are known to aggregate around the seabed during the day and disperse throughout the water column when light levels decrease at dusk in European waters (Nilsson *et al.*, 2003), and a similar diurnal rhythm in depth occurrence has also been found in sea bass, with increased vertical swimming apparent during daylight (Bégout Anras *et al.*, 1997). Although the depth distributions of these species have not been investigated in the study area, such patterns could be influencing changes in foraging activity of bottlenose dolphins throughout the diel cycle, both daily and on a seasonal basis.

Additionally, it should be noted that it is likely that such seasonal and diel variation in foraging activities and habitat selection will not only be associated with prey availability and distribution but also with underlying environmental variables such as water temperature and tidal cycle, and with physiological factors such as variation in dolphin energy requirements. Variables such as these should

also be considered when attempting to analyse patterns of foraging and dolphin presence.

Although a number of observations have been made in this study with regards to the diel and seasonal trends that appear to exist in bottlenose dolphin use of New Quay Bay as a habitat favoured for foraging activities, the limitations of this part of the investigation should be noted. Firstly the categorisation of behavioural state in the field should be considered. Defining the behaviour of wild cetaceans is inherently difficult, due to the fact that in most cases, such interpretations must be made from the observation of brief surfacing events. Furthermore, bias is introduced when judging the behaviour of a group of dolphins, as it is often assumed that all animals are in a similar behavioural state.

The four behavioural states considered in this investigation, that is foraging, travelling, foraging/travelling and resting were adapted from definitions cited by Viddi and Lescrauwaet (2005). These definitions provided a good basis for categorising the behaviour of bottlenose dolphins in New Quay Bay during the study period. Dolphins in the study area are rarely seen resting, and foraging is the most commonly observed behaviour for both individuals and groups of dolphins (Hanna Nuuttila, *pers.comm.*).

It was decided that the behavioural state of socialising, (usually described as undirected surface activity and obvious physical contact between dolphins (Jacobs *et al.*, 1993; Bearzi *et al.*, 1999; Viddi and Lescrauwaet, 2005)), which is often included as a behavioural category in similar bottlenose dolphin studies, would not be included in this study due to difficulties involved in judging when animals were engaged in this activity. In this study, it is likely that this behaviour was included in the category of 'quick' behavioural events, which although observed regularly, was not included in the acoustic analysis for practical reasons.

A further consideration that should be made is the values applied for mean ICI, train duration and number of clicks when categorising click trains as foraging or non-foraging. Whilst very significant differences were found between click trains emitted by foraging dolphins and those observed travelling or foraging/travelling for all echolocation variables, there was also some overlap. For instance, click trains produced by dolphins in the behavioural state of foraging may have similar characteristics to those produced by dolphins engaged in foraging/travelling activities in some instances. Although including values for all three click train variables reduces this type of error, it should be noted that suspected foraging click trains may not necessarily have been produced by dolphins in this behavioural state.

It should also be noted that the classification of foraging click trains was based on the matching of acoustic data with visual observations of dolphins during the day and in favourable conditions. It is possible that the characteristics of click trains detected in such conditions may not reflect those of click trains produced by dolphins in other circumstances, such as during the night or in turbulent sea states. As a result, examining variation in the number of click trains detected may not be representative of changes in the intensity of habitat use, but could potentially represent changes in echolocation rates and therefore dolphin behaviour.

Carlström (2005) has reported such diel variation in the echolocation rates of harbour porpoises in the waters of the Isle of Mull, Scotland. The results of that study revealed that at night, both echolocation encounter rate and minimum ICIs were higher than during the day. Several explanations were given as to the reasons for these differences, including an increase in echolocation rates at night due to a reduction in vision, and the possibility that porpoises were using echolocation more at night for navigational purposes, hence an increase in minimum ICI. It is not possible to conclude whether this is the case with the dolphins in my study, as such differences in sound production and behaviour between the day and night were not documented.

There are several limitations that need to be considered when monitoring cetaceans acoustically and the same applies when using T-PODs. Primarily, the use of T-PODs relies on dolphins echolocating. In the current study, it had to be assumed that the dolphin visually observed in closest proximity to the T-POD emitted the click train detected by the T-POD at that time. This is an assumption made in other T-POD studies where visual observations were incorporated (e.g. Ingram *et al.*, 2004; Reyes Zamudio, 2005), as the distance at which echolocation clicks will be detected is dependent on source level, directionality, and frequency of the sound (Richardson *et al.*, 1995). Thus, transmission loss will occur with increasing distance, depending on the initial strength of the echolocation signal amongst other factors.

Furthermore, whilst the height and location of the observation point in the study provided a good view of the Bay, it was not possible to observe dolphins that may have been present at greater distances on the far side of the T-POD units (see **Figure 2.7**). It was therefore necessary to assume that dolphins sighted by the observer produced the click trains detected on the T-PODs, which could have led to some misclassifications when matching visual and acoustic data.

In addition, several variables are thought to influence the acoustic detectability of dolphins, including acoustic sensitivity of the T-POD unit, ambient noise levels, dolphin acoustic behaviour and environmental factors affecting the propagation of sound, such as water depth, mixing, temperature and salinity. Patterns in the number of click trains detected by T-PODs, such as those found in this study are likely to be influenced by such parameters, and should be considered when comparing findings with those in other investigations.

A secondary aim of this study was to ascertain whether particular variables had any influence on the acoustic detectability of bottlenose dolphins by T-PODs. When examining the effects of directionality it was found that there was no significant variation in T-POD detection rates for dolphins observed with the

cross section of the head at the bearings of 0°, 45° and 90°. However, owing to small sample sizes, it was not possible to thoroughly investigate all bearings and, overall, the results of this part of the study were considered to be inconclusive.

The directional properties of bottlenose dolphin echolocation signals have been studied in detail in captive animals (e.g. Au *et al.*, 1986), but to the author's knowledge, this was the first attempt to explore the confounding influences of dolphin directionality on acoustic detection rates in the field. In terms of the methodology applied in this part of the study, the method of data collection was probably the most suitable for the setting in the study area. The high vantage point overlooking the position of T-POD gave a good view of the area around the unit and of any dolphins present. However, the accuracy of the data collected, when determining the directionality of dolphins by assessing the relative bearing from the cross section of the animal's head in relation to the T-POD buoy, remains uncertain.

