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Static acoustic monitoring of Cetaceans in Cardigan Bay, Wales

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STATIC ACOUSTIC MONITORING OF CETACEANS IN CARDIGAN BAY, WALES

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BY
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Summary

With ever increasing demands to develop coastal environments for sustainable use, particularly within UK government's renewable energy framework, policy makers and managers face growing pressure from conservation agencies as well as national and international regulatory bodies to comply with requirements to monitor the species and habitats in the areas under development or allocated for future use.

This work assesses one method of facilitating the monitoring of coastal cetacean species, and focuses on the two most common cetacean species in Wales, bottlenose dolphin (*Tursiops truncatus*) and harbour porpoise *(Phocoena phocoena*), both listed in the Annex II of the EU Habitats Directive, which requires reporting on their favourable conservation status. The study focuses on one static acoustic monitoring (SAM) device, the C-POD, which is already widely used in cetacean monitoring studies due to its practicality, ease of use and inexpensive set-up. Despite its popularity, some questions on its capabilities remain unresolved. This work aims to answer some of those questions.

Firstly the thesis estimates the effective detection area for harbour porpoises with C-PODs and examines the performance of both the hydrophone's click detection as well as the automated train detection algorithm. This is achieved with two different field experiments, comprising of playing back both artificial and real harbour porpoise sounds to the C-PODs at increasing distances. The results illustrate the ability of the C-POD to effectively log clicks, and the comparative performance of the train classification software. The effects of source level and distance from data logger on the detectability of porpoises are revealed, which enables the calculation of robust estimates of effective detection areas for future acoustic monitoring studies of the species.

Next the detection probability of bottlenose dolphins with C-PODs is examined using simultaneous visual observations and acoustic recordings and the effects of group size and behaviour on dolphin detection with acoustic devices is assessed. The analyses demonstrate a significant effect of both group size and behaviour on the detectability of dolphins consequently affecting the calculated effective detection radius and area. These findings pose a challenge for density estimation of dolphins using an overall detection function and emphasize the importance of prior knowledge of the activity and

behavioural patterns of target animals for developing appropriate experimental design, effective placement of data loggers and a meaningful analysis of SAM data.

The study also explored the difference in click train characteristics between broadband hydrophone recordings and C-POD recordings of bottlenose dolphins. A significant reduction in click rates was evident in the C-POD data, indicating that the C-POD train detection algorithm may not be logging the full range of dolphin echolocation, particularly those trains with long inter-click intervals.

The thesis then goes on to compare C-POD data with visual observations to assess whether the data can be used to discern behavioural information from the two species. The results confirm that regardless of the fact that the C-POD does not record the full vocal repertoire produced by these animals, it can reveal valuable behavioural information about its target species by detecting feeding or foraging events and identifying important feeding areas, particularly for harbour porpoise but also potentially for bottlenose dolphin.

This thesis supports the use of C-PODs in future monitoring efforts of both bottlenose dolphins and harbour porpoises. The findings will help analyse and interpret existing datasets and assist in designing effective and useful monitoring surveys for harbour porpoises and bottlenose dolphins and other species with similar behaviour and vocalisation characteristics.

Considering the already wide use of the device it is essential that future studies on the efficacy of the device continue. More detailed understanding of the effect of different behaviours and group sizes on the echolocation rate and characteristics for both species would be beneficial, particularly for the harbour porpoise. Further studies to extract dolphin feeding buzzes from C-POD data would increase the loggers’ ability to identify critical feeding sites. Improvements of the train classification algorithm would enhance the detection probability of dolphins with C-PODs, potentially overcoming the effects of behaviour and group size discovered here.

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This PhD would not have been possible without the generous help of many colleagues, students and volunteers and it was funded with a 125th Anniversary Bursary from the Bangor University. I thank my supervisors and advisors Drs John Turner, for agreeing to take this project on, Peter Evans for helping me see the bigger picture and believing in the project from the very beginning, Mandy McMath for helpful comments, Jim Bennell for acoustic advice, equipment and side scan, Len Thomas for statistical knowledge and Nick Tregenza, (and Jeff and Jan) for C-PODs and C-POD knowledge. Most of all, I am grateful to Dr Jan Hiddink for invaluable support without which the thesis would not be what it is today. Heartfelt thanks to Elisa Girola and Gemma James for everything – the project, the boat and a wonderful summer. Thanks also to Winnie Courtne-Jones, Paula Redman, Marta Sostres, Lucy Buckingham, Michelle Bradin, Melanie Wrigth, Claire Rowberry, Helene Roger-Berubet, Katie Green, Julia Sommerfield, Rhiannon Meier and Emily Cunningham for their efforts with data collection and handling; Brett Stones, Luke Saddler, Simon Williams and Remy Zyngfogel for invaluable help on the boat, sorting moorings and deploying and picking up C-PODs; SeaMôr Wildlife Tours and the Islander, along with Bethan and Derek Stones - my family in Wales! I thank the entire Cardigan Bay Acoustic Tracking Study team, C-CATS: Luke, Gemma, Winnie, Marta, Katrin and especially Jens Koblitz, Kati Brundiers and Felix Tschirschwitz of the German Oceanographic Museum for making the acoustic tracking and localisation project possible; the SAMBAH project for adopting me; Mats Amundin and Magnus Wahlberg for support and equipment; Jakob Tougaard and Line Kyhn for useful comments; everyone at SNAK, in Denmark for bats, decibels and Matlab; New Quay lifeboat station, Milford Haven and Swansea Coastguard and all fishermen and sea users in and around New Quay; Danielle Gibas, Gemma Veneruso and Daphna Feingold at Sea Watch Foundation, and the anonymous reviewers who helped improving the quality of the manuscripts presented here. I thank the SOS staff and **all** my friends and colleagues in Menai Bridge for support, stats and fun; climbing, office frisbee, yoga, salty liquorice, beach BBQs, midnight walks in Beaumaris and endless cups of herbal tea and coffee by the Menai Strait. Thanks to my wonderful family for encouragement and sisterly love, and Jaime for the climbing, surfing and sailing – and for reminding me to 'man up'. I also must make a special mention of Newborough beach – its space, solitude and simple beauty will stay with me long after this madness is forgotten.

⁂

I would like to dedicate my thesis to two very exceptional people who are no longer with us.

Firstly, to the memory of a colleague and a friend, Dr Mandy McMath, who encouraged me with her passion for marine conservation, her positive attitude, kindness and ability to dance till dawn. She was instrumental in setting up the Cardigan Bay acoustic monitoring project upon which this PhD was built.

⁂

And, with very heavy boots I would like to remember a fellow PhD student, Dr Eilir Hedd Morgan, whose infectious smile, positive attitude, determination and dedication to his work inspired me as it did so many people who were lucky enough to have known him. The arduous write up process was made so much more bearable with Eilir around for late night tea breaks and office football.

⁂

“Change the way you look at things, and the things you look at *will* change.”

-Dr Wayne Dyer

⁂

Chapters

Chapter 2 in preparation for Methods in Ecology and Evolution:

Nuuttila, H.K., Brundiers, K., Thomas, L., Courtene-Jones, W., Evans, P.G.H, Turner, J.R., Bennell,J. Hiddink, J.G., and Koblitz, J. (in prep.) **Defining an acoustic monitoring method for echolocating cetaceans: detection probability for C-PODs from playback experiments**

Chapter 3 submitted (in review) to Journal of the Acoustical Society of America:

Nuuttila,H.K., Thomas,L., Hiddink, J.G., Meier, R., Turner, J.R., Bennell, J., Tregenza, N.J.C. and Evans, P.G.H. (in review.) **Acoustic detection probability of bottlenose dolphins, *Tursiops truncatus*, with static acoustic data loggers in Cardigan Bay, Wales**

Chapter 4 in preparation for *Short notes* in Aquatic Mammals:

Nuuttila, Hanna, Winnie Courtene-Jones, Brundiers, Katharina, Jens Koblitz, Turner, J. Evans, P., Bennell, J. and Hiddink, J. (in prep.) **Comparison of broadband hydrophone and C-POD recordings of wild bottlenose dolphin echolocation clicks**

Chapter 5 accepted for publication to Aquatic Mammals:

Nuuttila, H.K., Meier, R., Evans, P.G.H, Turner, J.R., Bennell, J. and Hiddink, J.G. (in press) **Identifying feeding behaviour of wild bottlenose dolphins (*Tursiops truncatus*) and harbour porpoises (*Phocoena phocoena*) with static acoustic data loggers**

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Chapter 1 INTRODUCTION

Synopsis

In this introductory chapter, I present the rationale for this project, which investigates acoustic monitoring of bottlenose dolphins (*Tursiops truncatus*) and harbour porpoises (*Phocoena phocoena*) using static acoustic data loggers (C-PODs) in Cardigan Bay, Wales. I introduce reasons why monitoring distribution and abundance of cetaceans is required, describe my study area, Cardigan Bay Special Area of Conservation (SAC), and briefly introduce the two study species and their echolocation behaviour. I then describe the advantages and disadvantages of acoustic monitoring techniques versus traditional visual techniques and discuss the role that static, passive acoustic monitoring (SAM) can play in monitoring coastal cetaceans. I describe the data loggers used in this study, identifying some gaps in the current scientific knowledge about their use which this thesis sets out to address, and finish by summarising the main objectives of my PhD.

1.1 Rationale for monitoring cetaceans

Because many species of cetaceans face threats from anthropogenic activities such as by-catch, disturbance, marine seismic exploration, habitat degradation and pollution, they are now recognised as requiring specific conservation and management strategies implemented at national, regional and international levels (Reeves & Rejinders 2002; Compton *et al.* 2008; Evans & Teilmann 2009; Reynolds, III *et al.* 2009; Alter *et al.* 2010; Evans & Thomas 2011; Simmonds 2012). Impacts from climate change, such as loss of habitat, changes in prey availability and climate-induced changes in human activities put additional pressures on many cetacean populations (Alter *et al.* 2010). At a European level, monitoring of cetaceans is conducted under the European Union’s (EU) Habitats Directive (92/43/EEC 1992), and all cetaceans fall under Annex IV of the Habitats Directive requiring national reporting on their favourable conservation status. Annex II requires the establishment of Special Areas of Conservation (SAC) for harbour porpoise and bottlenose dolphin to form a network of conservation sites (termed the Natura 2000 network) (European Commission 2006; European Union 2007; Evans 2012). This is also now complemented through marine spatial planning and coastal zone management under the EU’s Marine Strategy Framework Directive, which requires governments, regulators and developers to assess the potential effect of their activities on the marine environment, including marine mammals (European Union 2012; Evans 2012). An important step towards designation of protected areas is to identify those key habitats of the target species, which are required for maintaining a healthy population (Hoyt 2004).

Monitoring cetacean population is all the more relevant in the context of the European Union directives requiring European member states to achieve 20 % of their energy from renewable resources by 2020 (Directive 2001/77/EC). As a consequence, there is a growing demand to develop offshore wind, tidal and wave technologies, which have the potential to cause substantial disturbance to coastal processes, benthic communities, and fish populations (Gill 2005; Hiddink *et al.* 2007; Shields *et al.* 2009; Alexander *et al.* 2013). These in turn can cause adverse effects on seabirds (Langton *et al.* 2011; Soanes *et al.* 2012) as well as marine mammals, in the form of reduced prey availability, noise pollution and habitat degradation or loss (Carstensen *et al.* 2006; Tougaard *et al.* 2009a; Dolman & Simmonds 2010; Simmonds & Brown 2010).

Cetaceans, as well as many other mobile marine species, are also affected by the construction and operation of various types of marine renewable energy extraction devices, which include offshore wind, wave and tidal power generators – both tidal barrages and tidal stream turbines (Carstensen *et al.* 2006; Wilson *et al.* 2007; Evans 2008; Brandt *et al.* 2011). Disturbance to cetaceans from renewable energy generators is caused by increased ambient noise, general habitat degradation from presence of the devices, potential changes in prey availability as well as the very real risk of collision with underwater devices, such as tidal turbines (Richardson *et al.* 1998; Madsen *et al.* 2006; Teilmann *et al.* 2006; Carstensen *et al.* 2006; Tougaard *et al.* 2009a). With such projects expected to increase due to the UK government's commitment to the EU to increase energy sourced from renewable resources in the next eight years, there will be a real necessity (as well as a legal requirement) to monitor the impacts of such projects on protected cetacean species and habitats (DECC 2011), especially when much of the impacts and the extend of potential impacts is still relatively unknown (Inger *et al.* 2009).

In the UK, the Joint Nature Conservation Council (JNCC) provides guidelines for management and conservation of protected species and habitats to achieve or maintain their favourable conservation status. The statutory national conservation agencies are required to assess whether selected species or habitats are in a favourable condition and this is achieved by collecting data on population status (Davies *et al.* 2001). Data should be used to assess population trends and to evaluate the impacts of anthropogenic pressures, such as habitat degradation, fisheries by-catch and disturbance from shipping or recreational activities, on the health and conservation status of populations (Ross *et al.* 2011).

One essential component of monitoring the population status of cetaceans is a reliable estimate of population size (abundance) or the number of animals per unit area (density), achieved through a continuous programme of systematic biological surveys of distribution and abundance (Thomas 2009). As most cetacean species are challenging to survey, indices of abundance derived from presence and absence data such as distribution, range and seasonal habitat have frequently been used in place of absolute density estimates (Evans & Hammond 2004). Acoustic data loggers are one such technique used for the monitoring of echolocating cetaceans in coastal waters, and the subject of this thesis.

1.2 Study species

Two cetacean species that are obvious targets for monitoring are the bottlenose dolphin and harbour porpoise. Both are regular inhabitants of the Cardigan Bay Special Area of Conservation in West Wales, one of three SACs established for bottlenose dolphin in the UK. This study was conducted off New Quay which lies within the Cardigan Bay SAC.

The harbour porpoise

The harbour porpoise (*Phocoena phocoena*, Linnaeus, 1758) is Britain’s smallest cetacean, measuring on average 1.5 m in length with a mean weight of 50-55 kg (Bjørge & Tolley 2009). It is inconspicuous, and due to its small size often missed by visual observers. It is easily identified by its rotund head, lack of distinct beak and small triangular dorsal fin (Figure 1.1). It inhabits large parts of the Welsh coast, with hot spots around Anglesey, the Llyn Peninsula, southern Cardigan Bay and the Gower

Peninsula (Baines & Evans, 2009; Figure 1.2). The abundance estimate from the July 2005 SCANS II survey for the entire Irish Sea was calculated at 15,200 (CV = 0.35) individuals (Hammond *et al.* 2008).

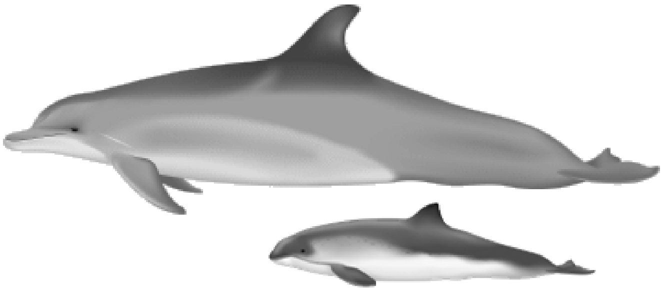

Figure 1.1 Illustration of a bottlenose dolphin (top) and a harbour porpoise (bottom). Adapted from the American Cetacean Society, www.acsonline.org

In Cardigan Bay, line transect surveys of the SAC indicate that the harbour porpoise population has been slightly increasing since systematic surveys began in 2001, with numbers ranging from 167 to 302 (Pesante *et al.* 2008; Veneruso & Evans 2012). Harbour porpoise are found in temperate shelf seas of 20-100 m depth and are commonly encountered in coastal bays and estuaries, near headlands with high rates of tidal flow (Evans *et al.* 2003; Evans & Hintner 2010; Isojunno *et al.* 2012). They are present year round in Welsh waters (Baines & Evans 2012), and in Cardigan Bay SAC site occupancy apparently increases over winter months (Simon *et al.* 2010). They are usually seen in the region in small groups of 2-10 animals, although congregations of larger numbers of animals are not uncommon (Pesante *et al.* 2008; Pierpoint 2008; Evans & Hintner 2010). Porpoises in the UK feed in the water column or on the sea floor on small schooling fish such as whiting (*Merlangius merlangus*), bib (*Trisopterus* spp.), pollack (*Pollachius* spp.), sandeel (*Ammodytidae* spp.) and gobies (of the family Gobiidae) (Santos *et al.* 2001, 2004; Santos & Pierce 2003). The harbour porpoise is exposed to many human activities, being the most commonly occurring cetacean within the nearshore area. In UK, its main identified causes of death are entanglement in fishing gear, infectious disease and bottlenose dolphin attack (Deaville & Jepson 2011).

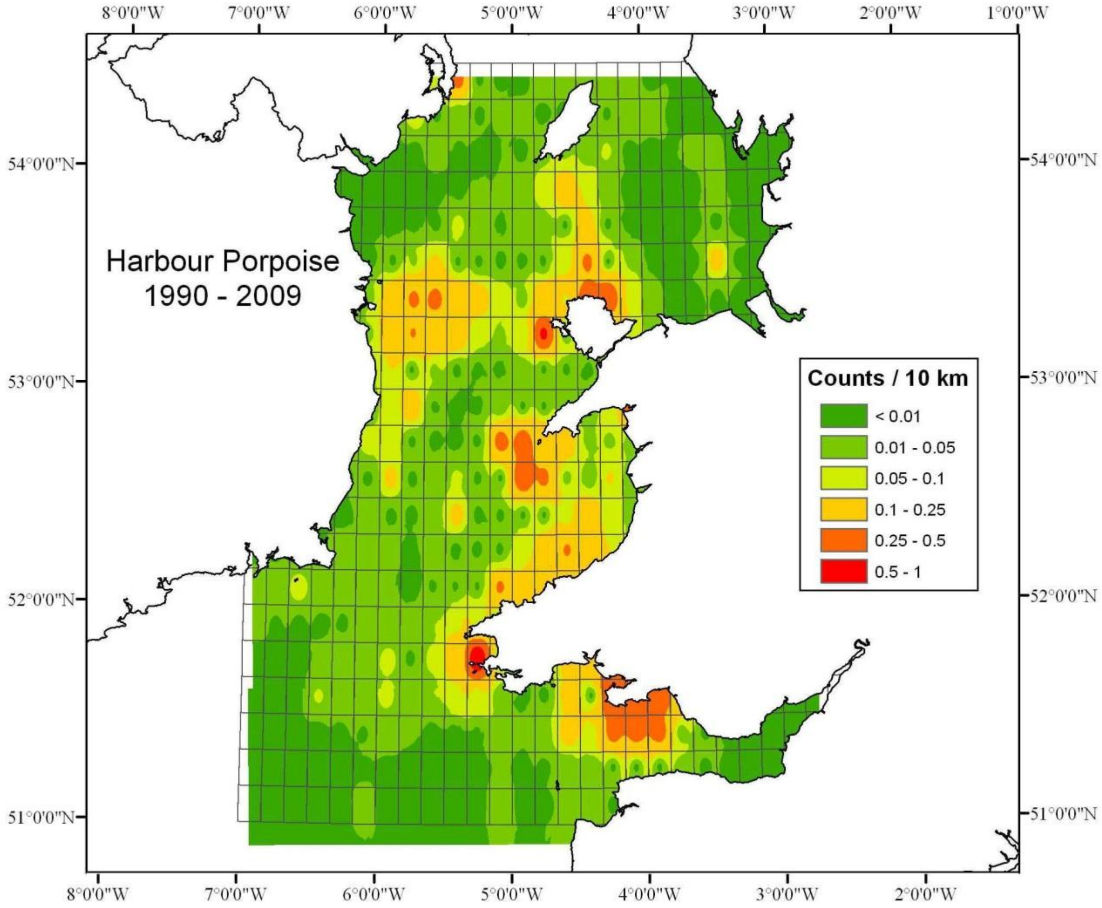

Figure 1.2 Long-term mean sightings rates (counts per 10 km distance travelled) of harbour porpoise in Welsh waters (Baines and Evans, 2012).