It was found during the pilot study that it would not be possible to determine the directionality of dolphins engaged in foraging activities, as the bearing of the dolphin's head when surfacing was unlikely to correspond with it's direction when submerged and hunting for prey. As a result, data collection was limited to the observation of travelling dolphins. However, whilst dolphins in this behavioural state are likely to surface more consistently than foraging dolphins, T-POD detection probabilities for travelling bottlenose dolphins have been found to be considerably lower than for dolphins engaged in feeding activities (Reyes Zamudio, 2005). As mentioned, it would appear that travelling dolphins have a lower echolocation rate due to the 'scanning' or navigational function of echolocation when in this behavioural state.

Furthermore, it was necessary to correct the directionality data to allow for discrepancies between the position of the reference buoys and the T-POD. Although such corrections are essential to lessen the error created by the

movement of the reference buoys, it is likely that the precision of the data for the bearing of the dolphin's head may have been compromised since such corrections cannot be totally accurate.

Whilst this directionality investigation was somewhat limited, it did provide a valuable insight into the suitability of such a methodology in the field. It was concluded that, although this is an area of research that is lacking in the field of acoustic monitoring, different techniques would be necessary to achieve a better understanding of the influences of directionality on T-POD detection rates. For instance, similar investigations would be better suited to study areas with clearer waters, where an assessment of the submerged dolphin could be made. Indeed, the use of underwater video cameras would be ideal for this type of investigation, to enable the precise determination of the bearing of the dolphin's head relative to the T-POD unit.

In order to broadly determine the possible effects of distance on T-POD detection rates, the distance that dolphins were sighted from the T-POD buoy was noted during the directionality measurements. However, no significant differences were found between acoustic detection rates for dolphins sighted either 0-100m away from the T-POD or 100-500m away, regardless of the bearing of the dolphin. When analysing the distances of dolphin sightings from the T-PODs for all sightings data during the study, it was found that the majority of dolphins were observed in the 100-500m distance category. Thus, when T-POD detection rates were analysed, it was found that the majority of dolphins acoustically detected were sighted within the 100-500m range of the T-POD. Dolphins sighted over 500m from the T-POD had the lowest detection rates. Unexpectedly low detection rates were revealed for dolphins sighted 0-100m from the T-POD.

During an investigation using a theodolite to track dolphins, Reyes Zamudio (2005) reported very similar findings in this study area. She found that acoustic detection probability decreased with increasing dolphin distance from the T-POD,

but also that a low rate of detection was evident for dolphins sighted in the 0-100m range. It was suggested that low detection rates at such close ranges were probably a result of a small sample size, which may also be the case in the current investigation, where only 2% of the total dolphin sightings were recorded within this distance of the T-POD. When tracking harbour porpoises, Tougaard *et al*, (2006) also found that animals observed within 100m of the T-POD were not always detected and suggested that this could be due to the highly directional nature of the porpoise echolocation beam.

When comparing distance estimates of cetaceans at sea, Gordon (2001) suggested that estimations by eye are considerably less accurate than measurements with reticulated binoculars or video cameras. Thus, the distance estimates for dolphins in relation to the T-POD units in this study may not be considered to be as accurate as distance readings obtained from, for instance, digital theodolite tracking of dolphins. Nevertheless, calculating distances from theodolite data can be erroneous, as several factors must be corrected for, including swell and tide height, the elevation of the observation platform, refraction and target distance. In addition, distance estimates by eye during land-based studies are considered to be less biased than those taken at sea (Kinzey and Gerrodette, 2003). However, the broad distance categories used in this study will have influenced the interpretations of detection rates and this should be taken into account.

With respect to group size, although a general increase in T-POD detection rates was apparent with increasing group size, no significant linear relationship was revealed. Lower than expected detection rates were revealed for groups of 4, 5 and 7 dolphins. These results support those of Jones and Sayigh (2002) who although noting a overall higher rate of echolocation production in bottlenose dolphins with increased group size, found that echolocation rates per individual dolphin decreased with increasing group size. It was suggested that this trend might be evidence for 'passive' echolocation, where members of a group share information, thus reducing the need for all individuals to echolocate.

Benoit-Bird and Au (2004) also found that the echolocation click rates of foraging Hawaiian spinner dolphins (*Stenella longirostris*) did not vary significantly with group size. It was suggested that clicks may not be emitted by all individuals of a group and could be used as some form of signal for group movements during feeding activities. It is possible that the reduced detection rates for group sizes of 4, 5 and 7 found in the current study may support the theory of passive echolocation, since the expected increase in detection rates with increasing group size was not observed. However, variable sample sizes for each group size will also have an influence on the resulting detection rate, and further work is needed in this area.

A recent suggestion for further improvements in static acoustic monitoring was the development of a method for the determination of group size from T-POD data (SAM Workshop, 2006). The possibility that dolphin echolocation rates or the number of clicks emitted by dolphins does not increase with increasing group size of animals could have implications for such work. Thus, research in the area of estimating group size from T-POD data may have to consider passive echolocation as a potential issue.

As discussed, increased rates of echolocation have been found in previous studies with foraging dolphins, when compared to dolphins engaged in other activities, such as travelling (e.g. Jones and Sayigh, 2002; Boisseau, 2005) For this reason, it was expected that the behavioural state of dolphins in the bay would influence acoustic detection rates. However, T-POD detection rates showed little variation with the observed behavioural state of dolphins in the current study. There are several possible explanations for these findings, including the potential for highly variable echolocation rates with behavioural state. However, further analysis indicated that numerous factors influence T-POD detection rates of the dolphins in New Quay Bay.

The collective evaluation of data obtained over the study period for the distance of dolphins from the T-POD, their observed group size and behavioural state, indicated that a combination of these variables affected T-POD detection rates. Highly variable results were revealed in acoustic detection rates during analysis. Generally, dolphins observed in all behavioural states were acoustically detected at a higher rate 100-500m from the T-POD than dolphins observed at other distances, regardless of group size. The exception to this trend was for foraging/travelling dolphin groups of 5 and 6 individuals, which were detected at a significantly higher rate than groups of the same size observed travelling or foraging in the 100-500m range.

In addition, it was revealed that the dolphin behavioural state and observed group size were especially important for acoustic detection rates at distances over 500m from the T-POD, although, again, the results were highly variable. Overall, increasing group size appeared to have the greatest influence on the acoustic detection of travelling dolphins, particularly when sighted within 100-500m of the T-POD where a trend for higher detection rates was revealed. It should be noted that these observations are of general trends and that no uniform patterns were revealed during analysis, possibly as a result of variable sample sizes for each category.

These findings may emphasise the flexible nature of bottlenose dolphin echolocation and behaviour, or perhaps the variability in the detection rates of T-PODs. The issue of T-POD sensitivity has been explored, particularly in the context of comparability between units and studies (e.g. Tregenza, 2006). The calibration of the T-PODs in this study means that there should have been minimal effects of variation in sensitivity between two units T-PODs. Nevertheless, the sensitivity of T-PODs can be affected in the field by other factors, particularly as a result of high levels of ambient noise (Tregenza, 2006), and this in turn could affect detection rates.

Despite the limitations discussed, it is evident that T-PODs can be used as a valuable tool in the monitoring of bottlenose dolphin habitat use. The current study benefited greatly from the fact that it was possible to visually observe dolphins from land whilst acoustically monitoring these animals, with relatively little effort. Thus, this combination of monitoring techniques did not disturb or influence the behavioural state of the dolphins in any way. Additionally, T-PODs also have an advantage over other acoustic monitoring techniques in that they can be left out at sea to collect data continuously, thereby reducing the labour and costs involved in monitoring.

## 4.2 Applications of the Study

Systematic studies that aim to determine the importance of particular habitats for protected or endangered species are essential for the conservation and management of such populations. As an SAC, Cardigan Bay is recognised as a high-quality conservation site and the bottlenose dolphins are afforded a level of protection from habitat deterioration (JNCC, 2006). Although long-term data indicate a steady increase within the SAC (Evans *et al.*, 2003; Sea Watch Foundation, *unpublished data*), marked changes in site usage and in the number of bottlenose dolphins observed in New Quay Bay has been noted in a long-term study, with results indicating prominent declines in group size and the number of calves observed between the years 2000 and 2002 (Bristow, 2004).

Although further research is needed in the area, it has been suggested that anthropogenic impacts, including increased levels of boat activity and the licensed discharge of shell waste, could negatively influence the frequency with which dolphins use New Quay Bay (Bristow, 2004). The present study has explored a methodology for the continuous monitoring of bottlenose dolphin foraging activities, and therefore has the potential to be used to monitor any long-term changes in dolphin behaviour. Consequently, it is possible that the acoustic monitoring of the echolocation behaviour of these dolphins could provide a means of monitoring fine-scale temporal changes in habitat use.

However, due to the variability in bottlenose dolphin behaviour, habitat use and echolocation behaviour with geographical location, similar field studies should incorporate a period of visual observations, to match the acoustic characteristics of click trains produced by dolphins in various behavioural states in the particular habitat of interest. In addition, considerations should be made for both the influences of dolphin behaviour, directionality, group size and distance, and environmental factors affecting T-POD detection rates, which are also likely to be habitat-specific.

Lastly, the interpretation of any changes in dolphin habitat use, through the use of T-PODs and the studying of echolocation behaviour, could contribute towards ensuring that management strategies and plans currently in place are achieving the targets set, and that any limitations of such conservation efforts are recognised.

### 4.3 Suggestions for Further Research

The findings of the present study have provided a foundation for future research in the area of T-POD use to study the echolocation behaviour of dolphins. The limitations of this study have been explored throughout and there is a need for further work in a number of the areas discussed. Suggestions for such research are outlined below:

- The data collected on each of the T-PODs in the bay could be analysed separately to examine any fine-scale variation in foraging activities within the study area.
- A similar methodology should be applied to study bottlenose dolphins observed in the vicinity of the other T-POD units in the Cardigan Bay SAC, if possible. This information could lead to a better understanding of bottlenose habitat use over a greater spatial and temporal scale.

- Furthermore, it would be interesting to examine click trains from dolphins observed in the various behavioural states from other sites in the UK and further afield, to determine whether click train characteristics exhibit variation with geographical location. This is an area of research that would be interesting to explore with bottlenose dolphins found in offshore habitats in particular.
- Other vocalisations from this dolphin population could be examined simultaneously, using a hydrophone, in relation to dolphin behavioural state, to determine the functional significance of such sounds and how they may relate to echolocation and communication.
- In addition to the effects of the diel cycle, the scope of this project should be increased to include the influences of other factors on patterns of dolphin foraging. For instance, other environmental variables such as sea surface temperature, primary productivity levels, and the tidal and lunar cycle should be examined in this context.
- Further research is needed to gain information about the diet and prey
  preferences of the bottlenose dolphins found in Cardigan Bay. This
  knowledge would allow for a greater understanding of how the
  distribution and behaviour of prey species influences that of the dolphins
  in the area.
- Recordings of underwater background noise in the SAC should be made for a number of reasons. Firstly, to gain a better understanding of the acoustic environment in areas frequented by dolphins (and porpoises), and the potential threat of increased underwater noise. Secondly, to quantify levels of ambient noise in these areas and determine how this may affect T-POD sensitivity. Lastly, to ascertain the possible masking effects of such noise on the echolocation and communication signals of cetaceans in the Bay.

- Although some results of the current study were inconclusive, it was
  determined that the concept of measuring the effects of directionality on
  acoustic detection rates is possible, and further work is needed in this area,
  as discussed
- More precise information on detection ranges could be obtained by watching dolphins from a greater elevation and using a theodolite for tracking of animals.
- Further investigation is needed on the socialising behaviours of dolphins in this study area, and the acoustic characteristics of click trains emitted whilst dolphin are in this behavioural state. Such work would further improve precision in the determination of dolphin behaviour from T-POD data.
- The capabilities of T-PODs for the acoustic monitoring of other odontocete species is now recognised and the findings of the current study could be applied to research with other echolocating species.

# 5. Conclusions

### 5. Conclusions

This study has found that bottlenose dolphins acoustically detected by two T-PODs in New Quay Bay produced echolocation click trains with click train parameters that varied significantly with observed behavioural state. Specifically, dolphins that were observed foraging produced click trains with significantly lower mean ICIs and total durations and a significantly higher number of clicks than dolphins engaged in travelling and foraging/travelling activities.

By applying these findings to T-POD data collected in the study area throughout the year, it was possible to determine diel and seasonal variation in dolphin foraging activities in New Quay Bay. The results suggested that dolphins are foraging in the study area both diurnally and nocturnally, and that peaks in feeding activity are evident at numerous points in the diel cycle. Additionally, analyses indicated significant differences in the number of foraging click trains detected between the diel phases within several of the months of the year, particularly during the summer.