The bottlenose dolphin

The bottlenose dolphin (*Tursiops truncatus*, Montagu, 1821) can easily be distinguished from the harbour porpoise by its distinct, stubby beak, large, sickle-shaped dorsal fin, and its much larger size (Figure 1.1). It has a stocky build and can grow to nearly 4 m in length – over double the length of the porpoise (Wells & Scott 2009). It is distributed across hemispheres in both tropical and temperate seas and its sub-populations are typically defined as either coastal or offshore populations. In the UK there are two semi-resident coastal populations; one in the Moray Firth, north-east Scotland and the other in Cardigan Bay (Wilson *et al.* 1997; Evans *et al.* 2003). In Wales, the bottlenose dolphin is the second most common cetacean species, typically seen close to shore with occasional offshore records. It is most frequently sighted in southern Cardigan Bay, Tremadog Bay and off the Isle of Anglesey (Baines & Evans 2012), (Figure 1.3). The abundance of the population inhabiting the Cardigan Bay SAC, as determined from line transect surveys has been estimated between 114 and 206 animals (Pesante *et al.* 2008; Veneruso & Evans 2012). Mark-recapture estimates from photo-ID studies indicate a population of around 150-300 animals occupying Cardigan Bay in summer in any one year (Veneruso & Evans 2012).

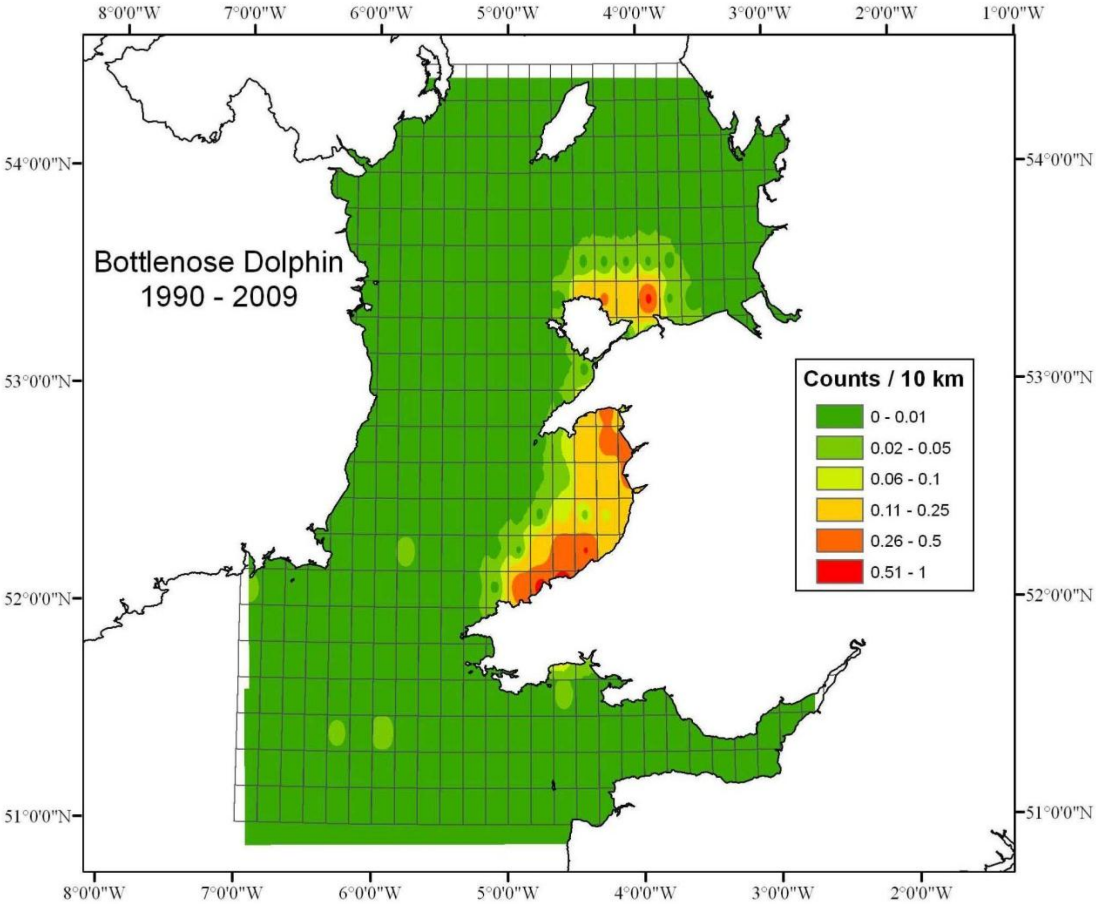

Figure 1.3 Long-term sightings rates (counts per 10 km distance travelled) of bottlenose dolphins in Wales (reproduced from Baines & Evans, 2012).

Coastal bottlenose dolphins are typically found around headlands, near areas of uneven topography and steep gradients as well as sandbanks, estuaries and areas of strong tidal current (Hastie *et al.* 2003a; b). Although seen throughout the year in Cardigan Bay, they exhibit seasonal preferences in habitat use occurring in southern and central Cardigan Bay in the summer, and dispersing northwards during winter months (Pesante *et al.* 2008; Baines & Evans 2012).

The bottlenose dolphin has a wide-ranging diet including a variety of fish and cephalopods, benthic and pelagic species. Stomach contents of stranded animals have included both solitary and schooling fish species, such as cod (*Gadus morhua*), pollack, whiting, haddock (*Melanogrammus aeglefinus*), salmon (*Salmo salar*), sprat (*Sprattus sprattus*), sandeels, flatfish (*Pleuronectidae* spp.) and cephalopods (Santos *et al.* 2001). In Wales, dolphins have been observed taking sea bass (*Dicentrarchus labrax*), salmon, conger eel (*Conger conger*), garfish (*Belone belone*), dragonet (*Callionymus* spp.) sandeel and small shark species but have also been associated with schooling herring and mackerel (Pesante *et al.* 2008; Evans & Hintner 2010). Only a small number of dolphins strand in Welsh waters and the cause of death is often not established, although relatively high levels of PCBs have been reported (Jepson 2005).

1.3 Study area

Cardigan Bay is the largest bay in the UK, situated between the western point of the Llyn Peninsula in the north (52° 47’ 45’’ N, 004° 46’ 00’’ W) and St David’s Head in the south (51° 54’ 10’’ N, 005° 18’ 54’’ W). It is a shallow bay, with water depths of less than 60 m throughout, very gentle slopes, and seasonally fluctuating salinity levels associated with freshwater inputs from rainfall, rivers and water masses from the Atlantic ranging from 34.2 in the summer to 33.3 in the winter. The sea surface temperatures vary from a minimum of 5°C in winter to a maximum of 16°C offshore and 20°C inshore in late summer (Evans 1995). The bay is exposed to the prevailing westerly and south-westerly winds and it has semi-diurnal tides with a mean spring tidal range of 4-5 metres (Evans 1995). The tidal currents are normally lower than 3.3 km/h flowing north during the flood, and south during the ebb. The substrate consists mainly of gravel in the strong current zone, and mud where the water energy is low (Evans 1995).

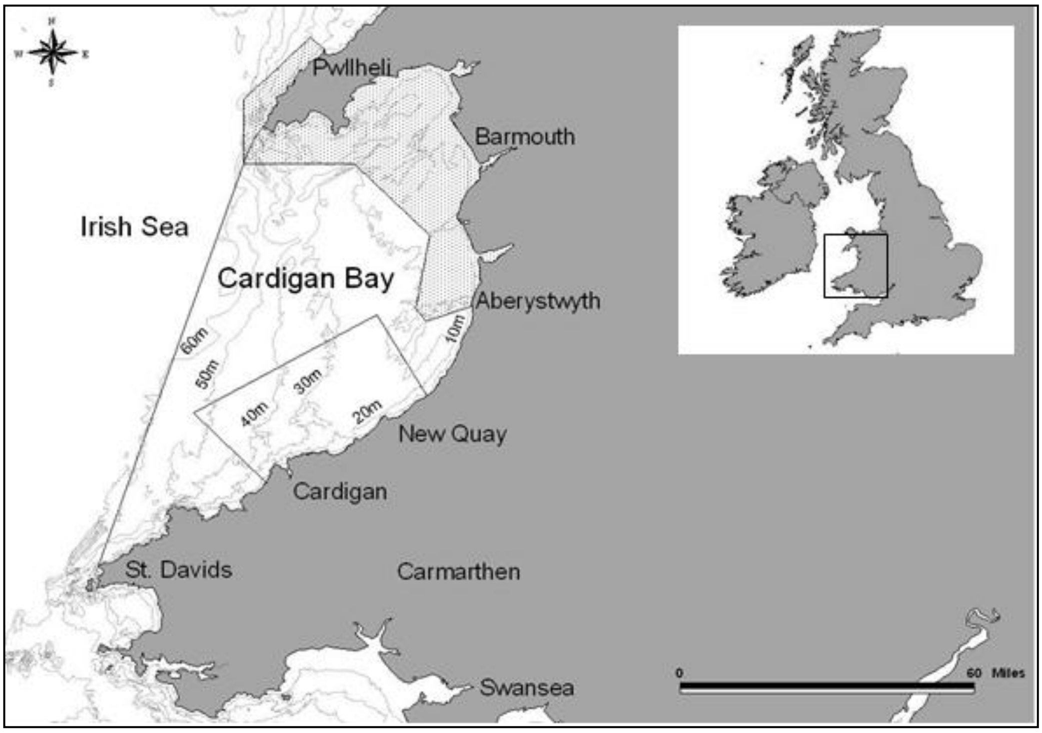

Figure 1.4 Cardigan Bay in West Wales with bathymetric contours; the diagonal line on the left delimits Cardigan Bay, the rectangle is the Cardigan Bay SAC, and the hatched, shaded polygon is the Pen Llyn a’r Sarnau SAC (reproduced from Pesante *et al.* 2008**)**.

The Bay has two Special Areas of Conservation (SAC) which are protected sites designated under the EU Habitats Directive and forming the Natura 2000 network. These are the Cardigan Bay SAC and the Pen Llyn a`r Sarnau SAC (Figure 1.4). Each SAC is designated for one or more habitats and species (called features) listed in the Directive, which also requires a management plan to be prepared and implemented to ensure the favourable conservation status of the selected habitats and species (Anon. 2001). Both SACs in Cardigan Bay have the bottlenose dolphin listed either as their primary or qualifying feature (Pesante *et al.* 2008). The study site, New Quay, is located in the middle of the Cardigan Bay Special Area of Conservation (SAC), and the two study species, the bottlenose dolphin (*Tursiops truncatus*) and the harbour porpoise (*Phocoena phocoena*), are both resident there (Pesante *et al.* 2008). Studies of these dolphins in the area have been conducted since the 1990’s (Lewis & Evans 1993; Bristow & Rees 2001; Bristow *et al.* 2001). More recent marine mammal research in the area has also included the harbour porpoise as its target species, despite not being a designated feature of the SAC (Pesante *et al.* 2008; Simon *et al.* 2010).

Both are suited for acoustic monitoring combined with visual observations as they often visit shallow near shore areas in the region (Pierpoint 2008; Pierpoint *et al.* 2009; Isojunno *et al.* 2012).

Both species are at risk from disturbance from anthropogenic activities, such as recreational boating, noise pollution, habitat degradation, reduction in prey availability and by-catch due to their year-round presence in coastal areas where the human presence and impact is at its highest (Baines & Evans 2012). Measured effects from anthropogenic causes include behavioural changes and decreased or modified site usage (Pierpoint *et al.* 2009; Veneruso & Evans 2012), all of which can lead to decreased feeding or breeding opportunities and affect the health of the population in the long-term (Lusseau & Higham 2004; Bejder *et al.* 2006; Lemon *et al.* 2006; Jensen *et al.* 2009a). Other observed effects are the increased inter-specific aggression between the two species in the area (Ross & Wilson 1996; Jepson & Baker 1998; Pesante *et al.* 2008).

1.4 Acoustic behaviour

Acoustic communication is an intrinsic part of all mammal behaviour but particularly so for cetaceans who have adapted to their marine existence by evolving special hearing and sound production mechanisms, not only for communication but also for purposes of navigation, foraging and feeding (Tyack & Miller 2002; Frankel 2010; Nummela 2010).

The two study species produce very different types of vocalisations. The bottlenose dolphin emits vocalisations in three broad structural categories: burst-pulse sounds, whistles and clicks (Caldwell *et al.* 1990; Tyack 1997). It uses echolocation clicks mainly for feeding and navigation, and burst-pulse sounds and whistles for communication (Mann *et al.* 2000; Janik 2009), although it has been suggested that clicks may also serve some communicative purpose (Tyack 1997). By contrast, the harbour porpoise produces only clicks, and uses these for navigation, feeding and communication (Koschinski *et al.* 2008; Verfuß *et al.* 2009).

Cetacean echolocation, and the sonar capabilities of the bottlenose dolphin in particular, have been much studied since the discovery of dolphin echolocation in the

1950s (McBride 1956; Kellogg 1958). The sound production in echolocating cetaceans takes place in the nasal complex in association with their respiratory system. Within this structure there is a pair of small lipid filled bursae surrounded by connective tissue lips and airsacs previously coined the monkey lips and dorsal bursae complex (MLDB), but now usually referred to as the phonic lips (Cranford *et al.* 1996). The clicks are generated via a pneumatic process when pressurised air is forced through the tight connective muscular tissue of the phonic lips, which open and close briefly to produce the sound. The clicks are then projected through the fat tissue bursae into the melon in the animal’s forehead. The air sacs and the skull help direct the sound into the melon, resulting in a narrow directed sound beam (Au 1993; Cranford *et al.* 1996; Madsen *et al.* 2010; Au *et al.* 2012).

Studies on dolphin echolocation have been conducted almost entirely with captive animals, and to date, the functional significance and details of echolocation in the wild are not yet fully understood. Echolocation clicks are typically described by the intensity of their source level, their peak frequency, click duration and inter-click interval (ICI). Here, the echolocation characteristics of dolphins and porpoises are listed, drawing as much as possible from studies conducted in the wild, with unrestricted animals.

Table 1.1 Echolocation click characteristics of harbour porpoise and bottlenose dolphin

	Harbour porpoise	**Bottlenose dolphin**
Mean source level dB re 1 µPa (peak-to-peak) @ 1 m	157 to 191	177-228
Click duration	77 µs	8-72 µs
Peak frequency	131 kHz	30-150 kHz
Beam width	13 °	9-10 °
Sources	(Au *et al.* 1999; Teilmann *et al.* 2002; Villadsgaard *et al.* 2007; Koblitz *et al.* 2012)	(Au *et al.* 1974, 2012; Au & Hastings 2008; Wahlberg *et al.* 2011).

In general, porpoise clicks are less varied than those of dolphins, with lower mean source levels, longer but more stable click lengths and peak frequencies. Dolphin clicks are shorter and more diverse in click duration and frequency, with very high source levels (Table 1.1). Inter-click intervals are context specific for both species. Dolphins decrease their ICIs steadily with decreasing distance to a target (Jensen *et al.* 2009b) and their echolocation rates (the number of clicks or click trains recorded in a time unit) vary according to different behaviours (Jones & Sayigh 2002). During foraging and feeding, they produce shorter and faster clicks with the shortest ICIs reported between 3.0 and 7.1 ms (Wahlberg *et al.* 2011).

Similarly, porpoise ICIs decrease progressively when ‘range locking’ upon a target during search phase, ending in a high rate ‘buzz’ of 300-500 clicks/s (DeRuiter *et al.* 2009; Miller 2010), with extremely short ICIs of around 1.5 ms (Villadsgaard *et al.* 2007; Verfuß *et al.* 2009) during the final prey capture (Figure 1.5). Some studies have also reported ICIs of around 50-60 ms from small data samples during the initial search phase (Au 1993; Akamatsu *et al.* 2005b; Villadsgaard *et al.* 2007).

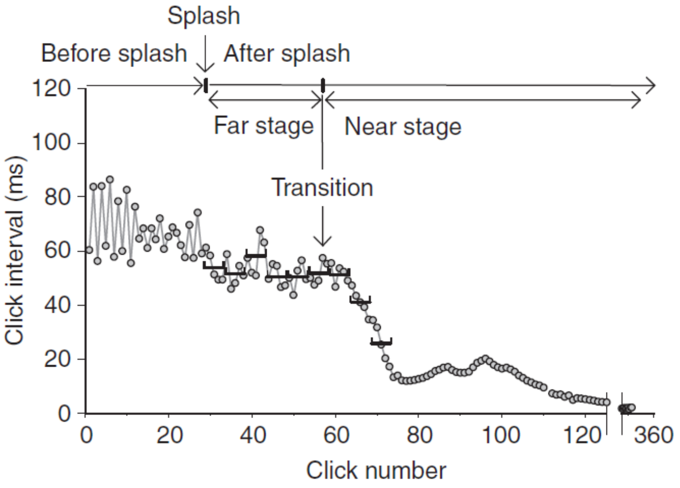

Figure 1.5 The sections of a (harbour porpoise) click train in a fish capture trial. ‘Splash’ refers to moment when fish or a boat hook hits the water creating a noise as cue for the animal. The after-splash section is divided into a far stage and a near stage, indicating animal’s distance from target, beginning with the transition to progressively shorter click intervals. Horizontal brackets indicate the mean click interval over five consecutive clicks. (Adapted from Verfuß *et al.* 2009)

Both species project their echolocation clicks in a directional beam with most of the acoustic energy directly in front of the animal, porpoise beam width being slightly wider than that of dolphins (Au *et al.* 2012; Koblitz *et al.* 2012). Dolphin clicks are very intense, short and broadband with energy across the frequency spectrum, 30-150 kHz (Figure 1.6), whereas porpoises produce very narrowband clicks centred around 130 kHz (Au 1993; Wahlberg *et al.* 2011; Koblitz *et al.* 2012). As a consequence, the higher frequency porpoise clicks are more rapidly absorbed by seawater, while the higher intensity and lower frequency dolphin clicks travel further – extending the area within which they are able to navigate and communicate, or be detected by researchers.