These findings further exemplify the importance of New Quay Bay as a habitat for the bottlenose dolphin population of this region. It can be concluded from the results of this study that the area is important for year-round foraging for this population, and that seasonal and diel variation in dolphin presence in the bay appears to be strongly influenced by such foraging activities. The limitations involved in the methodology and the use of T-PODs have been identified, and should be taken into account during subsequent interpretation of these results.

It has been found that T-POD detection rates appear to be influenced by a number of factors explored in this investigation, including directionality of the dolphin echolocation beam, the behavioural state and number of dolphins present, and the distance of dolphins from the T-POD. Further work is required to determine the extent to which each of these variables influences acoustic detection rates, and

how environmental variables may also contribute to the detection of echolocating dolphins.

The analysis of acoustic behaviour, in addition to other techniques, can provide a means of monitoring and gaining a better understanding of how cetaceans utilise a particular habitat. Both spatial and temporal patterns in the use of echolocation can be explored in this way to provide valuable information for the conservation, protection and management of this species.

# 6. Acknowledgements

### 6. Acknowledgements

I would like to thank the following people for providing their support, encouragement and expertise throughout the course of this project.

Many thanks to John Goold for his supervision and dedicated support throughout this project and for helping me to get to grips with the strange world of acoustics. I would also like to thank Hanna Nuuttila for all her fantastic help during the summer, especially with our many attempts to get the hydrophone working, and later with plenty of good advice and encouragement with my drafts. Also, many thanks to Peter Evans for the helpful advice he has provided and for spending so much time looking through my work.

I would especially like to thank my great friends Eleanor Stone and Tom Felce, without whom this project would have not been possible. Thanks for all those hours on 'the wall' and for a fantastic amount of advice, support and enthusiasm. A huge thank you to all the Sea Watch Foundation volunteers and staff for all their help and for making the summer so enjoyable. Thanks to my fellow New Quay MSc buddies Natalie and Edita.

Many thanks to Winston and Karl for the deployment of the T-PODs in the bay. I would also like to thank Nick Tregenza and Ruth Leeney for their POD advice.

I am also grateful to the Whale and Dolphin Conservation Society (WDCS) for providing financial support during the completion of this project.

Special thanks to all of my classmates for a brilliant year, in particular Eleanought, Simon, Kari, Meghan, Joana and Maja.

Last but not least, massive thanks to my mum, dad and sisters for their endless support and love. Also, many thanks to the Livermore family and to my boyfriend Richard for always being there and putting up with me being a poor, stressed out student.

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#### **Internet Resources**

ACS online (2006) URL: http://www.acsonline.org/factpack/btlnose.htm

JNCC (2006) URL: http://www.jncc.gov.uk/protectedsites/sacselection/SAC

Tide Tables (2006) URL: http://www.tourism.ceredigion.gov.uk

T-POD help pages (2001) URL: http://www.chelonia.co.uk

U.S. Naval Observatory (2006) URL: http://aa.usno.navy.mil/data

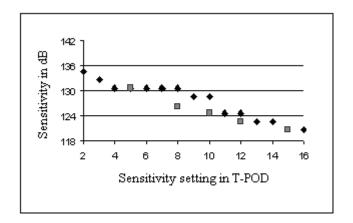
# 8. Appendices

**Appendix A:** T-POD Calibration

Calibrations were performed in the facilities of the German Oceanographic Museum, Stralsund. The applicable settings are described below:

T-POD ID	Sensitivity / Minimum Intensity	Absolute sensitivity
412	6	131 dB
420	6	129 dB

Settings for the reef (412) and fish factory (420) T-PODs deployed for field calibrations, based on the calibrations in the experimental set-up. The sensitivity and the minimum intensity are settings in the T-POD software. The absolute sensitivity of the T-POD hydrophone is given in dB re 1  $\mu$ Pa.

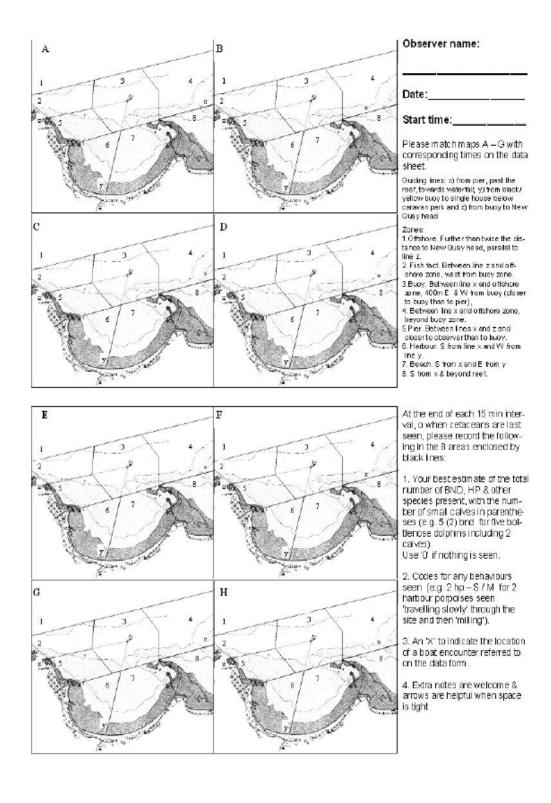


The sensitivity (in dB re 1  $\mu$ Pa) of a V4 T-POD to harbour porpoise clicks (black diamonds) and bottlenose dolphin clicks (grey boxes) at different sensitivity/minimum intensity settings. The sensitivity is given as the absolute sensitivity to harbour porpoise clicks and the relative sensitivity to bottlenose dolphin clicks. The figure shows that the differences in sensitivity between the sensitivity settings of the V4 T-POD are similar (within 4,5 dB) for clicks from the same two species.

**Appendix B:** Effort Form used by the Sea Watch Foundation (Ceredigion County Council)

Z	Name:				Location:	٠.			Da	Date:	
	IS MIN INT.		MEATHER		CETACEANS		Obsess/5	BOAT ENCOUNTER	TER atantol 75 mit		NOTES
NAP	StartTime	General	Who	Sea State	Species See 1	Type	Range / Distance	Total to. of boats with a 300m	Boat Fe Laubur	Cetacean Selation	
ď											
0											
٥											
ш											
_											
o											
Ŧ											
				The Nun	The Number of Different Boats Seen in 2 Hours	rent Boa	its Seen i	n 2 Hours	000		15(4)
	BOATTYPE	rPE		900	TOTAL			BOAT TYPE		901	TOTAL
MB	Recreations or the rs, dis	Recreational motor boat cabin	abit				VPE	Visitor Passenger Boat	Boat		
88/88	10000	Racing the spee docator RIB/ Water-skier	RIB/				o	Caloe			
SAIL	Any boat a	Any boat in densal heliding whick riter	641				n Jet	Jetski, personal water craft	ercraft		
O.	Comme	Commercial 1sting boat	Ħ				R GR	deace record boats rame)	boat : same)		

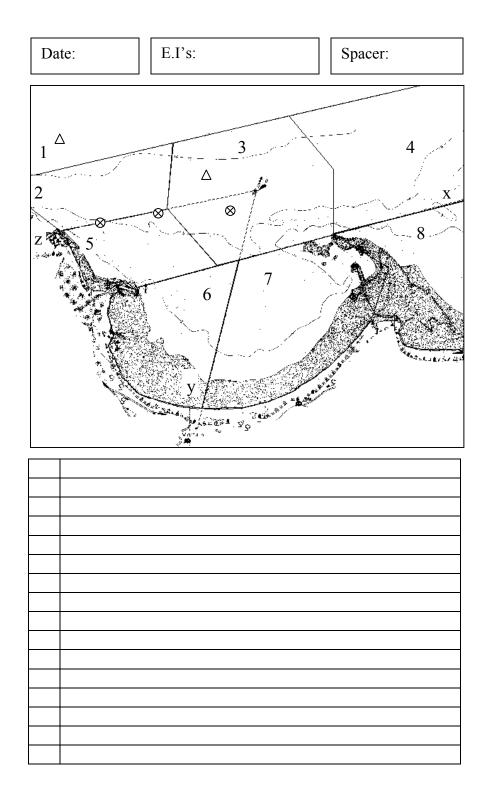
**Appendix C:** Sightings Form used by the Sea Watch Foundation (Ceredigion County Council)



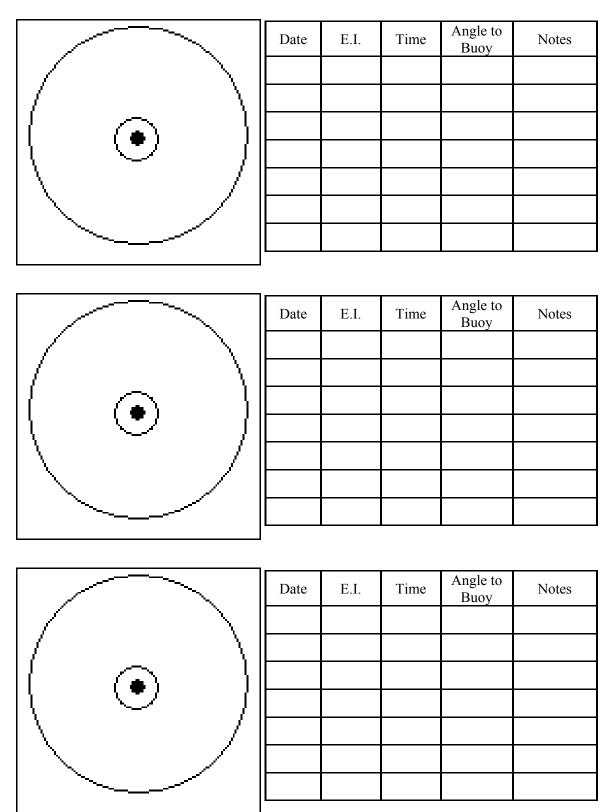
**Appendix D:** Effort Form (Form 1)

EI	TIME	TIDE	SS		В	BOAT TALL	Y	
El	TIME	TIDE	33	MOTOR	SPEED	FISHING	SAIL	CANOE

# **Appendix E:** Sightings Form (Form2)



**Appendix F**: Directionality Form (Form 3)



#### **Appendix G:** Statistical Analysis

#### **Acoustic Data**

### a) Inter-click Intervals

#### Kruskal-Wallis Test: Mean ICI versus Code

Kruskal-Wallis Test on Mean ICI

```
Code
          N Median Ave Rank
1
        221
             40.10
                       145.0 -9.32
         81
              96.76
                        264.3
                               7.02
                        237.2
3
         75
              72.07
                               4.28
Overall 377
                        189.0
H = 89.31 DF = 2 P = 0.000
H = 89.31 DF = 2 P = 0.000 (adjusted for ties)
```

### Mann-Whitney Test and CI: Mean ICI F, Mean ICI T

```
N Median
Mean ICI F 221 40.10
Mean ICI T 81 96.76

Point estimate for ETA1-ETA2 is -58.10
95.0 Percent CI for ETA1-ETA2 is (-73.93,-43.85)
W = 27913.0
Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at 0.0000
The test is significant at 0.0000 (adjusted for ties)
```

### Mann-Whitney Test and CI: Mean ICI F, Mean ICI FT

```
N Median

Mean ICI F 221 40.10

Mean ICI FT 75 72.07

Point estimate for ETA1-ETA2 is -38.01

95.0 Percent CI for ETA1-ETA2 is (-51.12,-25.55)

W = 28673.0

Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at 0.0000

The test is significant at 0.0000 (adjusted for ties)
```

### Mann-Whitney Test and CI: Mean ICI FT, Mean ICI T

```
N Median
Mean ICI FT 75 72.07
Mean ICI T 81 96.76

Point estimate for ETA1-ETA2 is -17.27
95.0 Percent CI for ETA1-ETA2 is (-39.50,0.49)
W = 5353.5
Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at 0.0584
The test is significant at 0.0584 (adjusted for ties)
```

#### b) Total Duration of Click Train

#### Kruskal-Wallis Test: Tr Dur versus Code

Kruskal-Wallis Test on Tr Dur

```
Code N Median Ave Rank Z
1 221 52.28 158.1 -6.56
2 81 114.43 243.2 5.05
3 75 86.32 221.6 2.89
Overall 377 189.0

H = 44.53 DF = 2 P = 0.000
H = 44.53 DF = 2 P = 0.000 (adjusted for ties)
```

### Mann-Whitney Test and CI: Foraging, Travelling

```
N Median
Foraging 221 52.28
Travelling 81 114.43

Point estimate for ETA1-ETA2 is -52.12
95.0 Percent CI for ETA1-ETA2 is (-71.54,-34.27)
W = 29525.0
Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at 0.0000
The test is significant at 0.0000 (adjusted for ties)
```