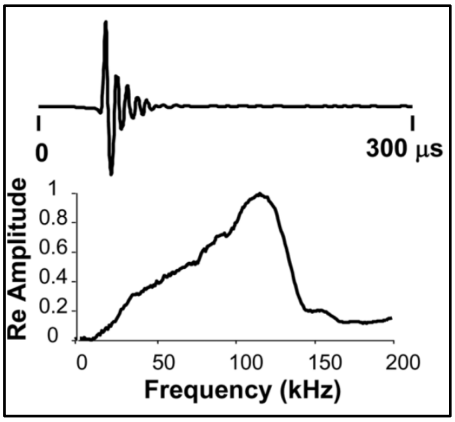

Figure 1.6 Example of a typical dolphin click time signal (top) and relative amplitude spectrum (bottom). Most of the energy is spread between 50 and 150 kHz. (Adapted from Au *et al*. 2012)

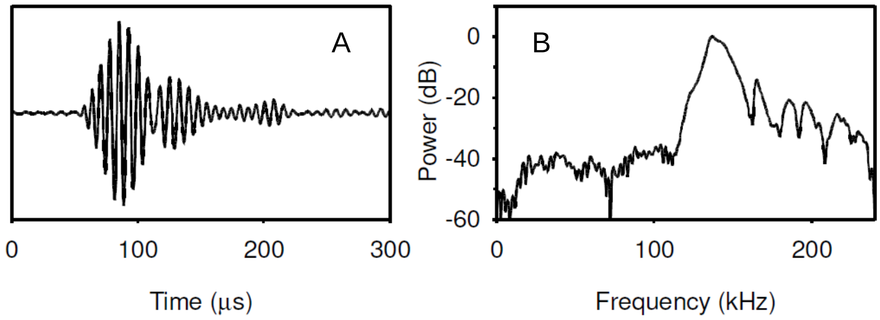

Figure 1.7 Example of a typical porpoise click time signal (A) and power spectrum (B). There is virtually no energy present below 100 kHz (the curve below 100 kHz represent background noise of the recording). (Adapted from Tougaard *et al*. 2005)

Most of the literature describing dolphin or porpoise echolocation focuses upon clicks recorded near to the beam axis, the so called “on-axis” clicks. However, the further away from the beam axis the clicks are recorded, the more altered they become. These “off-axis” clicks from dolphins have generally lower frequency and amplitude to the on-axis clicks (Au & Hastings 2008). This can result in a high number of clicks with dominant frequency in the lower part of the frequency range. The narrowband, high frequency clicks of the porpoise exhibit much less off-axis click frequency variability.

Despite the distinct characteristics of clicks, there are occasions when dolphin clicks can appear very similar to porpoise clicks (Simon *et al.* 2010).

Both species alter their vocalisations according to function and behaviour, and many studies have examined the types of vocalisations used for different behaviours (Nowacek 1999, 2005; Acevedo-Gutiérrez & Stienessen 2004; Quick & Janik 2008; Janik 2009; Simard *et al.* 2011) or environmental characteristics, such as water depth (Simard *et al.* 2010) For porpoises which produce only one type of vocalisation (the high frequency click), differences in click train characteristics, particularly the ICI, relate to the behavioural context (Akamatsu *et al.* 1994; Verfuß *et al.* 2009; Clausen *et al.* 2010).

1.5 Acoustic studies of cetaceans

In cetacean studies, ‘bioacoustics’ can be described as the use of acoustics to study a variety of aspects of cetacean biology including auditory capacities, sound production, and communication or feeding and foraging behaviour. Light, thermal, and electromagnetic energy attenuate quickly in water, but acoustic energy propagates efficiently over large distances underwater, and it is the most effective method for cetaceans to communicate, navigate and locate prey or conspecifics, or avoid their predators (Au & Hastings 2008). Acoustic methods to study cetaceans include underwater microphones (hydrophones) and recorders to receive sound or transducers to emit sound.

Acoustical techniques can be used to detect and track marine animals as well as to assist in the study of their environment and behaviour, including feeding, mating and social interactions (Johnson *et al.* 2006; Au & Hastings 2008). A common approach is to study the types of vocalisations produced by cetaceans and how these relate to their behaviour or group size, or try to ascertain the functions of particular sounds (Janik & Slater 1998; Nowacek 2005; Villadsgaard *et al.* 2007).

Many studies have concentrated on describing the hearing abilities of marine mammals and how anthropogenic noise might affect them (Kastelein *et al.* 2002; Gannon *et al.* 2005). Static acoustic gear has also been used to measure presence and absence of animals to assess the impacts of marine developments such as wind farms and shipping or fishing gear on the abundance, distribution or behaviour of cetaceans (Lesage *et al.* 1999; Cox *et al.* 2004; Carstensen *et al.* 2006; Holt *et al.* 2009; Tougaard *et al.* 2009a; b). Acoustic methods, such as towed or stationary hydrophones have also been used to detect vocalisations of cetaceans to study their range, distribution and to estimate their abundance (McDonald & Fox 1999; Barlow & Taylor 2005; Berrow *et al.* 2009; Marques *et al.* 2009, 2012).

1.6 Visual versus acoustic studies of cetaceans

The fact that marine mammals have evolved to utilise sound as their main means of communication and navigation enables us to study animals which otherwise can be extremely hard to detect. Small odontocetes (toothed whales) in particular can be difficult to locate by eye sight (Akamatsu *et al.* 2008) as only a small portion of them is visible for a brief period of time. Many small cetaceans have fast swimming speeds - up to 1.2–5.0 m/s for harbour porpoises (Hanson & Baird 1998; Akamatsu *et al.* 2002) with a dive duration of 4-6 min and potentially longer when feeding - up to 10-15 min (Otani *et al.* 1998; Teilmann *et al.* 2007), and hence they can travel several hundred metres underwater without being observed visually at the surface (Akamatsu *et al.* 2008). Large cetaceans, such as baleen whales and sperm whale, are easier to spot when they are on the surface, but many are fast swimmers and can spend long times submerged (up to an hour for sperm whales) which can seriously affect one’s ability to sight them (Whitehead 2003).

Visual studies of cetaceans often use shipboard or aerial survey methods which are generally limited to calm weather conditions and daylight hours. There are serious constraints which can introduce bias to visual surveys, including sea state (Clark 1982; Barlow 1988; Evans & Hammond 2004), observer variability (Young & Pearce 1999; O’Brien *et al.* 2009), optics and platform used, and the eye height above sea level, adding uncertainty to the data collected. The level of experience, the number of observers, and the environmental conditions will all affect how well or how quickly animals are sighted (Figure 1.8). For some species, the probability of detecting animals in sea states above Beaufort scale 2 is considerably reduced, and the size, noise, speed or mere presence of the vessel used can bias the study, with animals either being attracted towards it or avoiding it. All these factors affect the sighting rates, initial sighting distances and subsequent estimates of abundance based on them (Palka 1996; Teilmann 2003).

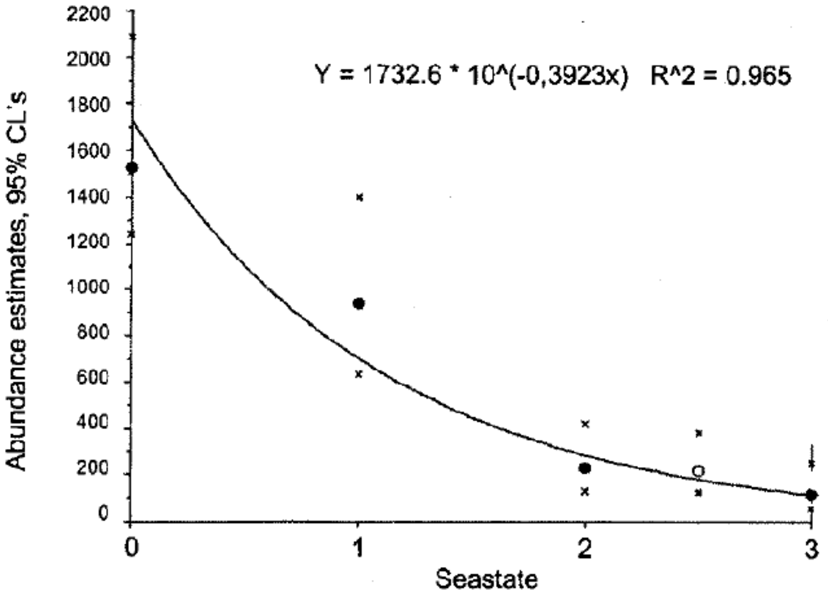

Figure 1.8 Abundance point estimates for harbour porpoise (black dots) for sea states 1, 2, and 3 with 95% confidence intervals (x symbols). (Adapted from Teilmann 2003)

When shipboard or aerial surveys are used for density estimates, the above biases must be taken into account, necessarily resulting in a complex detection function for the animals. Traditionally, the main assumption of these surveys is that all animals on the track line are detected, so that the detection probability (*g*) at distance 0 is 1, (g(0) =1); this is difficult or impossible to achieve with many diving animals, and must be corrected for, e.g. using dive data from tagged animals. Furthermore, cetacean surveys have generally low coverage in space and time, which contributes significantly to the variability, adding bias from likely changes in diurnal and seasonal diving patterns, as most surveys are conducted in the summer months when the weather is most suitable (Evans & Hammond 2004). Together with observer variability and the density estimates obtained from visual surveys have potentially very large margins of uncertainty.

Acoustic studies have several distinct advantages over visual observations. They can be used outside daylight hours and in more varied weather conditions especially with static acoustic gear that is left moored on the seabed. The equipment used can be standardised and made independent of each observer's abilities which may allow independent comparisons between several detection methods. A hydrophone array can be used to accurately determine both the distance and direction to a vocalising animal, whereas determining distance in particular is notoriously difficult for even the most experienced observers. Static acoustic methods also allow monitoring to be carried out without any interference from observer variables or the presence of a boat. Because acoustic detection methods do not need to rely on human observers, they are useful as an independent detection method during visual transect surveys (Akamatsu *et al.* 2008).

However, acoustic methods do have important limitations. The main disadvantage is that only vocalising animals will be detected and animals that are silent for long periods will be missed, making certain species more suitable for acoustic monitoring, e.g. the harbour porpoise, which echolocates almost continuously (Akamatsu *et al.* 2007). Furthermore, estimating abundance for species where call rate and detection function are not quantified is still problematic. If acoustic line transect methods are used, expensive survey platforms (boats and ships) are still required. Several species-specific factors including the frequency range of the target species need be taken into account when planning acoustic surveys. Low frequency sounds such as those of mysticetes (usually below 1 kHz) have significantly less seawater absorption loss than sounds emitted by odontocetes (typically above 10 kHz), and this greatly affects their detection distance. Large species, like the sperm whale, produce long range sonar clicks with extremely high source levels up to 223 dB *re* 1 µPa/root mean square (RMS) at centroid frequencies of 15 to 20 kHz where energy absorption is low, and which can be detected several kilometres away (Møhl *et al.* 2000; Madsen *et al.* 2002). In contrast, most species of porpoises produce narrow band high-frequency (NBHF) clicks of around 130 kHz, and these are disadvantaged by a high rate of absorption around 40 times higher than those of sperm whale clicks so that they are only functional or detectable at short distances (Kyhn *et al.* 2009).

The probability of detecting an animal will also depend on its vocal behaviour, the rate of sound production, and the source levels of the vocalisations. Importantly for echolocating cetaceans, the directionality and beam width of the sound emitted as well as the actual direction of the head of the vocalising animal will have an important effect on the detectability of the signal, as on–axis clicks will be more intense and thus more easily detectable (Figures 1.9 and 1.10). Foraging and feeding vocalisations tend to vary from those emitted during resting or socialising. Dolphins produce specific foraging calls, and both dolphins and porpoises increase their echolocation rate when feeding (Janik 2000; Johnson *et al.* 2006; Verfuß *et al.* 2009). Intense vocalisations with a lot of energy across the frequency spectrum will have a greater likelihood of reaching the recording hydrophone without the loss of much acoustic energy through absorption or refraction in the water column (Au & Hastings 2008). Vocal behaviour can vary with gender, age and season; humpback whales are well known for the songs produced exclusively by males in their wintering grounds (Darling & Bérubé 2001). Although visual observer bias can be eliminated, and acoustic data can be collected in more varied weather conditions, the detection function will still vary according to the ambient noise levels from wind, waves and rain, and therefore must be quantified. In Another very important factor to consider is the ambient noise at the time of recording. Vocalisations with low source levels will be masked by the ambient noise in the same frequency band, being only detectable at close range to the hydrophone (Akamatsu *et al.* 2008). This is of particular concern in noisy environments such as shipping lanes or areas with high tidal flow and increased noise from mobile sediments (Hamilton *et al.* 1956), but in fact applicable to all recordings.

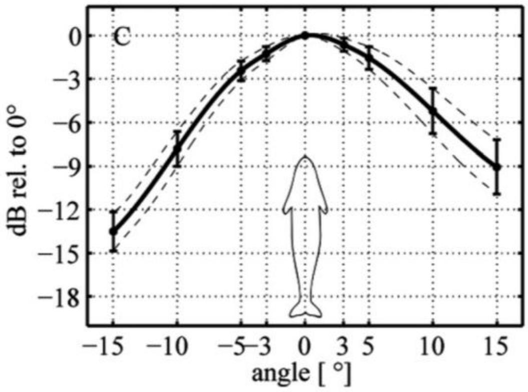

Figure 1.9 Averaged horizontal beam pattern for harbour porpoise clicks. Error bars show mean and 1 standard deviation of the measurements for each receiver. Black solid line is the averaged interpolated beam pattern. One standard deviation of all interpolated beams is depicted by the black dashed line. (Reproduced from Koblitz *et al.* 2012)

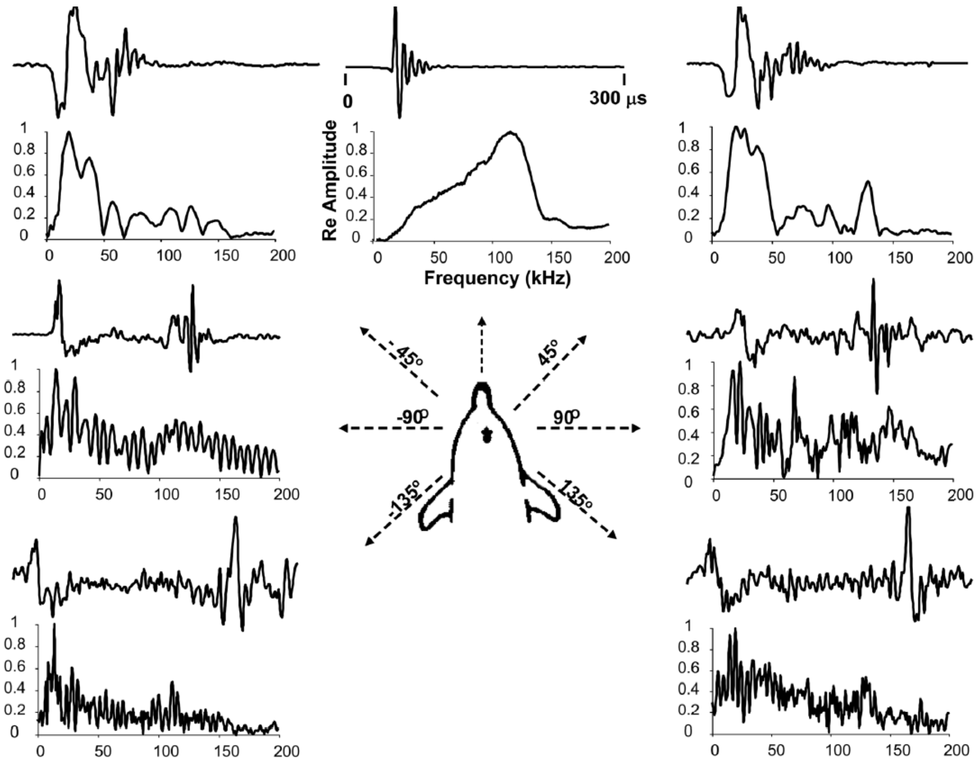

Figure 1.10 An example of a single bottlenose dolphin echolocation click measured by hydrophones at different angles in the horizontal plane, showing the click time signal and the varying frequency content and relative amplitude. (Reproduced from Au *et al*. 2012)

1.7 Acoustic methods to study cetaceans

Generally, acoustical techniques available for cetacean studies can be described as either passive or active. Acoustic methods can also be described as real time or archived, static or mobile. Active acoustic methods typically produce and transmit a sound and consequently analyse the returning echo (SONAR). Active acoustics can be used to find and track animals in the water column in real time or to explore the environment in which the animals live (Similä & Ugarte 1993; Similä 1997; Benoit-Bird *et al.* 2009). For example, acoustic echo sounders have been used to detect localised concentrations of migrating sound scattering layers of micronektonic animals to study patterns in beaked whale foraging (Figure 1.11). Many dolphin species feed on this layer so active acoustics can be used to study the predator and its prey simultaneously (Johnston *et al.* 2008).

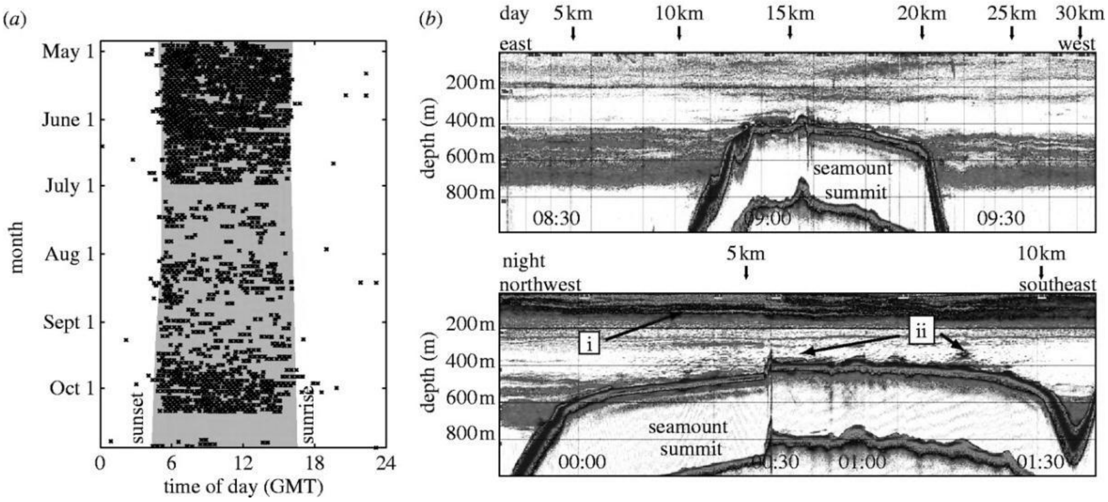

Figure 1.11(a) Detection of beaked whale clicks, primarily at night, at Cross Seamount, Hawaii. Each black mark indicates a detection, and the grey region represents local night. (b) Day and night echogram snapshots illustrating the nocturnal enhancement of prey fields (i and ii) at Cross Seamount. (Reproduced from Johnston *et al.* 2008)

Passive acoustic techniques are much more widely used in cetacean studies, and can be further divided into fixed or static versus mobile acoustic sensors. Passive acoustic techniques allow the localisation of animals for the purpose of abundance and density estimation (Clark & Ellison 1988). Mobile methods include hydrophones towed behind a ship or other mobile platform (Mellinger *et al.* 2007). For multiple hydrophone arrays, the number and position of hydrophones in an array can be modified according to target species and task at hand. Towed hydrophones can be used alone, or in combination with visual surveys, to estimate abundance and density of cetaceans (Leaper *et al.* 2000; Akamatsu *et al.* 2001; Hastie *et al.* 2003b; Barlow & Taylor 2005; Lewis *et al.* 2007; Berrow *et al.* 2009), using the same or slightly modified methodology as in visual line transect surveys (Buckland *et al.* 2001).