### Mann-Whitney Test and CI: Foraging, F/T

```
N Median
Foraging 221 52.28
F/T 75 86.32

Point estimate for ETA1-ETA2 is -32.59
95.0 Percent CI for ETA1-ETA2 is (-48.07,-19.88)
W = 29941.5
Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at 0.0000
The test is significant at 0.0000 (adjusted for ties)
```

#### Mann-Whitney Test and CI: F/T, Travelling

```
N Median

F/T 75 86.32

Travelling 81 114.43

Point estimate for ETA1-ETA2 is -17.90

95.0 Percent CI for ETA1-ETA2 is (-43.13,4.36)

W = 5454.0

Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at 0.1246
```

### c) Number of Clicks

#### Kruskal-Wallis Test: No Clx versus Code

Kruskal-Wallis Test on No Clx

```
Code N Median Ave Rank Z
1 221 14.00 204.5 3.29
2 81 11.00 165.8 -2.17
3 75 12.00 168.4 -1.83
Overall 377 189.0

H = 10.84 DF = 2 P = 0.004
H = 10.89 DF = 2 P = 0.004 (adjusted for ties)
```

### Mann-Whitney Test and CI: Foraging, Travelling

```
N Median
Foraging 221 14.000
Travelling 81 11.000

Point estimate for ETA1-ETA2 is 2.000
95.0 Percent CI for ETA1-ETA2 is (1.000,4.000)
W = 35327.0
Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at 0.0061
The test is significant at 0.0060 (adjusted for ties)
```

### Mann-Whitney Test and CI: Foraging, F/T

```
N Median
Foraging 221 14.000
F/T 75 12.000

Point estimate for ETA1-ETA2 is 2.000
95.0 Percent CI for ETA1-ETA2 is (0.000,4.000)
W = 34401.0
Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at 0.0135
The test is significant at 0.0133 (adjusted for ties)
```

### Mann-Whitney Test and CI: F/T, Travelling

```
N Median

F/T 75 12.000

Travelling 81 11.000

Point estimate for ETA1-ETA2 is 0.000

95.0 Percent CI for ETA1-ETA2 is (-0.999,2.000)

W = 5924.5

Test of ETA1 = ETA2 vs ETA1 not = ETA2 is significant at 0.8970

The test is significant at 0.8966 (adjusted for ties)
```

### a) Diel Variation in Echolocation Behaviour

### Test for Equal Variances: Foraging versus Hrs After Sunrise

95% Bonferroni confidence intervals for standard deviations

```
Hrs
After
Sunrise N Lower StDev Upper
1 18 175.212 242.797 387.802
2 16 97.358 137.325 227.679
```

```
F-Test (normal distribution)
Test statistic = 3.13, p-value = 0.032
```

### Two-Sample T-Test and CI: Foraging, Diel Phase

```
Two-sample T for Foraging
```

Diel				SE
Phase	N	Mean	StDev	Mean
1	18	306	243	57
2	16	256	137	34

```
Difference = mu (1) - mu (2)
Estimate for difference: 49.7292
95% CI for difference: (-90.5203, 189.9786)
T-Test of difference = 0 (vs not =): T-Value = 0.72 P-Value = 0.475 DF = 32
Both use Pooled StDev = 200.3923
```

### **G-Test (Hours After Sunrise)**

Hour	Trains	Hour*Trains	Observed	Expected	Ratio	In ratio
0	430	0	430	36.96	11.634	1055.185
1	416	416	416	184.92	2.250	337.285
2	744	1488	744	462.57	1.608	353.583
3	799	2397	799	771.41	1.036	28.077
4	592	2368	592	964.84	0.614	-289.167
5	479	2395	479	965.42	0.496	-335.714
6	475	2850	475	805.00	0.590	-250.575
7	270	1890	270	575.34	0.469	-204.268
8	277	2216	277	359.81	0.770	-72.449
9	286	2574	286	200.01	1.430	102.277
10	226	2260	226	100.07	2.259	184.123
11	134	1474	134	45.51	2.944	144.702
12	78	936	78	18.97	4.111	110.261
13	83	1079	83	7.30	11.366	201.744
14	73	1022	213	3.86	55.150	854.142

	1275	85	15
G = 4438.41	800	50	16
	85	5	17
P = 0.000000			
	27525	5502	

Mean = 5.003

### **G-Test (Hours After Sunrise)**

Hour	Trains	Hour*Trains	Observed	d Expected	Ratio	In ratio
0	351	0	351	18.257	19.226	1037.649
1	445	445	445	98.823	4.503	669.613
2	359	718	359	267.463	1.342	105.668
3	296	888	296	482.593	0.613	-144.689
4	291	1164	291	653.069	0.446	-235.232
5	412	2060	412	707.012	0.583	-222.490
6	397	2382	397	637.843	0.622	-188.240
7	360	2520	360	493.235	0.730	-113.357
8	300	2400	300	333.735	0.899	-31.969
9	233	2097	233	200.723	1.161	34.743
10	138	1380	138	108.651	1.270	32.997
11	194	2134	194	53.466	3.628	250.028
12	211	2532	211	24.118	8.749	457.640
13	67	871	67	10.042	6.672	127.159
14	40	560	40	3.883	10.302	93.293
15	1	15	1	1.401	0.714	-0.337
						G = 3744.952

4095 22166

P = 0.000

Mean=5.413

### b) Interannual Variation in Echolocation Behaviour

### **G-Test (Foraging click trains v Month)**

Month	Observed	Expected Ratios	Expected Freq	Ratio	In Ratio
Jan	68.611	1	63.359	1.083	5.464
Feb	72.443	1	63.359	1.143	9.705
Mar	63.221	1	63.359	0.998	-0.138

Apr	62.097	1	63.359	0.980	-1.249
May	65.120	1	63.359	1.028	1.785
Jun	61.547	1	63.359	0.971	-1.787
Jul	69.469	1	63.359	1.096	6.395
Aug	61.070	1	63.359	0.964	-2.247
Sep	56.727	1	63.359	0.895	-6.273
Oct	50.652	1	63.359	0.799	-11.338
Nov	61.410	1	63.359	0.969	-1.919
Dec	67.945	1	63.359	1.072	4.748
	760.31	12.00			G= 6.292

P = 0.853

## G-Test (Day phase v Month)

Month	Observed <sup>l</sup>	Expected Ratios	Expected Freq	Ratio	In Ratio
Jan	57.159	1	52.170	1.096	5.220
Feb	44.375	1	52.170	0.851	-7.181
Mar	55.427	1	52.170	1.062	3.357
Apr	54.865	1	52.170	1.052	2.764
May	47.168	1	52.170	0.904	-4.754
Jun	59.716	1	52.170	1.145	8.067
Jul	64.784	1	52.170	1.242	14.029
Aug	60.232	1	52.170	1.155	8.655
Sep	58.558	1	52.170	1.122	6.764
Oct	42.941	1	52.170	0.823	-8.360
Nov	43.533	1	52.170	0.834	-7.879
Dec	37.281	1	52.170	0.715	-12.527
	626.04	12.00			G = 16.311