Another type of mobile acoustic technique is the acoustic tag where the animal itself is used as the recording platform. Acoustic tags provide information on the acoustic behaviour of the animal itself but also of its conspecifics, and can be used to collect other auxiliary information on dive times, depth, and movement as well as environmental information (Akamatsu *et al.* 2005a; Zimmer *et al.* 2005; Johnson *et al.* 2006). Digital tag recordings have also been used in conjunction with the U.S. Navy underwater test ranges such as the Atlantic Underwater Test and Evaluation Center’s

(AUTEC) bottom mounted hydrophones to track beaked whales, and to provide auxiliary data for long term passive monitoring (Ward *et al.* 2008).

Hydrophones can also be fixed to set locations for long time periods. Advantages of mobile acoustic receivers are the larger spatial coverage and simplicity in combining acoustic detection with visual surveys. The main benefit of fixed systems is the longer temporal coverage, allowing continuous monitoring around the clock, between years and seasons, and they are typically a lot less expensive than shipboard surveys (Marques *et al.* 2009).

Fixed (static) acoustic methods

The main types of static equipment used to capture sound are cabled hydrophones in permanent or semi-permanent installations, radio linked hydrophones, sonobuoys and autonomous recorders (Mellinger *et al.* 2007). Static acoustic methods have long been used to locate and track cetaceans, and to provide information on the relative abundance (in terms of presence over time) and habitat use of cetaceans. Recently, static acoustic methods have also been used to provide population estimates of abundance and density within specified areas using a variety of techniques including modified distance sampling methods (Marques *et al.* 2010, 2011, 2012; Küsel *et al.* 2011).

Fixed cabled hydrophones are usually placed on the sea floor in permanent configurations, and have the capability to be continuously powered by an external source and to continuously send data to a receiving station. They are expensive and usually only used by governmental agencies, such as the U.S. Navy's low frequency Sound Surveillance System (SOSUS) or the AUTEC) in the Bahamas (Mellinger *et al.*, 2007). Studies have used data from existing fixed hydrophone arrays designed for other purposes (usually military) in order to study cetacean distribution and occurrence, both short term and spanning very long time periods and over ocean basins (Stafford *et al.* 1998, 2007; Simard *et al.* 2008). These have proved very useful especially for large, sparsely distributed species like humpback (*Megaptera novaeangliae*) and sperm whales (*Physeter macrocephalus*) (Tiemann *et al.* 2006), Blainville's beaked whales (*Mesoplodon densirostris*) (Marques *et al.* 2009), and minke whales (*Balaenoptera acutrostrata*) (Marques *et al.* 2010). In general, the military or governmental sources can provide near real time data and have hydrophones in pelagic areas otherwise often inaccessible for scientists.

Another kind of passive acoustic device available for marine mammal scientists is the sonobuoy which oceanographers have long used to record noise in the oceans, and the U.S. Navy has used for several decades to record the sound of submarines (Northrop 1973, 1975). The sonobuoy can be deployed either from an aircraft or a surface ship, and includes a single underwater hydrophone and a radio transmitter to send the recorded signals back to the aircraft or ship. By deploying multiple sonobuoys in a pattern, the location of the “target” can be determined. Sonobuoys have been used in ocean exploration as well to record marine mammal calls and listen for earthquake activity (Levenson 1974).

Radio-linked or cabled hydrophones can also be used for marine mammal surveys; these consist of a hydrophone receiver on a mooring with a connection through a radio link or cable to a shore station or a ship, and data captured real time (Rankin *et al.* 2005). Examples of such systems include the Comprehensive Test Ban Treaty Organization’s (CTBTO) International Monitoring System and the WHOI/Cornell Right Whale Detection Buoy System, which has been designed specifically to study marine mammals.

Autonomous recorders contain a hydrophone and a battery powered recording and data storage system. Some devices record sound directly but others record only selected characteristics of sound, either continuously or following a duty cycle. Recorders are typically moored to the sea bed or float from the surface and require the equipment to be recovered for the data to be downloaded (Dudzinski *et al.* 2011). One such autonomous system is the C-POD.

1.8 Static acoustic monitoring with autonomous click loggers

Static acoustic monitoring (SAM) of cetaceans encompasses a wide variety of fixed, mainly passive, acoustic methods, some of which were mentioned earlier. One type of automated click logger is the C-POD (Chelonia Ltd.). The C-POD, and its predecessor, T-POD, were developed to detect small odontocetes such as the harbour porpoise which produces a stereotypical narrowband high frequency (NBHF) signal and is particularly well suited for automated detection (Dudzinski *et al*. 2011).

Figure 1.12 Photograph of a C-POD prior to deployment attached to a rope and weights.

C-PODs and T-PODs as monitoring tools

T-PODs and C-PODs are self-contained omni-directional static acoustic click detectors comprising a hydrophone, filter and digital memory (Figure 1.12). The first versions of the *Chelonia* click detector were tested more than a decade ago (Baines *et al*. 1999; Tregenza 2009), and one of their initial uses was to detect and monitor harbour porpoise and fisheries interactions, specifically their movements around pingers (Cox *et al*. 2001).

They automatically detect and record the time and duration of echolocation clicks. The T-POD, the predecessor of C-PODs, scans through six frequency channels per minute, which can be adjusted by the user to the desired frequency band. The T-POD has two band-pass filters, the target filter and the reference filter. Clicks are logged when the acoustic energy in the target filter surpasses that of the reference filter by a predefined ratio (Kyhn *et al*. 2008; Dudzinski *et al*. 2011). This ratio is set by the ‘click bandwidth’ (version 4) and ‘selectivity (Ratio A/B)’ (version 3). The minimum sound pressure level picked up by a T-POD is adjusted with the ‘threshold’ (version 4) and ‘sensitivity’ (version 3) settings (Simon *et al.* 2010).

The C-POD uses digital waveform characterisation within a frequency band of 20-160 kHz to detect click signals with brief spikes in sound intensity, and logs the time, centre frequency, intensity and bandwidth of each cetacean click. Instead of scanning through the six channels like the T-POD, the C-POD logs all clicks continuously and stores data onto a removable SD card, allowing more data to be collected and making rapid servicing at sea possible. The C-POD has a much lower false negative rate, in particular for bottlenose dolphins, and is more suitable for recording in areas of high levels of background noise where T-PODs would fail to detect cetaceans (Tregenza 2009). The data collected from both types of data loggers have to be extracted from the loggers using specific software (*T-POD.exe* and *C-POD.exe* respectively, available at http://www.chelonia.co.uk/downloads). Once data area extracted, the software, comprising a train detection algorithm, filters through the raw click data, identifies cetacean click trains, and estimates their probability of arising by chance from a non-train producing source (like rain or a boat propeller). This probability, p is determined by Poisson distribution of the prevailing rate of arrival of clicks, the size of the interval between each click and the regularity of the trains. The probability of an entire identified train arising by chance from random sources will be the product of successive p values (Chelonia Ltd 2012b). The software then assigns the click trains to categories by species and their probability of being from cetacean origin, as High, Medium and Low quality (Thomsen *et al.* 2005).

Comparability of units

Several versions of the T-POD hardware and software were developed and used in monitoring studies before being replaced by the C-POD, and although they have been shown to be a very useful tool with both porpoises and dolphins, there are still concerns over the comparability of data across regions and how differences in the sensitivity of different versions, different train algorithms or even individual loggers affect the performance of the equipment and outcome of the analysis. Despite calibration of hydrophone sensitivity and omni-directionality during the manufacturing process, the early versions (v.1 - v.3) of the T-POD had large variations in their sensitivities and detection thresholds (Kyhn *et al.* 2008; Bailey *et al.* 2010).

Essentially, data collected with different versions of the T-POD or analysed with different versions of the train algorithm varied greatly and were not comparable without cross-calibrating the equipment (Dudzinski *et al.* 2011; Kyhn *et al.* 2012). The C-PODs are now manufacturer calibrated to strict standards and tank calibrations are no longer considered necessary prior to deployment (Chelonia Ltd 2012a). The C-PODs used in chapters 2 and 4 were tank calibrated by the German Oceanographic Museum, and those used in chapters 3 and 5 similarly tank calibrated by the manufacturer, both before and after the deployment period.

The manufacturer calibrated the instruments an acoustic tank using a standard signal, by rotating the complete instrument in a sound field, and adjusted to achieve a radially averaged, temperature corrected, maximum sound source pressure level (SPL) reading within 5% of the standard at 130 kHz (±0.5 dB). The radial values were not averaged and were taken at 5 degree intervals. This is in contrast to many hydrophone manufacturers who publish a rolling mean value that reduces the apparent range between minimum and maximum values. The sensitivity of each C-POD was adjusted to record an average sound pressure level (SPL) value of 45 for the signal (equivalent to 2 Pascals (peak to peak) which equates in water to 120 dB re 1 µPa @ 1m) (Chelonia Ltd 2012a). After two years of near continuous deployment the recalibration revealed that the sensitivity of the C-PODs had shifted between 0.0-1.1dB (mean of 0.55 dB). Regardless of such small changes, it is sensible to cross-correlate collected data across units and, if logistically possible, conduct field calibrations between units prior to embarking on a long-term monitoring study. The calibration and standardisation process are described in detail on the manufacturer’s website (www.chelonia.co.uk).

Deployment

The T-PODs and C-PODs can be left underwater, moored to the seabed, for up to four months at a time. They are small cylindrical devices in polypropylene casing, which are positively buoyant and powered by alkaline batteries. They can be moored to small weights, and deployed and picked up by hand from small boats in shallow and sheltered coastal environments (Simon *et al.* 2010), or be attached to large deep water moorings in shipping lanes and around wind farms (Verfuß *et al.* 2007; Tougaard *et al.* 2009b).

T-PODs have been used in several studies to assess the effect of varying types of fishing gear, pingers or chemically enhanced nets on porpoises (Cox *et al.* 2004; Carlström 2005) and bottlenose dolphins (Lauriano & Bruno 2007; Leeney *et al.* 2007). The presence and absence data recorded with the T-PODs have successfully been used in studies of environmental impacts of noise producing operations, such as for monitoring the effects of wind farm construction and operation (Teilmann *et al.* 2002); and both T-PODs and the new generation C-PODs have become one of the most widely used marine mammal monitoring tools for wind farm impact assessments in Denmark, Germany and The Netherlands, particularly at offshore sites where other survey methods are difficult or too expensive (Diederichs *et al.* 2003; Carstensen *et al.* 2006; Tougaard *et al.* 2009a; b; Lucke *et al.* 2009; Brandt *et al.* 2011). They have also been used to monitor effects of gas pipeline installations and tidal power generators (Fisher & Tregenza 2003; Englund *et al.* 2006; Philpott *et al.* 2007).

The click loggers detect echolocation clicks between 9 kHz and 170 kHz for the T-PODs and 20-160 kHz for the C-PODs, making them ideal for monitoring almost all odontocete species, except for the sperm whale whose clicks have energy at too low a frequency band. In addition to harbour porpoises and bottlenose dolphins, T-PODs and C-PODs have been used to detect various other species such as Hector’s dolphins (*Cephalorhyncus hectori*) (Rayment *et al.* 2009), finless porpoises (*Neophocaena phocaenoides*) (Jefferson *et al.* 2002), dusky dolphins (*Lagenorhynchus obscurus*) (Fisher 2005), Cuvier’s beaked whales (*Ziphius cavirostris*) and striped dolphins (*Stenella coeruleoalba*) (Ludwig *et al.* 2010), and Heaviside’s dolphins (*Cephalorhyncus heavisidii*) (Leeney *et al.* 2011), amongst others. Although they were not designed to discriminate clicks of various delphinid species from each other, they have successfully been used to study harbour porpoise and bottlenose dolphins simultaneously (Bailey *et al.* 2010; Simon *et al.* 2010).

Click detectors can reveal patterns of localised habitat usage and perform well in areas of both low and medium density as is the case with harbour porpoises in the Danish and German Baltic (Teilmann *et al.* 2002; Verfuß *et al.* 2007), and porpoises and bottlenose dolphins in relatively high density areas around the UK and Ireland (Berrow *et al.* 2009; Bailey *et al.* 2010; Simon *et al.* 2010). Currently a large international project is utilising over 300 C-PODs to estimate the density of the endangered Baltic harbour porpoise, which is present at very low densities over most of its range (Carlström *et al.* 2012). The click loggers are particularly useful in long-term monitoring and detecting trends in abundance across seasons and years. Visual surveys on the other hand, are typically conducted seasonally and often many years apart and thus have a lower ability to estimate long term trends.

1.9 Estimating density with static data loggers

Many conservation objectives encompass a requirement to estimate animal density in a given area. Marine mammal abundance estimates are traditionally achieved by line-transect surveys with *Distance* sampling methods using data from visual observations, either from headlands, ships or low flying airplanes (Akamatsu *et al.* 2008). Techniques also exist to extract information on animal positions from acoustic data, either from towed hydrophone arrays, or arrays of fixed hydrophones on the seabed (McDonald & Fox 1999; Barlow & Taylor 2005; Lewis *et al.* 2007).

In many areas static acoustic monitoring (SAM) devices, and specifically the automated click loggers, such as T-PODs and C-PODs have been selected as the study methodology of choice, usually due to inaccessibility of the location or lack of funds to carry out more expensive visual or acoustic line transect surveys. Its value as an additional method to visual surveys has been widely recognised, and there is huge demand to develop SAM further, especially in the field of density estimation. Tougaard *et al.* (2006) were the first to explore the idea of using T-PODs for density estimation, conducting preliminary studies on the radial detection probability and distance detection function of the T-POD (Tougaard *et al.* 2006). This was a breakthrough study utilising the SAM device as a point sample location, developed further by Kyhn et al. (2012), who demonstrated the ability to estimate detection probability and calculate density estimations with T-PODs for harbour porpoises.

To develop static data loggers for the application of density estimation requires using each SAM unit as an individual sampling point. The data logged can either be collected over a continuous time period or divided into snapshots of shorter time periods. The analytical approaches vary depending on the detection target, but what is required is exactly the same as for the other passive acoustic studies described above: the known point sample area, termed ‘effective detection radius’ or EDR, derived from the detection function, the rate of acoustic cue production and its decay, and the detection capabilities of the data logger used.

If individual animals cannot be distinguished using acoustic data, an alternative density estimation method exists based on detecting acoustic cues instead of animals themselves (Marques *et al.* 2009; Küsel *et al.* 2011), a method commonly used for song-birds obscured by vegetation. The vocalisations of birds are counted instead of the birds themselves, and converted into abundance using song rates (Buckland *et al.* 2001). For this method further auxiliary data on cue rates and vocal behaviour are required in addition to the detection probability. Techniques have also been developed to estimate animal density from fixed sensors without the need to estimate animal position and distance from the recorder (Marques *et al.* 2010).

1.10 Developing data loggers into an effective monitoring tool

Effect of distance from data logger and the source level of vocalisations on detection probability

The newer C-POD train detection algorithm detects a wider variety of signals, not just the NBHF clicks, and has less variability across units. The software now allows more detailed assessment of the resulting train data, including manual verification of individual click trains and species (Dudzinski *et al.* 2011). The detection range of the T-POD and its optimum settings for porpoises and dolphins have been studied to some extent (Philpott *et al.* 2007; Simon *et al.* 2010; Elliott *et al.* 2011b), but no such data have yet been published for C-PODs. In previous studies with T-PODs where acoustic data have been validated with visual observations, bottlenose dolphins have been detected from 1246 m (Philpott *et al.* 2007) and 1313 m away (Elliott *et al.* 2011b), and the effective detection radius (EDR) for dolphins estimated at 266 m (95% CI 222-317 m) (Elliott *et al.* 2011b). For harbour porpoises, the effective detection radius with T-PODs has been calculated to be between 22 and 104 m depending on the T-POD version (Kyhn *et al.* 2012).

Playback studies have been conducted with artificial porpoise-like clicks to estimate detection ranges and effective detection radii for C-PODs (Brundiers *et al.* 2012) but no studies on the detection probability of wild animals with C-PODs have been published so far. Apart from ambient noise and distance from datalogger, the source level of emitted clicks affects how well and how far away they can be detected (Au *et al.* 2007; Kyhn *et al.* 2009; DeRuiter *et al.* 2010). This concept can be explored through the basic passive sonar equation, which, in its various forms, describes the performance of a sonar system (Au & Hastings 2008; Zimmer 2011). It enables the estimation of how far a sonar device (in this case the C-POD) will be able to hear and detect the sound producing animal. This is achieved by utilising the relationship between acoustic intensity (dB) at one meter from the source (source level = SL), the amount of intensity (dB) lost during transmission from source to the receiver (transmission loss = TL), and the received acoustic intensity (dB) (received level = RL). In one of its simplest forms this can be expressed as

$$\mathrm{RL} = \mathrm{SL} - \mathrm{TL}.$$

However, only those signals which are above both the equipment detection threshold (DT in dB) and the background (ambient) noise level (NL in dB) can be detected. This can be expressed as

$$\mathrm{RL} = \mathrm{SL} - \mathrm{TL} > \mathrm{NL} > \mathrm{DT}$$

The properties of the receiver (the C-POD) are of interest here, including the threshold at which the C-POD is able to detect clicks (and correctly classify them) and the range that they can effectively operate, which of course depends on the noise levels of the deployment site.

Studies have attempted to measure the source levels of clicks emitted by both harbour porpoises (Villadsgaard *et al.* 2007) and bottlenose dolphins (Wahlberg *et al.* 2011) in the wild. Studies using C-PODs should aim to determine the extent to which the detection distance and probability are affected by changes in source levels of vocalisations, and crucially, how variable the emitted source levels are for the target species.

Effects of behaviour, group size and echolocation rate on detection probability

Detection of echolocation clicks by the data loggers is not only dependent on animal distance from the data logger, noise levels and the source level of acoustic emissions; the vocal behaviour of the animal may also affect detection if vocalisation rate, acoustic beam pattern and orientation and other movement patterns vary between different behaviours. For example, resting animals are likely to vocalise less, making them less detectable to the loggers (Linnenschmidt *et al.* 2012).

Several studies have looked at the effect of group size on detection rates with acoustic devices (Akamatsu *et al.* 1992, 1994, 2008). Some studies found no effect of group size on bottlenose dolphin and Hector's dolphin detections (Philpott *et al.* 2007; Rayment *et al.* 2009) similar results were reported with harbour porpoises (Koschinski *et al.* 2008). However, increased group size was found to be correlated with increased detections of Yangtze finless porpoise (*Neophocaena phocaenoides*) (Wang *et al.* 2005). Contrasting findings have been made with one of the largest echolocating dolphins, the orca (*Orcinus orca*), where the echolocation rate per individual decreased with increasing group size, suggesting that individuals share information within a group (Barrett-Lennard *et al.* 1996), interpreting echolocation signals of others (Dawson 1991). This could potentially result in the number of clicks generated by a group being relatively constant and independent of the number of members. For humpback dolphins, the number of vocalisations (whistles and echolocation clicks) increased with group size (Van Parijs *et al.* 2002).

Some studies suggest that porpoises in particular produce clicks almost continuously (Akamatsu *et al.* 2007; Verfuß *et al.* 2009). However, recent studies with captive porpoise have found that harbour porpoises can remain silent for up to 20 minutes at a time (Linnenschmidt *et al.* 2012). A C-POD study on bottlenose dolphins in Turkey (James *et al.* 2012) found periods with a distinct lack of echolocation within the diel cycle. Silent animals will not be detected, so this must be factored into the research design of any acoustic study, especially if it is known that there are certain times of the day or tidal cycle when the animals might be more vocal than others (Akamatsu *et al.*

1992, 1995). Increased vocalisations during night time have been found for porpoises with T-PODs (Carlström 2005; Todd *et al.* 2009) and acoustic tags (Linnenschmidt *et al.* 2012), although some studies found no such increase (Kastelein *et al.* 1995). Investigating how group size and behaviour affect the rate of vocalisations, and subsequently, the detection probability of the study species, would substantially strengthen inferences that can be drawn from the click detector data (Rayment *et al.* 2009).

Quantifying the quality of data recorded with C-POD

As detailed earlier, the C-PODs are click detectors designed to detect clicks which stand out from background noise and which then use a train detection algorithm to identify cetacean vocalisations (Dudzinski *et al.* 2011). To enable high quality data to be produced only those clicks that can be assigned to distinctive click trains are used. Furthermore, click trains are also classified for purposes of species identification. Consequently, some clicks and click trains will inevitably be excluded from the final output to ensure a low rate of false positive detections. As neither the click detection process nor the train detection algorithm is available for public inspection, researchers must test data empirically to fully understand what proportion of echolocation clicks may be missed. Understanding what kinds of clicks maybe missed by the C-POD and how this will affect the data collected is crucial for effective interpretation of monitoring data.

Identifying behavioural information from C-POD data

If the echolocation click or click train carries behavioural information, it may be possible to distinguish behaviour with click loggers. Studies of echolocation rates for harbour porpoise found that these typically varied with water depth and location, reflecting possibly either porpoise behaviour or prey abundance (Cox *et al.* 2004), but most likely both. Some previous studies have attempted to describe communication signals of echolocating cetaceans from the click characteristics by assessing the variation in the inter-click intervals (ICI) of the echolocation clicks logged by T-PODs and other hydrophones (Koschinski *et al.* 2008; Clausen *et al.* 2010). In addition to the communication clicks, the echolocation clicks themselves vary between different functions, especially those emitted during feeding or foraging (Verfuß *et al.* 2009). By investigating changes in the ICI, train duration, and the total number of clicks per time unit, it may be possible to identify potential feeding events from the click train data, and consequently identify critical feeding areas and trends in feeding patterns.

1.11 Aims and objectives of this study

Static acoustic monitoring with data loggers is already an established methodology for many species of cetaceans. Density estimation with acoustic methods has had great successes with terrestrial mammals such as elephants (Thompson *et al.* 2009), as well as large whales using extensive hydrophone arrays across ocean basins (Marques *et al.* 2012), but smaller scale static systems are also becoming more popular. This thesis assesses one method of monitoring of two of the most common cetacean species in Wales, the bottlenose dolphin (*Tursiops truncatus*) and the harbour porpoise *(Phocoena phocoena*). The study focuses on a popular static acoustic monitoring (SAM) method, the C-POD, widely used in cetacean monitoring studies due to its practicality and cost-effectiveness. It is increasingly used either in place of, or simultaneously with, traditional visual methods, to assess animal presence and habitat use, and can facilitate mandatory monitoring of protected species within marine protected marine areas such as SACs.

Regardless of its popularity, some questions on its capabilities remain unresolved. Although C-PODs are in common use by many research projects, there have been no published results on the ability of the device to detect the vocalisations of the two species, including types of clicks detected, maximum detection threshold and range and the effective detection area. A gap exists in our knowledge on how the C-POD's hydrophone performs in detecting clicks, as well as what proportion of detected clicks the automated train detection algorithm classifies as cetacean click trains. Likewise, questions remain on the performance of individual C-PODs in comparison to each other. There is also a critical lack of information on the effect of group size and behaviour on dolphin and porpoise vocalisations, particularly of call rates and silent periods, which will all affect C-POD detections, and be of crucial importance to any studies attempting to estimate animal density with these devices.

The general aim of this study was to increase our knowledge of how static click loggers detect harbour porpoises and bottlenose dolphins, specifically by examining the performance of both the click detection and the train classification algorithm. The overall hypothesis is that C-PODs are capable of detecting the echolocation clicks of both bottlenose dolphins and harbour porpoises but that their detection probability is affected by animal behaviour, and group size. Furthermore, we hypothesise that although C-PODs probably do not detect *all* echolocation clicks emitted they are still able to record enough detail to enable feeding and foraging behaviour to be distinguished from other activities.

To address these hypotheses the thesis describes the detection probability as a function of distance and, for the harbour porpoise, the source level. The study also examines how group size and behaviour affect the detectability of bottlenose dolphins, comparing C-POD detections with simultaneous and broadband recordings, and assesses whether the loggers can be used to discern porpoise and dolphin behaviour.

It was not possible to study the two species in an exactly the same manner. Insufficient visually observed porpoise data were acquired to examine the effects of group size and behaviour on porpoise detection probability and unfortunately no successful recordings of wild harbour porpoise echolocation clicks were made. Likewise it was not practical to conduct a playback study with simulated bottlenose dolphin clicks because of the enormous variability in dolphin clicks, making it difficult to characterise a ‘typical’ dolphin click. Consequently the research objectives and methodologies are slightly different for the two species.

Specific objectives of the research, and more detailed hypotheses addressed, were:

- To define the optimum distances at which the C-POD detects harbour porpoise echolocation clicks by estimating the effective detection radii and effective area using artificial and real playback signals at various distances and source levels
- To define the optimum distances at which the C-POD detects bottlenose dolphin echolocation clicks by estimating the effective detection radii and effective area using visual observations of wild bottlenose dolphins
- To assess the performance of both the click detection of the C-POD and the train classification algorithm of the accompanying software for harbour porpoises by

comparing the detections of the playback study on both raw click data files and those produced by the train classification algorithm

- To test the hypothesis that behaviour and group size affect acoustic detection of bottlenose dolphins, and to evaluate the effect of both behaviour and group size on the effective detection distance of dolphins with C-PODs
- To test the hypothesis that C-PODs do not detect all kinds of echolocation clicks by examining the difference between clicks recorded by the C-POD with those recorded with a broad-band hydrophone
- To determine whether bottlenose dolphin and harbour porpoise behaviours, particularly feeding, can be distinguished from C-POD data
- To make recommendations on C-POD use for acoustic monitoring of bottlenose dolphins and harbour porpoises

Chapter 2 describes the detection probability of harbour porpoises for C-POD data loggers as a function of distance and source level, through extensive field-experiment using artificial and real recorded porpoise clicks. It also assesses the performance of both the click detection of the C-POD and the train classification algorithm of the accompanying software.

Chapter 3 explores the C-POD detection probability of bottlenose dolphins with regards to the effects of distance from the data logger, animal behaviour, and group size. It also assesses the performance of paired C-PODs in comparison to each other, and whether variation between individual C-PODs will have an effect on the overall detection probability.

Chapter 4 compares bottlenose dolphin echolocation clicks recorded from free swimming animals using a broadband hydrophone with data logged by C-PODs, in order to examine differences in the logged click characteristics between the two, and to assess whether certain types of clicks may not be recorded by the data logger.

Chapter 5 compares C-POD data with visual observations of bottlenose dolphin and harbour porpoise behaviour to assess whether SAM data can be used to extract behavioural information of the target species.

And finally, **Chapter 6** summarises the findings of the thesis, setting them in the context of current developments in acoustic monitoring, and provides recommendations for further research.

Chapter 2 DETECTION PROBABILITY OF HARBOUR PORPOISE (*PHOCOENA PHOCOENA*) FOR C-PODS FROM PLAYBACK EXPERIMENTS

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Author's contribution

This experiment was part of a fieldwork organised jointly by Jens Koblitz and myself from the German Oceanographic Museum (GOM) to acoustically localise and track cetaceans with a hydrophone array. It was funded by the German Federal Ministry for the Environment, Nature conservation and Nuclear Safety, Bangor University and myself. Jens Koblitz, Len Thomas, Katharina Brundiers and I designed the experiment and the playback methodology based on an earlier playback trial conducted in Germany by Jens and Katharina.

Jens, Katharina and the team from GOM designed, built and transported from Germany to Wales an array of hydrophones, several transducers, and all the recording and playback equipment. I organised the day to day logistics of the fieldwork, the two boats used and the team of volunteers (please see acknowledgement) for land and boat work. Kati and I organised the deployment of C-PODs and T-PODs, and Kati was in charge of setting and maintenance of the PODs.

Kati, Winnie Courtene-Jones and I conducted the visual analysis of the C-POD data, although Kati did the lion's share of that work. I compiled the data and conducted all the analyses and wrote the manuscript. Len Thomas helped with statistical analysis and R script, and comments from Jan Hiddink and Peter Evans greatly improved the structure of the manuscript. All authors proofread the manuscript and offered helpful suggestions before submission to the Journal.

2.1 Abstract

Harbour porpoises (*Phocoena phocoena*) have been extensively monitored using static acoustic data loggers, but few studies have quantified what fraction of animal vocalisations these devices capture and how animal distance and source level affect their detection probability. Knowing the effective detection area of the device is imperative for designing and implementing effective monitoring studies. Here we assessed the effectiveness of the C-POD's hydrophone in detecting porpoise clicks using artificial signals played at varying distances and source levels to the data loggers, and measuring the fraction of acoustic detections recorded in each C-POD. Additionally, to assess the C-POD's performance for wild animal signals, recorded porpoise clicks were played at increasing distances from the

C-PODs and their detection rate on each device was calculated. Furthermore, the performance of the C-POD software in correctly identifying porpoise click trains was examined. Generalized Additive Mixed Models (GAMM) were used to create the detection function and estimate the effective detection radius (EDR) and effective detection area for each C-POD for both artificial and real porpoise clicks. Both source level and distance from data logger influenced the detection probability, whilst differences between C-PODs were evident across the study. Maximum distance for detecting real porpoise clicks was 566 m. The average EDR for the real recorded porpoise sequence using a directional transducer was 188 m (95% CI: 135-241) and the effective detection area 0.111 km^2. For detections which were correctly assigned as harbour porpoise trains, the EDR was reduced to 72 m and the area to 0.016 km^2.The mean EDR for artificial porpoise like clicks at 184dB re 1 µPa @ 1m (peak-peak) was 187 m (95% CI: 173-200) resulting in an average effective detection area of 0.1098 km^2. Differences between C-PODs were likely due to site specific variation in environmental characteristics. Such differences in detection probability will affect monitoring studies and specifically the density estimates based on these figures and estimating an average EDR across several C-PODs for each study site is recommended. The method described here is applicable to most cetaceans recorded by C-PODs and will greatly facilitate statutory monitoring of protected species.

2.2 Introduction

The harbour porpoise (*Phocoena phocoena*, Linnaeus, 1758) is one of the most common cetaceans off the North East Atlantic coastline. It is the only regularly seen cetacean in the Baltic where the subpopulation is increasingly threatened by human activities and listed as ‘critically endangered’ in the IUCN Red List (Hammond *et al.* 2008). To effectively conserve and manage porpoise populations it is imperative that the population status, including the density is assessed. The harbour porpoise is small and inconspicuous and difficult to monitor using traditional visual techniques because of its size and cryptic behaviour. In recent years many studies have used static acoustic data loggers to monitor the presence of porpoises in both coastal and offshore areas (Verfuß *et al.* 2007; Todd *et al.* 2009). Harbour porpoise lends itself well to acoustic studies because it emits stereotypical high frequency, narrow-band echolocation clicks and produces near continuous vocalisations apart from short periods of rest (Linnenschmidt *et al.* 2012). Automated echolocation click loggers such as C-PODs and their predecessors, T-PODs record the times and duration of clicks. C-PODs also additionally log the frequencies of the recorded clicks. The specific software then classifies detected clicks into series of clicks called click trains, based on known characteristics of cetacean vocalisations. These trains are further categorised based on their likely origin: boat sonar, dolphin, or porpoise click trains, which the C-POD software’s species identification process calls “Narrow Band High Frequency“ (NBHF) click trains.

C-POD data are easy to analyse as daily or hourly detections, train durations or total number of trains and clicks detected. This type of data are now widely used in studies evaluating presence and absence of cetaceans (Verfuß *et al.* 2007; Bailey *et al.* 2010; Simon *et al.* 2010) and assessing disturbance to porpoises from wind farms, shipping, fisheries and coastal development (Carstensen *et al.* 2006; Carlström *et al.* 2009; Todd *et al.* 2009; Tougaard *et al.* 2009a; Brandt *et al.* 2011) but can also be used to estimate animal density (Kyhn *et al.* 2012).

To use C-POD data in density estimation, the area around the C-POD within which the porpoises are effectively detected, is calculated from the effective detection radius (EDR), derived from the detection function, which defines the detection probability of porpoises as a function of animal distance from the logger (Marques *et al.* 2009). Kyhn *et al.* (2012) calculated the EDR for harbour porpoises detected with T-PODs between 22 and 104 m depending on the T-POD version. The C-PODs outperform T-PODs in porpoise detection due to their more sensitive hydrophones and lower between-logger variation (Dudzinski *et al.* 2011). Although no studies have been conducted on the detection probability of real porpoises with C-PODs, the EDR for an artificial, porpoise like click of 176 dB re 1 µPa/V @ 1m (peak-peak) was found to range between 151-196 m in controlled field experiments (Brundiers *et al.* 2012). Many factors may affect the detection probability of cetaceans with acoustic data loggers, including animal behaviour and activity state, vocalisation rate, intensity and frequency of emitted sounds, direction of movement, and orientation in the water column. Animals searching prey on the seabed may direct their sonar beams into the sediment and resting animals are likely to vocalise less, making them less detectable to the loggers (Linnenschmidt *et al.* 2012). Besides these, ambient noise, water temperature, pressure and salinity as well as the physical characteristics of the immediate surroundings of the logger are likely to affect the detection probability of porpoise sounds, due to transmission loss of sound, absorption into sediment and potential shadowing from physical objects (Au 1993; Au & Hastings 2008; Zimmer 2011).

Furthermore, the C-POD’s ability to detect a cetacean click depends on several processes – firstly the detection and logging of the actual click by the hydrophone and secondly the correct identification of clicks into click trains of cetacean origin and thence into the correct species classification.

Because the EDR depends on so many physical characteristics, it is likely to vary at each study site, and ideally should be estimated for every site. Here we present a standardised method based on established distance sampling theory (Buckland *et al.* 2001) to estimate EDR for several C-PODs for one study site, which can be repeated at other locations, across varying environmental characteristics, such as bottom composition and water depth. However, this process can be costly and difficult to accomplish for many smaller projects with no access to required acoustic equipment. Therefore we hope that our results may be of use to other projects where estimating EDR is not practical or logistically possible.

The first objective of this study was to assess the performance of the data logger’s hydrophone in detecting porpoise clicks. This was done by playing back artificial, porpoise like clicks of varying source levels to the C-PODs at increasing distances from the loggers. The detection probability of each playback click was estimated as a function of increasing distance and decreasing source level. From this, the average effective detection radius of C-PODs for the playback signals was then calculated. An artificial signal was used to create a repeatable signal with a known source level that could be manipulated to cover the intensity range of harbour porpoise vocalisations.

The second objective was to examine the performance of the train classification and species identification software, and involved playing real porpoise click sequences to the C-PODs and calculating the detection rate not only of the clicks detected but also of identified trains.

2.3 Materials and methods

Eighteen tank calibrated acoustic echolocation click loggers (C-PODs) were deployed off New Quay, Wales, of which fifteen were single C-PODs bottom moored in five stations of three loggers each in a triangle formation, at depths of 13 - 20 m of water, approximately 50-75 m apart and further three C-PODs attached together were used as a control and deployed in the middle of each station for every playback trial (Figure 2.1). The control C-PODs were deployed at each station to assess potential variability in playback signal, and were deployed at each station before the playback trials begun. All the playbacks were conducted in sea states 2 or less, to ensure safety and stability of the recording set up and the accuracy of the distance measurements. A side scan survey of the area was conducted prior to the study, revealing a generally even, sandy bottom substrate.

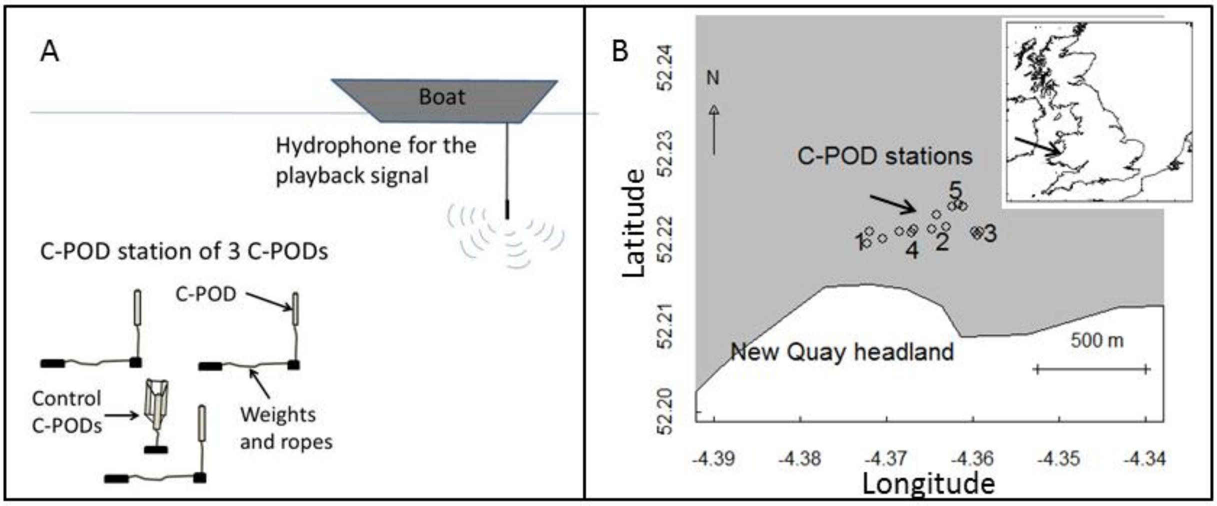

Figure 2.1 A diagram of a C-POD mooring set up for one station (A) and the map of the deployment site of all the C-PODs (B). Each station had three C-PODs moored on the sea bed and the three control C-PODs (C1, C2 and C3) were temporarily deployed in that station during the playbacks. The playback hydrophone was suspended from the boat.