# G-Test (Night phase v Month)

Month	Observed	Expected Ratios	Expected Freq	Ratio	In Ratio
Jan	32.841	1	37.830	0.868	-4.644
Feb	45.625	1	37.830	1.206	8.548
Mar	34.573	1	37.830	0.914	-3.113
Apr	35.135	1	37.830	0.929	-2.597
May	42.832	1	37.830	1.132	5.319
Jun	30.284	1	37.830	0.801	-6.738
Jul	25.216	1	37.830	0.667	-10.228
Aug	29.768	1	37.830	0.787	-7.134
Sep	31.442	1	37.830	0.831	-5.816
Oct	47.059	1	37.830	1.244	10.273
Nov	46.467	1	37.830	1.228	9.556
Dec	52.719	1	37.830	1.394	17.496
	453.96	12.00			G = 21.842

P = 0.026

## G-Test (Diel Phase v Month)

Month	Diel Phase	Observed	Expected Ratios	Expected Freq	Ratio	In Ratio
Jan	Day	57.165	1	45	1.270	13.679
	Night	32.835	1	45	0.730	-10.349
						G = 6.660
						P = 0.010
Feb	Day	44.370	1	45	0.986	-0.626
	Night	45.630	1	45	1.014	0.635
						G = 0.018
						P = 0.894

Mar	Day	55.427	1	45	1.232	11.552
	Night	34.573	1	45	0.768	-9.113
						G = 4.877
						P = 0.027
Apr	Day	54.878	1	45	1.220	10.890
	Night	35.123	1	45	0.781	-8.704
						G = 4.372
						P = 0.037
May	Day	47.179	1	45	1.048	2.231
	Night	42.821	1	45	0.952	-2.126
						G = 0.211
						P = 0.646
Jun	Day	59.736	1	45	1.327	16.922
	Night	30.264	1	45	0.673	-12.006
						G = 9.832
						P = 0.002
Jul	Day	64.747	1	45	1.439	23.557
	Night	25.253	1	45	0.561	-14.589
						G = 17.935
						P = 0.000
Aug	Day	60.199	1	45	1.338	17.517
Aug	•	29.801	1	45 45	0.662	-12.282
	Night	29.001	1	45	0.002	G = 10.472
						P = 0.001
						1 = 0.001
Sep	Day	58.565	1	45	1.301	15.430
	Night	31.435	1	45	0.699	-11.277
	3					G = 8.306
						P = 0.004
Oct	Day	42.936	1	45	0.954	-2.016
	Night	47.064	1	45	1.046	2.111
						G = 0.189
						P = 0.663

Nov	Day	43.510	1	45	0.967	-1.465
	Night	46.490	1	45	1.033	1.515
						G = 0.099
						P = 0.753
Dec	Day	37.287	1	45	0.829	-7.011
	Night	52.713	1	45	1.171	8.339
						G= 2.657
						P = 0.103

## **3.2.2.3 Directionality**

## **G-Test (Angle v Detection Rate)**

Angle	Observed	Expected Ratios	Expected Freq	Ratio	In Ratio
0	40.92	1	37.49	1.091	3.577
45	32.33	1	37.49	0.862	-4.790
90	39.23	1	37.49	1.046	1.778
	112.48	3			G = 1.129
					P = 0.569

# G-Test (Angle, Distance v Detection Rate)

Angle	Observed (Angular)	Expected Ratios	Expected Freq	Ratio	In Ratio
0	35.24	1	35.11	1.004	0.133
45	32.33	1	35.11	0.921	-2.669
90	37.76	1	35.11	1.075	2.747
	105.34	3			G = 0.422
					P = 0.810

### 3.2.2.4 T-POD Detection Rates

### a) Distance from T-POD

### Regression Analysis: detection rate versus distance

```
The regression equation is detection rate = 22.3 - 2.50 distance
```

```
        Predictor
        Coef
        SE Coef
        T
        P

        Constant
        22.33
        18.08
        1.23
        0.433

        distance
        -2.500
        8.372
        -0.30
        0.815
```

```
S = 11.8392  R-Sq = 8.2%  R-Sq(adj) = 0.0%
```

Analysis of Variance

Source	$_{ m DF}$	SS	MS	F	P
Regression	1	12.5	12.5	0.09	0.815
Residual Error	1	140.2	140.2		
Total	2	152.7			

### b) Group Size

### Regression Analysis: Detection rate versus Group size

```
The regression equation is
Detection rate = 21.1 + 1.87 Group size
```

```
        Predictor
        Coef
        SE Coef
        T
        P

        Constant
        21.129
        5.660
        3.73
        0.014

        Group size
        1.871
        1.266
        1.48
        0.199
```

```
S = 6.69665 R-Sq = 30.4% R-Sq(adj) = 16.5%
```

#### Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	98.06	98.06	2.19	0.199
Residual Error	5	224.23	44.85		
Total	6	322.29			

### c) Behavioural State

### **G-Test (Behaviour v Detection Rate)**

Behaviour	Observed	Expected Ratios	Expected Freq	Ratio	In Ratio
Foraging	29.13	1	28.63	1.017	0.503
Travelling	28.04	1	28.63	0.979	-0.586
F/T	28.73	1	28.63	1.003	0.093
	85.90	3			G = 0.021
					P =0.989

## d) Comparison of Factors Affecting Detection Rates

## G-Test (Behaviour, Group Size, Distance v Detection Rate)

Distance	Group Size	Behaviour	Observed	Expected Ratios	Expected Freq	Ratio	In Ratio
0-100	1	F	0.00	1	14.02	0.000	0.000
100-500	1	F	28.17	1	14.02	2.009	19.648
>500	1	F	13.90	1	14.02	0.991	-0.123
			42.07	3			G =39.050
							P =0.000
0-100	1	Т	35.26	1	25.2633	1.395875	11.761
100-500	1	Т	28.22	1	25.2633	1.116857	3.118
>500	1	Т	12.31	1	25.2633	0.487268	-8.850
			75.79	3			G = 12.059