Theoretical detection distance

To appreciate the effect of transmission loss on porpoise like signals, and to determine the required playback distances a simplified theoretical detection distance was modelled for a C-POD with a detection threshold of 114 dB peak-to-peak re 1uPa at 130 kHz detecting a typical harbour porpoise click at source levels from 178 to 205 dB re 1µPa peak-to-peak (Villadsgaard *et al.* 2007) in sea water of 20 °C. The model was constructed using the transmission loss (TL) based on spherical spreading (Zimmer 2011): $TL = 20*\log10(R) + (R)*a$, where R is the distance to animal in meters and a is the frequency-dependent absorption, estimated at ~0.04 dB/m at 135 kHz (Fisher & Simmons 1977).

Artificial porpoise-like signal

Series of artificial clicks were played back with an omni-directional transducer at various different source levels and distances from 0-1500 m from the C-PODs to assess the effect of varying intensity on detection probability and to estimate the effective detection area for porpoise signals for the C-PODs. Artificially constructed porpoise-like clicks were used to ensure standard, repeatable signal for which source level could be controlled. The signal consisted of 15 cycles of 130 kHz frequency, generated via National Instruments 6356 usb-box and played back using Labview software. The signals were fed through an amplifier (gain 26dB), which drove a Reson TC4033, and an omni-directional transducer with a projective sensitivity of 137 dB re 1 µPa/V for 130 kHz signal, suspended from the side of the boat to 2 m below water surface. The set up was powered using external car batteries via an inverter.

The playback consisted of four separate sequences. One playback sequence contained eleven blocks of ten clicks (90 ms duration with 60 ms between each block), each block with a different source level (SL), decreasing in 3 dB steps over a range of 30 dB from 176 dB re 1 µPa/V @ 1 m (peak-peak) to 146 dB re 1 µPa/V @ 1m (peak-peak). At each source level, ten clicks were emitted (Figure 2.2). To increase the source levels further and cover as much as possible of the range of source levels emitted by the porpoise, the first two sequences were played back with an additional 20 dB gain, in an attempt to achieve source levels up to 196 dB re 1 µPa/V @ 1m (peak-peak). Unfortunately, unknown to the playback operators at the time, the hydrophone used as the transducer could not cope with source levels higher than 184 dB re 1 µPa/V @ 1m (peak-peak) - which now remains the highest source level tested. It is also important to bear in mind that even this source level may have suffered some distortion and further testing of the reported source levels is required. However, at the time of writing this, the 184 dB re 1 µPa/V @ 1m used here was considered sufficiently accurate for this analysis.

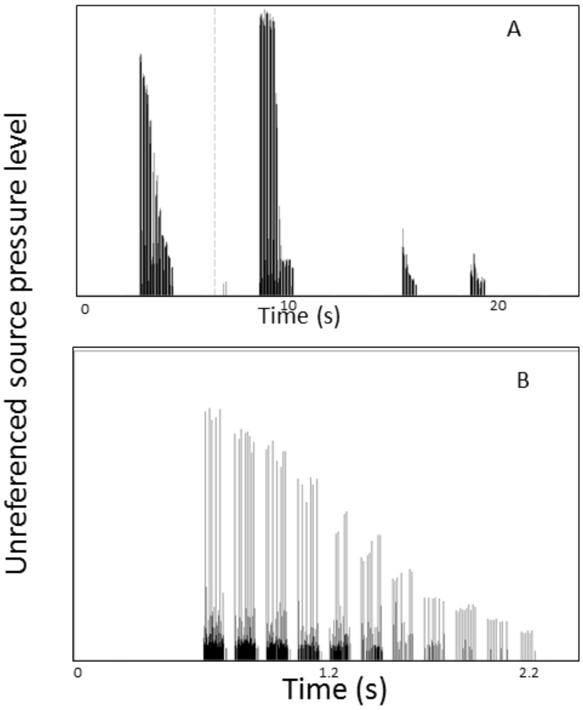

Figure 2.2 Artificial playback sequence as a screenshots from C-POD.exe: Above is a set of four sequences with first two sequences played with 20dB amplitude gain (A). Below is a zoomed in recording of a sequence where the 11 blocks of decreasing amplitude can be seen in progressively shorter length of clicks recorded in each block (B).

Real porpoise click

To assess the detection probability of actual harbour porpoise vocalisations, and the performance of the train detection algorithm as well as the hydrophone's ability to detect clicks, real porpoise clicks were recorded from captive porpoises at Fjord & Bælt Center, Denmark, and compiled into an 18 s long sequence of clicks. The recordings contained both weak and intense clicks, and the constructed signal had varying amplitude and frequency ranges, with source levels between 182 and 152 dB (peak-peak) re 1 µPa, representing some of the known variability in both click rate and source level of real porpoise vocalisations (Figure 2.3). It was played using a similar set up as above but without an amplifier and through a directional transducer, a Reson TC2130 with a transmitting sensitivity of 158.5 dB re 1 µPa/V @ 1 m (peak-peak) (for 130 kHz signal) and a projection directionality similar to a porpoise beam (12.25° for 150 kHz signal). The playbacks were played from distances ranging from 0 to 640 m from the C-PODs with an additional gain of 20 dB generated through the computer, resulting in a maximum source level of 179 dB re 1 µPa/V @ 1 m (peak-peak). A directional transducer was used to replicate a real porpoise to imitate the directionality and beam width of the animal. As opposed to the omni-directional transducer used with the artificial playbacks, this would emit sounds in narrow beam only. During playbacks it was moved from side to side in (arbitrarily selected) 90° angle, pointed towards the middle of each C-POD station, imitating the sweeping movement of a porpoise head (shown for finless porpoise by Akamatsu *et al.* 2010), whilst the playback boat was moving away from the station.

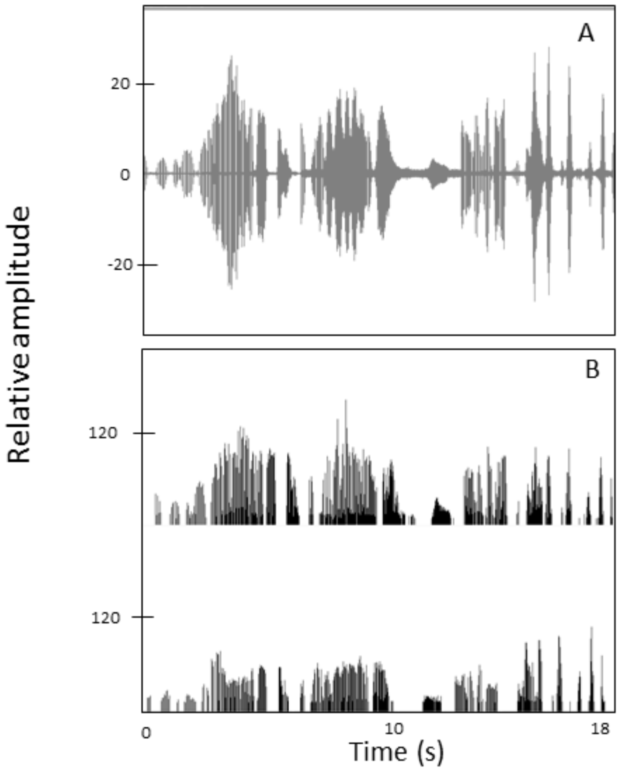

Figure 2.3 The porpoise playback click sequence (A) and the same sequence logged by two C-PODs simultaneously (B). Y-axis depicts a relative amplitude as recorded by the C-POD.

Play-back procedure

Each C-POD station contained three C-PODs, approximately 50-75 m apart and before the playback trials were commenced, the control station was deployed to the seabed, in the middle of the three C-PODs (Figure 2.1). The boat then moved away from the station with the tidal current, playing the signal at approximately 10-50 m steps from 0 to 1500 m distance for the artificial playbacks and 0-640 m distance for the real porpoise clicks, to achieve a dataset of clicks recorded on C-PODs with gradually increasing distances from the data logger to a distance where they were definitely no longer detected. The distance between the playback vessel and the C-POD was determined using the spherical law of cosines as follows:

$$d = \cos^{-1} (\sin(lat_1) .\sin(lat_2) + \cos(lat_1) .\cos(lat_2) .\cos(long_2 - long_1)) .R$$

where the position of the boat was defined as lat_1 and $long_1$ and the position of the C-POD was defined as lat_2 and $long_2$ and R is the mean radius of the earth (6371 km). Formulas were obtained and adapted from http://moveable-type.co.uk/scripts/latlong.html (Veness 2010).

Data analysis

The data were visually inspected using bespoke C-POD software (*CPOD.exe* v.2.026) to note whether each of the playbacks were detected by the C-PODs. For each artificial playback sequence, the C-POD raw click files (CP1 files) were examined and the number of clicks from each series and each block was counted. Only those playbacks with more than one click recorded out of each block of ten were used for the analysis. For the real porpoise click sequence, the observers noted whether or not the sequence was detected on the C-POD or not - only those playbacks with a clear recording of the whole or part of the sequence were considered as detected. For the real porpoise recording, also the classified train files (CP3 files) were examined to assess the performance of the train classification algorithm in identifying the playback sequence as a cetacean train and more specifically, a porpoise click train. The distance between the playback transducer and the C-PODs were calculated from the GPS latitude and longitude coordinates (Veness, 2012, www.movable-type.co.uk)

The curve depicting the probability of detecting a porpoise click, if within a distance *x*, is called the ‘detection function’ or *g(x)*. To estimate the detection function, from which the effective detection radius (EDR) could be calculated, the resulting datasets of detected clicks and sequences were analysed using a Generalized Additive Mixed Model (GAMM) in mgcv and gamm4 package in R (Wood 2006) with binomial error structure. ‘Detected’ or ‘not detected’ was the binary response variable and distance and source level the explanatory variables with smoothers, C-POD ID as an explanatory factor variable and playback as random variable. The playbacks were not independent as each playback was used multiple times – once for each different C-POD. Variance and 95% confidence intervals (CIs) were calculated using a nonparametric bootstrap, treating each playback as the unit for resampling with 1000 bootstrap replicates.

Effective detection radius and effective area

The effective detection radius (EDR, also denoted $\hat{\rho}$), was calculated by obtaining the *average* probability ($\hat{P}$) of detecting each click or click sequence within distance w of the data logger, derived from the detection function (Kyhn *et al.* 2012) assuming uniform probability of detection from around the data logger and by integrating out the distance:

$$\hat{P} = \int_0^w \frac{2\pi x g(x)dx}{\pi w^2}$$

$$= \frac{2}{w^2}\int_0^w xg(x)dx \qquad (1)$$

The effective detection radius, $\hat{\rho}$, was then calculated using 500 m as the truncation distance:

$$\hat{\rho} = \sqrt{\hat{P}w^2} \qquad (2)$$

The effective area was calculated as a circular plot around the C-POD using EDR as the radius (r):

$$A = \pi r^2 \qquad (3)$$

2.4 Results

Artificial playbacks were successfully conducted on all five stations, but playbacks with real click data were only conducted on four stations (1, 2, 3, 4) due to time and weather constraints. Although all bottom moored C-PODs yielded full datasets, of the control deployment with the three closely attached C-PODs, only one functioned throughout the entire playback experiment – the other two were not restarted properly after having been downloaded and only limited data were acquired from them.

Theoretical detection distance

The modelled detection distance by a C-POD for an average porpoise click of 135 kHz was estimated at 337 m for 178 dB, 554 m at 191 dB and 819 m for a sound of 205 dB source level (all re 1µPa peak-to-peak) (Figure 2.4). Based on this relatively simple model for ideal conditions, and for “on-axis” clicks (the most intense clicks emitted within the narrow acoustic beam of the animal, as opposed to “off-axis” clicks which can originate off the main acoustic beam), we were confident that conducting the playback at distances up to 1500 m would cover the entire range of the C-POD.

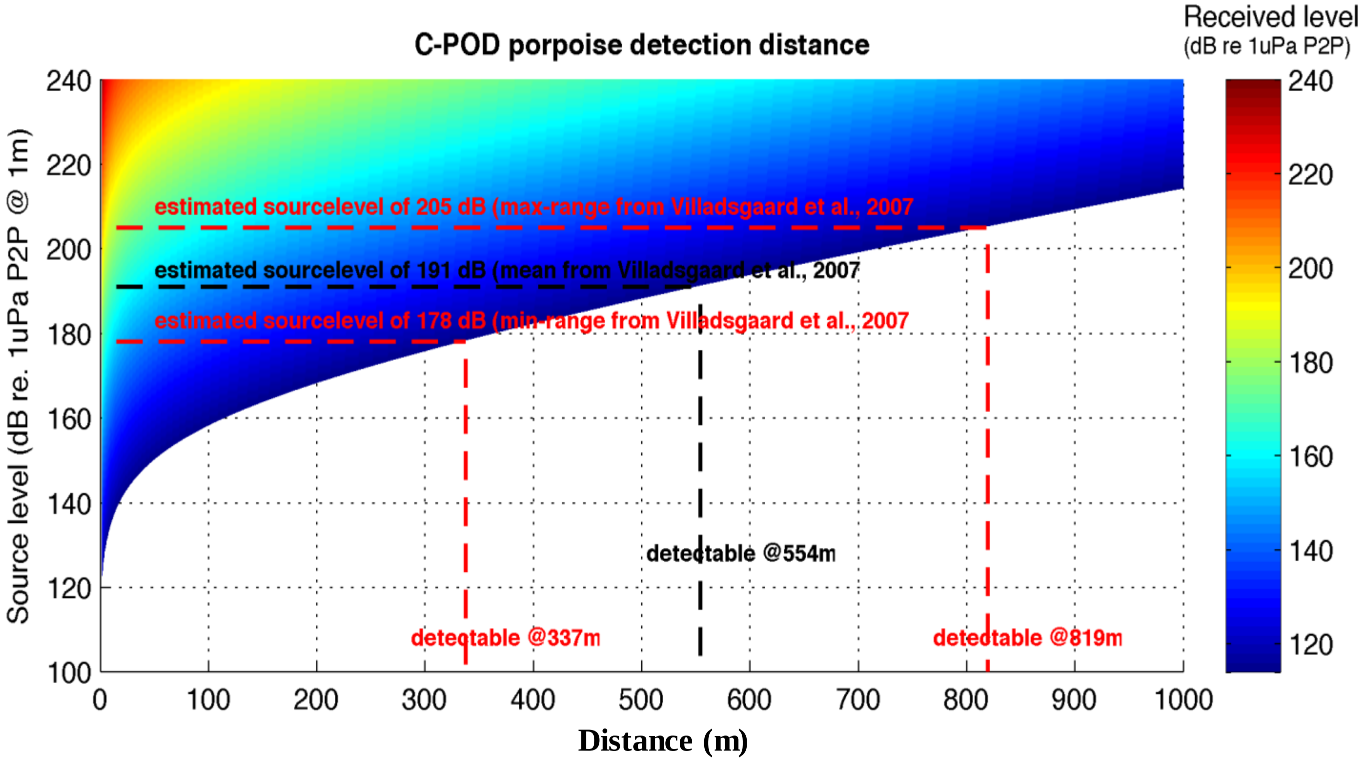

Figure 2.4 Theoretical detection distance for a porpoise click at 135 kHz for different source levels based on spherical spreading loss.

Playbacks with artificial porpoise clicks

For the artificial playbacks, the detection of every click sequence was assessed on all the C-PODs, as the use of omni-directional transducer meant that the sound would travel to all directions. Thus a total of 343 artificial playbacks (4 sequences of 11 blocks each consisting of 10 clicks, each block emitted at a different source level) played at the 18 C-PODs produced over 16000 recorded playback blocks which were visually assessed. Only playback source levels up to 184 dB re 1 µPa @ 1 m (peak-to-peak) were usable for the analysis due to saturation of the transducer to the extreme high voltages at the highest source levels.

The dataset consisted of a binary response variable (whether each click that was emitted was detected), explanatory variables (distance from data logger, source level and C-POD

ID) and a random effect of each playback. The GAMM was run separately for each station. For each dataset, the model with lowest AIC values included all three variables and the random effect. The smoothers for the covariates of distance and source level were significant for all stations ($P < 0.001$). Additionally, the parameter, C-POD ID, significantly contributed to the model for each dataset. The models for each station explained between 39.3 and 68.8 % of the deviance in the datasets. Appendix 2.1 lists the results of the GAMM. As expected, there was a negative effect of increasing distance and decreasing source level of the playback signal on the detection probability (Figure 2.5). The detection function curves were similar in shape for all C-PODs apart from those in station 2, which had peaks of higher detection probability at longer distances than any other C-POD. Despite careful checking, no anomalies or outliers in the dataset were discovered. A possible explanation for this could be an error in the distance calculations. For the rest of the C-PODs, the detection probability falls sharply between 100 and 200 m distance from the data logger, although slight variations between C-PODs are evident. The effect of source level on detection probability increases sharply for clicks over 160 dB re 1 µPa/V @ 1m (peak-peak) for all C-PODs, apart from station 2, where the source level seems to have little effect on detection probability, further indicating an existence of a potential error in the dataset. Figure 2.6 depicts the estimated smoothers for each covariate for station 4. The smooth plots for each station are listed in the Appendix 2.3.

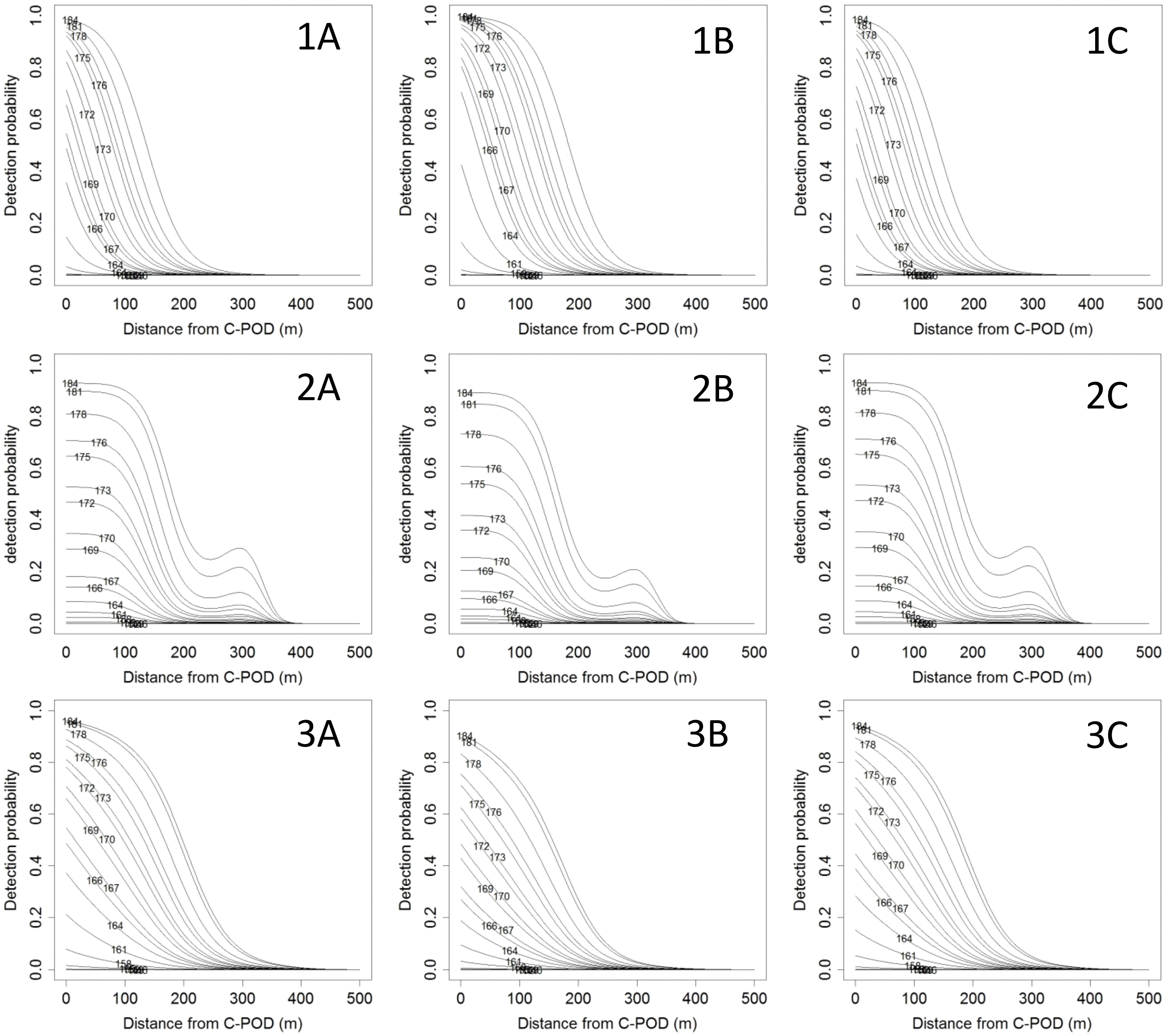

Figure 2.5 Fitted probability curves for the detection of artificial porpoise-like playback clicks at different distances for source levels between 184 and 147 dB re 1 µPa/V @ 1 m (peak-peak) for all C-PODs. Each line depicts the fitted probability for one dB value.

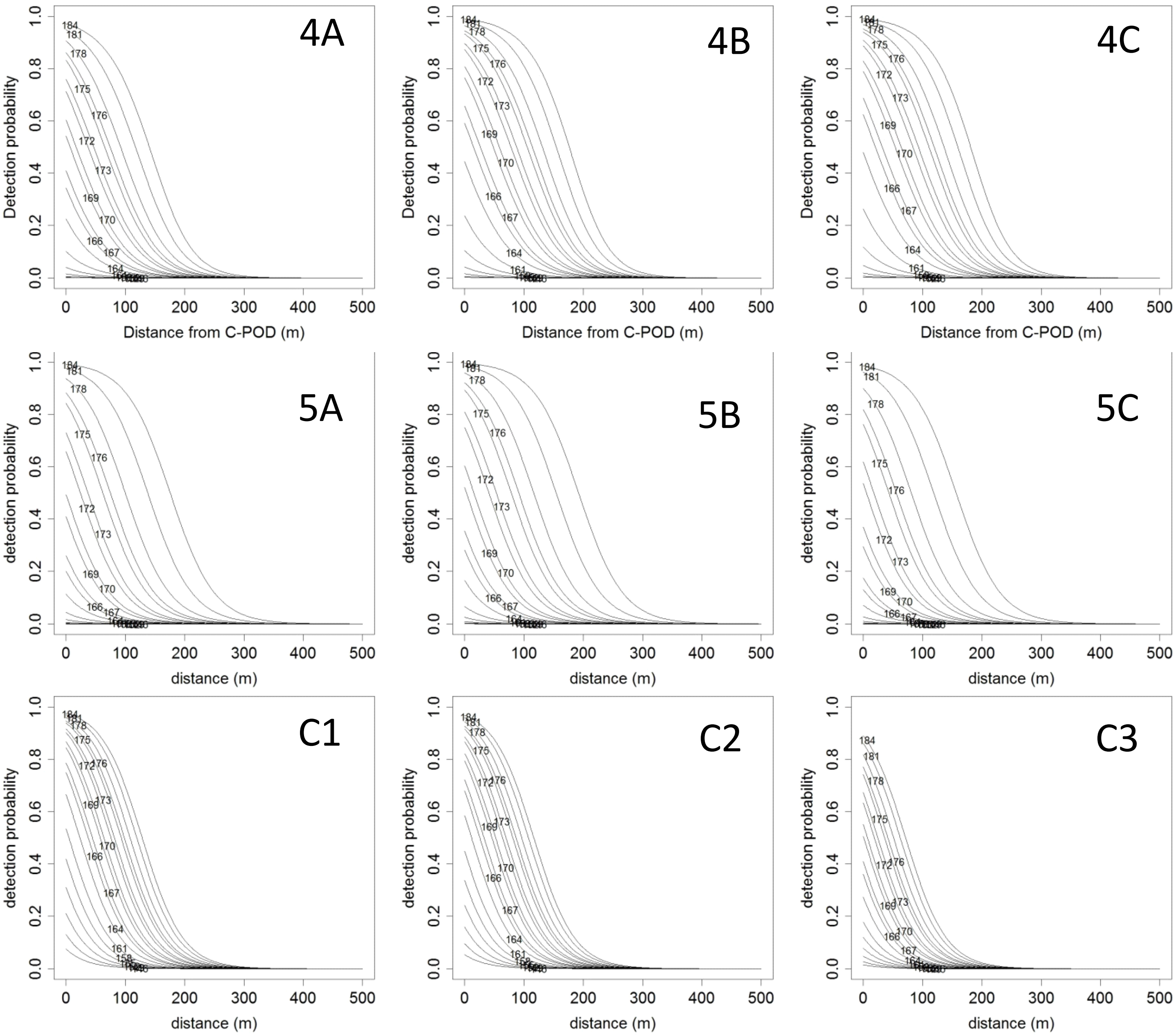

Figure 2.5 (continued from previous). Probability of detection of artificial porpoise-like playback clicks at different distances for source levels between 184 and 147 dB re 1 µPa/V @ 1 m (peak-peak) for all C-PODs.

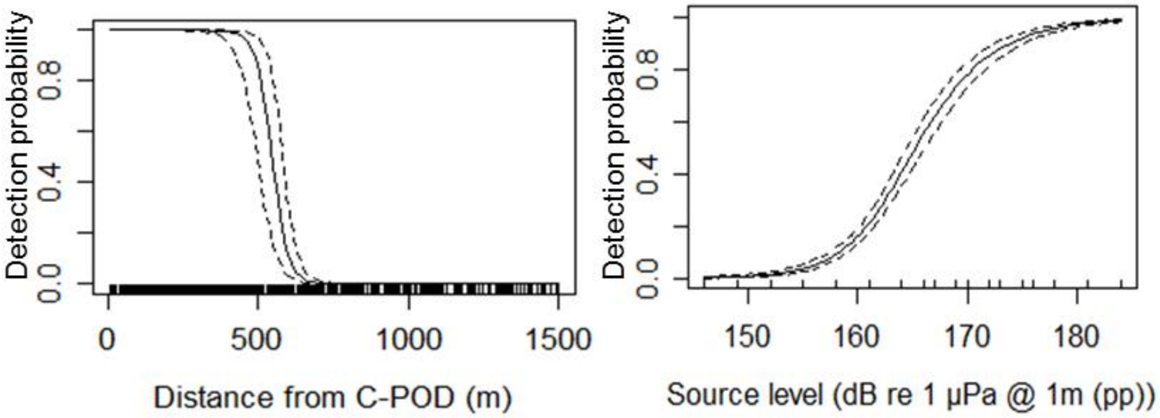

Figure 2.6 The effect of distance from C-POD and signal source level on the detection probability of artificial playback signal in the GAMM model for Station 4. Dashed lines indicate two standard errors; y-axis is transformed to the response variable scale, and the lines on x-axis show the distribution of the values of predictors in the underlying dataset.

The calculated effective detection radii (EDR) for artificial clicks with the highest emitted source level (184dB re 1 µPa @ 1m (peak-peak)) varied from 207 to 142 m for the main C-PODs, with a mean of 187 m (95% CI: 173-200) and an average effective detection area of 0.1098 km^2. The EDR for the control C-PODs was much lower varying from 137 to 94 m, probably due to the different mooring set up with three C-PODs in close proximity to each other, which may have caused a shadowing effect on the hydrophones.. A 20 dB reduction in the source level of the artificial playback signal reduced the effective detection radius to 107 m, and clicks of source level 170 dB re 1 µPa @ 1m (peak-peak) or less had less than 100 m detection radius (Figure 2.7). The EDR values with 95% confident intervals (CI) and coefficients of variation (CV) for each C-POD for different source levels are listed in Appendix 2.3.

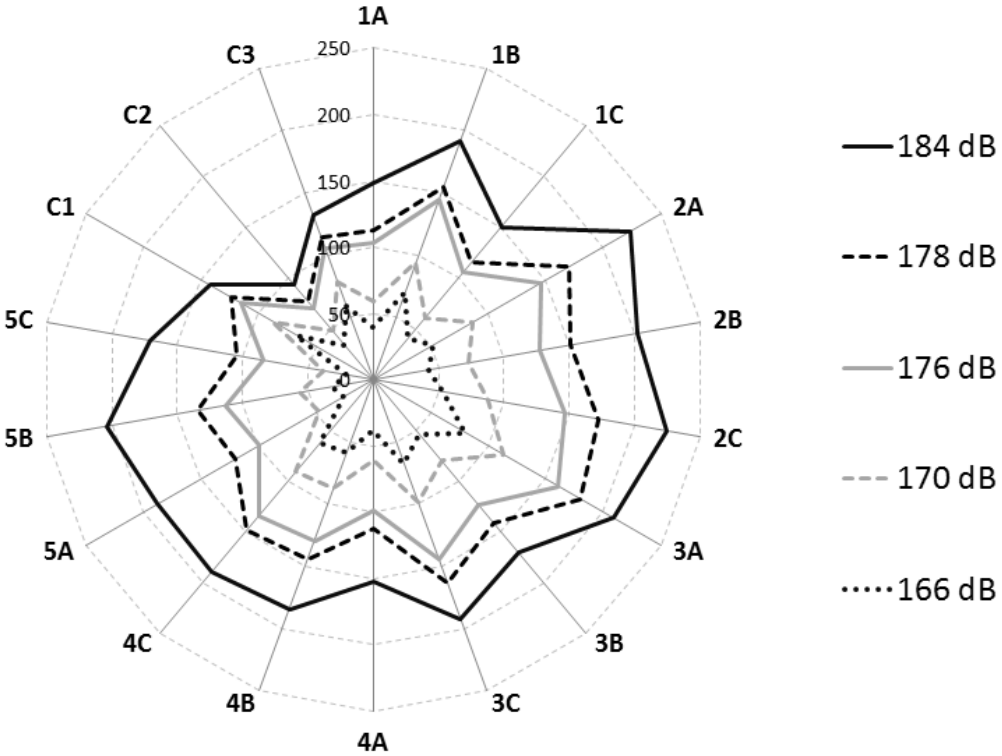

Figure 2.7 The estimated average effective detection radii for different source levels for a single artificial porpoise click for each C-POD. C1, C2 and C3 were the control C-PODs, re-deployed at each station for the duration of the playback trials. Axis in meters. Source level reference dB re 1 µPa/V @ 1m (peak-peak).

Playbacks with real porpoise clicks

For the real playbacks, only those sequences played back at the direction of each station were usable, as the directional transducer would only emit sounds at a narrow beam width of 12.5°. This resulted in a total of 715 porpoise click sequence times to be assessed across distances up to 640 m from the data loggers. From the 715 total sequences, 289 (40 %) were recognised and logged as clicks by the C-PODs, 186 (26 %) identified as train and 149 (21 %) classified as harbour porpoise trains. The average rate of detection for clicks in raw data files (CP1s) was 40 % across the C-PODs.

The GAMM was run for three datasets: 1) detections of playback sequence on raw click files (CP1); 2) detections as trains (CP3); and 3) detections as porpoise trains (CP3). For all three, the detection probability of the playback sequence was significantly affected by distance, and the GAMM model with lowest AIC values included the C-POD ID as a factor variable and the playback as random effect. The smoother for distance was significant for all raw datasets ($P < 0.001$). The GAMM results are displayed in Appendix 2.1. The three models explained between 13.3 and 22.2 % of the deviance in the datasets, notably less than the models for the artificial playbacks. Figure 2.8 depicts the detection function curves for the real porpoise playback sequences for all stations, for raw click data as well as for classified trains. Lowest detection probabilities for click data (CP1) were recorded for C-PODs 1A, 1C, 2A and 2B. High detection probability of clicks did not always correspond to high detection of classified porpoise trains (see 4C in Fig. 2.8).

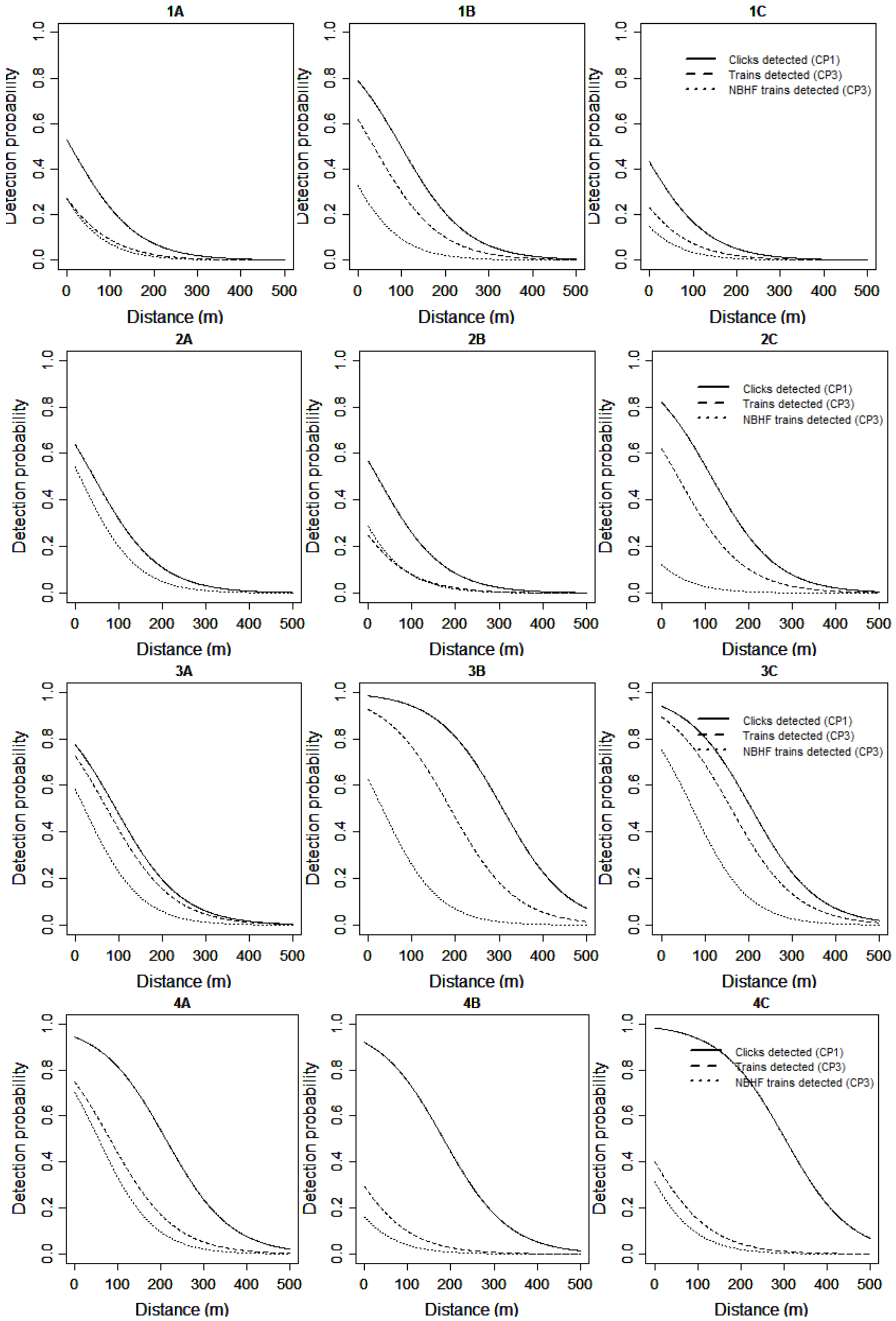

Figure 2.8 Detection probability of real harbour porpoise clicks recorded by C-PODs and the probability of click trains classified using the C-POD.exe software for each C-POD (A,B,C) at each station (1,2,3,4). Solid line = all clicks detected, dashed line = trains classified and dotted line = trains classified as porpoises (NBHF).

The calculated mean effective detection radii (EDR) of real porpoise signals was 188 m (95% CI: 135-241) for all clicks detected (CP1 files), 116 m (95% CI: 80-152) for classified trains and 72 m (95% CI: 52-92) for classified porpoise trains (Figure 2.9). This reflects the increasing detection threshold required for the train and species classification, a task that is more demanding of higher signal to noise ratio. The calculated effective detection area, using the clicks detected from the raw click files (CP1), was 0.111 km^2. When taking only those detections into account that were correctly assigned as harbour porpoise trains by the algorithm, the reduced EDR of 72 m yielded an effective area of 0.016km^2. The mean difference in EDR from detected clicks to correctly detected species was 105 m (95% CI: 66-144), demonstrating the rather larger difference in how the clicks are detected by comparison to the correct species identification.

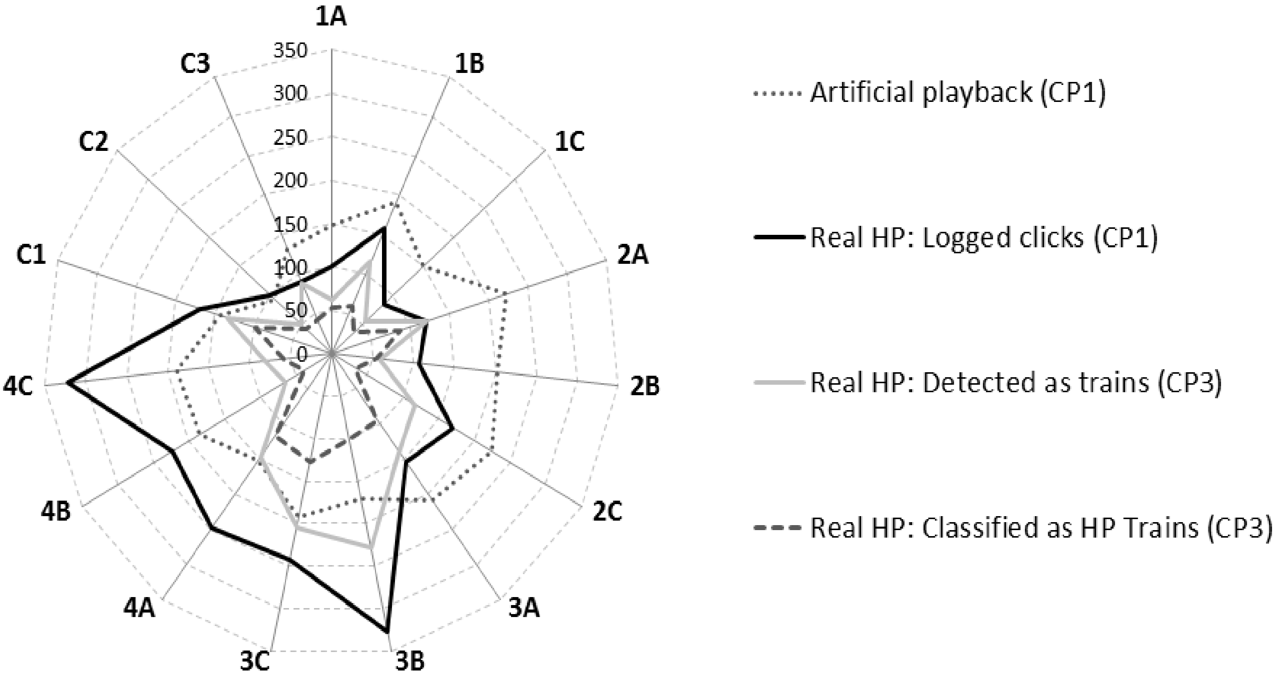

Figure 2.9 The estimated effective detection radii for real porpoise playback sequence for all logged clicks (black line), for all detected trains (grey line), and for all detected porpoise trains (dashed line). The average EDR of a single artificial click for the highest source level is shown with dotted line. C-PODs C1, C2 and C3 were the control C-PODs, re-deployed at each station for the duration of the playback trials. Axis in metres.