0-100	1	FT	0.00	1	13.56723	0	0.000
100-500	1	FT	30.00	1	13.56723	2.21121	23.806
>500	1	FT	10.70	1	13.56723	0.78879	-2.539
			40.70	3			G = 42.534
							P = 0.000
							P = 0.000
Distance	Group	Behaviour	Observed		Expected	Ratio	In Ratio
Distance	Size	Bellavioui	Obscived	Ratios	Freq	Ratio	mitado
0-100	2	F	35.26	1	33.03	1.068	2.320
100-500	2	F	36.41	1	33.03	1.102	3.536
>500	2	F	27.42	1	33.03	0.83	-5.109
			99.1	3			G = 1.494
							P = 0.474
							P = 0.474
0-100	2	Т	0.00	1	8.855033	0	0.000
100-500	2	Т	26.57	1	8.855033	3	29.185
>500	2	Т	0.00	1	8.855033	0	0.000
			26.57	3			G = 58.369
							P =0.000
Distance	Group Size	Behaviour	Observed	Expected Ratios	Expected Freq	Ratio	In Ratio
0-100	3	F	0.00	1	17.04	0.000	0.000
100-500	3	F	32.69	1	17.04	1.918	21.292
>500	3	F	18.43	1	17.04	1.082	1.450

51.12 3

P =0.000

G = 45.484

0-100	3	Т	0.00	1	30	0	0.000
100-500	3	Т	45.00	1	30	1.5	18.246
>500	3	Т	45.00	1	30	1.5	0.000
			90.00	3			G = 36.492
							P = 0.000
0-100	3	FT	90.00	1	45.56203	1.975329	61.266
100-500	3	FT	46.69	1	45.56203	1.024671	1.138
>500	3	FT	0.00	1	45.56203	0	0.000
			136.69	3			G = 124.808
	C=====			Cymaeted	Even a stand		P = 0.000
Distance	Group Size	Behaviour	Observed	Expected Ratios	Expected Freq	Ratio	In Ratio
					•		
100-500	1	F	28.1791	1	31.70	0.889	-3.316
100-500	2	F	36.3912	1	31.70	1.148	5.024
100-500	3	F	32.7088	1	31.70	1.032	1.026
100-500	4	F	30.00	1	31.70	0.946	-1.652
100-500	5	F	35.24	1	31.70	1.112	3.737
100-500	6	F	24.12	1	31.70	0.761	-6.590
100-500	7	F	35.24	1	31.70	1.112	3.737
			221.89	7			G = 5.469
							P = 0.485
100-500	1	Т	28.2478	1	26.29	1.074	2.027
100-500	2	Т	26.5651	1	26.29	1.010	0.274
100-500	3	Т	45	1	26.29	1.712	24.183
100-500	4	Т	39.23	1	26.29	1.492	15.701
100-500	5	T	0.00	1	26.29	0.000	0.000
100-500	6	T	45.00	1	26.29	1.712	24.183
100-500	7	Т	0.00	1	26.29	0.000	0.000
			184.04	7			G = 52.968

							P = 0.000
Distance	Group Size	Behaviour	Observed	Expected Ratios	Expected Freq	Ratio	In Ratio
100-500	1	FT	30	1	33.98	0.883	-3.736
100-500	2	FT	26.1329	1	33.98	0.769	-6.861
100-500	3	FT	46.7199	1	33.98	1.375	14.877
100-500	4	FT	30.00	1	33.98	0.883	-3.736
100-500	5	FT	45.00	1	33.98	1.324	0.000
100-500	6	FT	60.00	1	33.98	1.766	34.116
100-500	7	FT	0.00	1	33.98	0.000	0.000
			237.85	7			G = 8.559
							P = 0.200
100-500	1	F	28.1791	1	28.80897	0.978136	-0.623
100-500	1	FT	30	1	28.80897	1.041	1.215
100-500	1	Т	28.2478	1	28.80897	0.980521	-0.556
			86.4269	3			G = 0.073
							D 0004
							P = 0.964
>500	1	F	13.9356	1	12.2695	1.135792	1.774
>500	1	FT	10.6256	1	12.2695	0.866	-1.528
>500	1	T	12.2473	1	12.2695	0.998191	-0.022
2 300	·	•		•	. 2.2000	2.000101	0.022
			36.8085	3			G = 0.447
							P = 0.800

Distance	Group Size	Behaviour	Observed	Expected Ratios	Expected Freq	Ratio	In Ratio
100-500	2	F	36.3912	1	29.6964	1.225441	7.398
100-500	2	FT	26.1329	1	29.6964	0.880	-3.341
100-500	2	T	26.5651	1	29.6964	0.894556	-2.960
			89.0892	3			G =2.195 P =0.334
>500	2	F	27.4152	1	16.26793	1.685229	14.308
>500	2	FT	21.3886	1	16.26793	1.315	5.853
>500	2	Т	0	1	16.26793	0	0.000
			48.8038	3			G =40.323 P = 0.000
100-500	3	F	32.7088	1	41.4571	0.788979	-7.752
100-500	3	FT	46.6625	1	41.4571	1.126	5.519
100-500	3	Т	45	1	41.4571	1.085459	0.000
			124.3713	3			G = 4.466 P = 0.107
>500	3	F	18.4349	1	21.14497	0.871834	-2.528
>500	3	FT	0	1	21.14497	0.000	0.000
>500	3	Т	45	1	21.14497	2.128166	33.987
			63.4349	3			G = 62.917
							P = 0.000
100-500	4	F	30	1	33.07717	0.90697	-2.929
100-500	4	FT	30	1	33.07717	0.90697	-2.929
100-500	4	Т	39.2315	1	33.07717	1.18606	6.694
			99.2315	3			G = 1.671

Distance	Group Size	Behaviour	Observed	Expected Ratios	Expected Freq	Ratio	In Ratio
100-500	5	F	35.2441	1	26.74803	1.317633	9.7216
100-500	5	FT	45	1	26.74803	1.682367	23.4090
100-500	5	Т	0	1	26.74803	0	0
			80.2441	3			G = 66.261
							P = 0.000
		_					
100-500	6	F	24.0436	1	43.01453	0.558965	-13.985
100-500	6	FT	60	1	43.01453	1.394877	19.968
100-500	6	Т	45	1	43.01453	1.046158	2.031
			129.0436	3			G = 16.027

## **Appendices 1-6**

CD Rom containing sightings, effort, directionality and T-POD data used during the study. Includes acoustic detection data and click train parameter data used in analyses.

This box should contain a data CD Rom