Notably, the control C-PODs had the lowest EDRs and detection distances in both experiments, most likely due to their method of deployment. This consisted of attachment of three C-PODs in close proximity to each other, which we now believe probably decreased their detection rates due to shadowing effect. Hence the EDRs of the control C--PODs were not used to calculate the overall means and confidence intervals for either experiment.

Despite the between-C-POD variation in detection probability for the three different datasets: raw clicks, click trains and porpoise trains, the control C-POD displayed a very gradual and regular decrease in detection probability across the sites (Figure 2.10). Furthermore the control C-POD showed little difference in the overall detection probability across each station, with the exception of porpoise train detections at station 4 (Figure 2.11). The EDR values with 95% confident intervals (CI) and coefficients of variation (CV) for each C-POD are listed in Table 2.1.

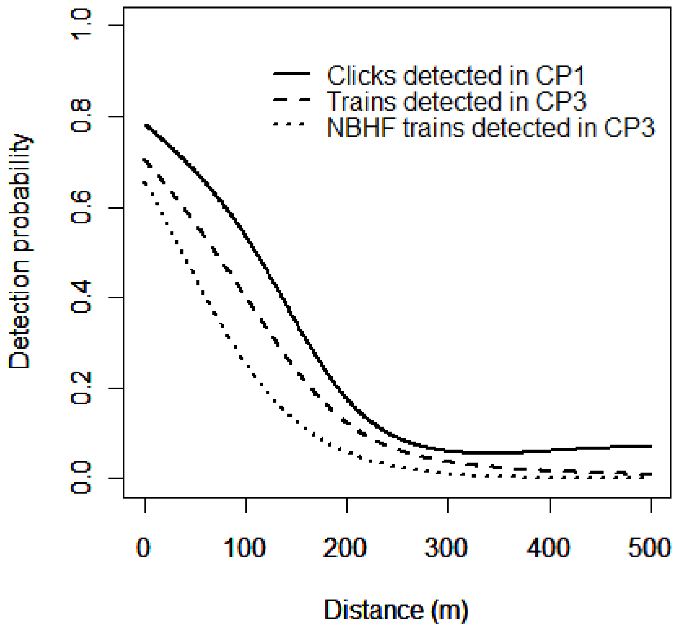

Figure 2.10 The probability of real harbour porpoise clicks and click trains detected with the control C-POD (C1). Solid line depicts all clicks detected in the C-POD raw data, dashed and solid lines depict the probability of these clicks being classified into trains (dashed line) and into porpoise (NBHF) click trains (dotted line) for all real porpoise click playback from all the stations on the control C-POD.

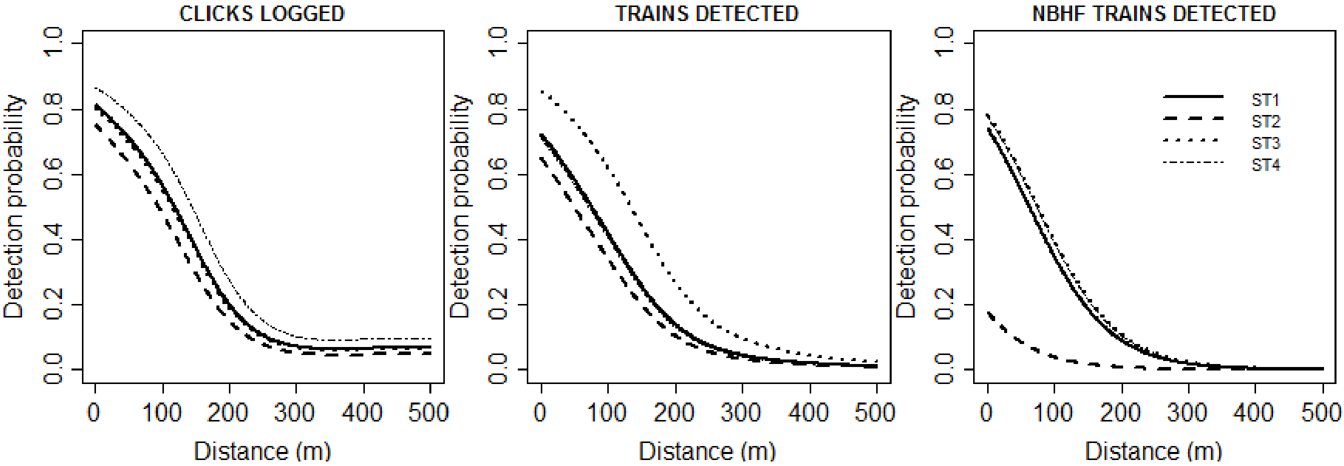

Figure 2.11 The probability of real harbour porpoise clicks logged, all click trains detected and porpoise (NBHF) trains detected with the control C-POD (C1) at each station. Station1 (solid line), station2 (dashed line), station 3 (dotted line) and station 4 (dots and dashes)

Table 2.1 Effective detection radius and effective detection area with bootstrapped 95% confidence intervals and coefficient of variation (CV) for the recorded porpoise playback signal for each of the C-PODs tested

POD	EDR (m)	2.50%	97.50%	CV	EF. AREA (km^2)	2.50%	97.50%	CV
1A	101	53	167	0.29	0.03	0.01	0.09	0.09
1B	158	113	217	0.17	0.08	0.04	0.15	0.03
1C	85	55	137	0.25	0.02	0.01	0.06	0.06
2A	119	61	207	0.31	0.04	0.01	0.13	0.10
2B	107	64	173	0.26	0.04	0.01	0.09	0.07
2C	170	109	245	0.20	0.09	0.04	0.19	0.04
3A	155	99	233	0.22	0.08	0.03	0.17	0.05
3B	327	236	418	0.15	0.34	0.18	0.55	0.02
3C	243	169	327	0.17	0.19	0.09	0.34	0.03
4A	247	191	308	0.12	0.19	0.11	0.30	0.02
4B	223	173	282	0.13	0.16	0.09	0.25	0.02
4C	322	265	381	0.09	0.33	0.22	0.46	0.01
CTRL 1	168	142	208	0.11	0.09	0.06	0.14	0.01
CTRL 2	91	63	126	0.18	0.03	0.01	0.05	0.03
CTRL 3	100	69	144	0.19	0.03	0.02	0.07	0.04

Maximum detection distances

Maximum detection distances where acoustic detections were still made depended on the source levels of the emitted signals. The longest maximum theoretical modelled distance of

819 m was based on an estimated source level of 205 dB re 1 µPa @ 1m (peak-peak) (Villadsgaard *et al.* 2007). Unfortunately we were not able to cover such high source levels in this experiment. The maximum artificial click source level emitted was 184 dB re 1 µPa @ 1m (peak-peak), yielding a maximum detection distance of 545 m (recorded with C-POD 3B) and a mean of 402 m (95% CI: 371-429), which corresponds to what was expected based on the modelled theoretical distances (Figure 2.4).

The highest source level of the real recorded porpoise signal was 179 dB re 1 µPa @ 1m (peak-peak), yielding a maximum detection distance of 566 m (C-POD 4C). The mean maximum distance for all the C-PODs was 248 m (95% CI: 181-316), which reflects much reduced detection rates due to the directional transducer used, emulating more closely the real-life scenario of actual porpoise movement patterns and sonar beam width. For both experiments, the shortest maximum distances were recorded with the same C-POD, (C2) - 268 m for the artificial playbacks and 105 m for the real porpoise playbacks.

2.5 Discussion

Static data loggers such as C-PODs are one of the most common methods for studying and monitoring harbour porpoises in Europe, and understanding the distance at which porpoises are detected by C-PODs and how source level affects their detectability is crucial for quantifying cetacean area use. Accurate estimates of effective detection radius are essential for density estimation using static acoustic data loggers. This is the first experimental study to estimate harbour porpoise detection probability for C-PODs using both artificial and real porpoise clicks. The use of an artificial click sequence allowed us to assess the performance of the C-POD’s hydrophone in detecting clicks in a standardised and repeatable way, whereas the use of real clicks enabled us to evaluate the performance of the train classification algorithm.

As expected, the detection probability and the effective detection radius decreased with increasing distance from data logger and with decreasing source level of the artificial signal. No detections were made beyond 545 m from the logger and signals below 161 dB re 1 µPa/V at 1 m (peak-peak) had less than 0.2 probability of being detected even at distances of less than 50 m from the C-POD.

We calculate that the C-POD is capable of effectively detecting a porpoise-like click around 187 m radius for the most intense signal measured, (184 dB re 1 µPa/V at 1 m peak-peak), yielding a detection area of 0.11 km^2, which is somewhat lower than those calculated in previous studies (Brundiers *et al.* 2012), probably due to lower levels of ambient noise in a non-tidal environment and a slightly different technique for calculating detections, both of which may have increased the number of detections in their study. It is important to note that transmission loss and noise levels will vary between sea states and site and therefore ideally should be measured prior to C-POD deployment. Additionally, further research is recommended to assess detection probability with varying levels of ambient noise, such as those caused by wind and waves, using either existing data on noise level change with sea state or repeating the present experiment in higher sea states, something that was not possible here due to equipment and boat configuration used.

The same pattern of decreasing detection probability with distance was evident with real porpoise click sequences, with an almost equivalent EDR of 188 m. The real clicks had generally higher detection probability and were detected from further away (up to 566 m) than the artificial clicks. This was expected considering that the detection probability for an artificial signal is estimated for a *single* click, whereas the detection probability of the real porpoise click was calculated for the entire 18 s long sequence, despite the fact that the real clicks were played out with a directional transducer and at lower maximum source level (179 dB re 1 µPa/V @ 1 m peak-peak). No published EDR values for porpoise clicks exist for C-PODs, but for T-PODs (the predecessors of C-PODs), the reported mean EDR for wild porpoises detected as cetaceans was 47 m, varying slightly with T-POD type and sensitivity (Kyhn *et al.* 2012). Here, the mean EDR for detecting real porpoise clicks as porpoises, was much improved at 72 m. There was a clear reduction in detection probability and EDR for correctly classified porpoise trains (mean EDR: 72 m) in comparison to the EDR of the clicks logged (mean EDR: 188 m).

When examining the modelled detection distances for a typical porpoise click, it is interesting to note that the mean maximum distance recorded for the artificial click sequences matched closely the theoretical distance, indicating that at such short ranges the transmission loss is well described simply by spherical spreading, although at deeper depths and longer ranges, sound-speed profile, bathymetry, bottom properties, and multipath acoustic propagation will also affect the transmission loss, requiring more complex calculations to estimate the sound propagation (DeRuiter *et al.* 2010).

Click detection vs. train classification

As expected from the higher signal to noise ratio required for a more complex task, the detection probability decreased progressively from detected clicks to classified trains, and again to correctly classified species (Figure 2.10). Although the raw click files (CP1) had high detection rates of porpoise clicks and maximum detection distances close to those modelled here with transmission loss based on spherical spreading, the detection rates of the correctly classified click trains were greatly reduced in comparison. Variations between units for the probability of correct species classification were high in contrast to the overall detection probability (Figure.2.8) The challenge remains for the developers of the software to improve the train classification algorithm to more closely match the click detection abilities of the device, which would greatly increase its effective detection area – in the case of the real porpoise click sequence used in this study, this would be a five-fold increase from 0.02 to 0.1 km^2. However, it is unlikely that this can be achieved at all, since more complicated signal (trains and species classification) will always require more information (more intense clicks and larger number of them) than just detecting a click – and therefore the detection probability of click trains will always lower than that of clicks.

Differences between C-PODs

Although there was only little variation in detection probability across the stations, as measured by the control C-POD, and the confidence intervals around the mean EDRs were relatively small, specifically for the artificial playbacks, there were some differences between individual C-PODs in how they detected clicks and click trains. This could be due to either site or C-POD unit variation, or unforeseen slight alterations in playback or data handling protocol.

The C-PODs were calibrated with comparable sensitivity levels within 0.5 dB (no range given) of each other (www.chelonia.co.uk), which would result in variation of 56 m in detection distance. For the artificial playbacks a variation in the region of ±10 m was found, and therefore we do not think that much of the variation seen here was a result of differences in C-POD sensitivities. A likely cause of variation in detection probability could be due to random site specific differences, such troughs in the seabed or variation in the substrate type, which cannot be ruled out despite the side scan survey of the area. A further cause of variation could be unforeseen errors during playback procedure or data handling, given that very large amounts of data were processed by a small team. Even with a double checking procedure in place to avoid such errors, we cannot exclude the possibility of observer error in our visual assessments, and have to accept a small likelihood of both false positive and false negative detections in the dataset. However, with such large sample sizes we expect the effect of these errors to be minimal.

Wild harbour porpoise source levels

The source levels used in this study were based upon limited data from recordings of wild porpoises (Villadsgaard *et al.* 2007), which may not reflect the real variation in source levels, likely to be affected by behavioural context and variation in habitat characteristics, such as ambient noise, as demonstrated for the beluga whale (*Delphinapterus leucas*), which adapts the source level and frequency of its echolocation clicks according to noise levels of its surroundings (Au *et al.* 1985). Lower source levels have been reported since, but from captivity. In the study by Koblitz et al. (2012) all harbour porpoise clicks recorded were within 132–140 dB re 1 µPa range. Here, the maximum source level emitted was 184 dB re 1 µPa/V @ 1 m (peak-peak) for the artificial playbacks and 179 dB re 1 µPa/V @ 1 m (peak-peak) for the real porpoise playbacks, which are considerably less than the maximum estimated level of 205 dB re 1 µPa/V @ 1 m (peak-peak), or even the mean of 191 dB re 1 µPa/V @ 1 m (peak-peak), although within those recorded from captive porpoises. Hence the EDRs reported here will not represent the full detection range of wild porpoises. Nevertheless, it should be noted that these high source levels have been calculated for the most intense, "on-axis" clicks of the animals, whereas static acoustic data-loggers will by definition detect all clicks emitted and projected into the water column. If the animal moves its head frequently and both on and off-axis clicks are equally as likely to be received by the C-PODs, it is imperative that the detection probability of data loggers is based on the full range of clicks projected, including both on- and off-axis clicks, and consequently clicks of varying source levels. Thence we believe that the highest levels measured here probably represent a reasonable average source level arriving at a C-POD in low ambient noise conditions and the results can therefore be of practical use in studies of similar environmental conditions throughout the harbour porpoise range.

Designing effective sampling regimes

Kyhn *et al.* demonstrated how to estimate density around a single T-POD using the estimated EDR. However, typically one would want to cover a larger area. The area surveyed will depend on the nature of the research question and the target species. It is not practical or useful to try and cover the whole area with C-PODs and typically systematic sampling is the preferred method whilst ensuring that the detection ranges of each C-POD do not overlap. The maximum detection distance recorded for porpoise click trains was 256 m whilst the mean maximum detection distance across C-PODs was 163 m (95% CI: 132-194). To monitor an area whilst excluding the possibility of simultaneous recordings of porpoises from two C-PODs, one would need to deploy the C-PODs beyond their maximum detection range, yet close enough to achieve best possible coverage. Allowing 250 m between each C-POD would satisfy these criteria, for the source levels used here requiring a total of 16 C-PODs to cover a sampling site of 1 km^2. However, as the source levels of wild animals have been reported to be much higher, this would need to be taken into account here too.

The narrowband nature of the porpoise’s echolocation click (at 130kHz) means that it will be unlikely to cause simultaneous detections with the same click trains more than 54 m apart, based upon a beam width of 12.25° at 250 m from the C-POD. Obviously, any added side-to-side head movement would increase this. For example, if the porpoise head side-to-side movement is 45° with a beam width of 12.25°, the beam at 250 m from the animal would cover a maximum range of 388 m – although, as seen from the maximum detection ranges, at these distances there is insufficient information arriving at the C-POD to allow for effective detection of porpoise click trains.

When planning for practical deployment distances, considerations must also include the potential swim speed of the animals. Using a maximum swim speed of 2 m/s (Westgate *et al.* 1995; Otani *et al.* 2001), the porpoise might cover a distance of 120 m in a minute. If the C-PODs are deployed more than 265 m apart (to ensure no simultaneous detections) and the data are sampled in no longer than one minute periods (to ensure that the animal does not move into the EDR of another C-POD), it will be possible to arrive at a crude density estimate for a series of consecutive sampling snapshots in the study area, providing the average group size is known (or estimated).

Typically a sampling design does not aim to cover the entire area but rather to sample systematically in a representative manner, to cover any variation in the study area (such as depth or bottom substrate). Hence, the amount of sampling points required will depend on the nature of the area of interest, the target species and indeed the question asked.

The challenge for the C-POD is not detecting the clicks – as seen from the results of the artificial click experiment, the C-PODs hydrophone detects porpoise clicks extremely well. However, due to inherent characteristics of signal detection of complex signals, the train detection algorithm and the species identification software have a lower detection threshold and thus a lower EDR. In areas of low porpoise density, where there are no other cetaceans present, (and if false positive rate is low and can be quantified) it might be useful to use the raw click data or the train classification results, without species identification, improving the overall detection rate and enlarging the effective detection area. However in areas where dolphins are present this approach is not workable and species classification is the most practical way of distinguishing species, regardless of the reduced EDR, after all it is always more useful to have a lower rate of true positives than risk recording many false positives, as long as the rate of missed detections can be quantified – as this is much easier to quantify and correct for in the analysis.

To fully establish detection probabilities for small cetaceans we need to gain a thorough understanding of the effect of behaviour and group size on vocalisation rates, including the portion of time that animals rest and spend silent, which will obviously affect their detection. Currently, we have limited information on wild porpoise vocalisation rates, and can only conclude that they vary according to time of day (Carlström 2005; Todd *et al.* 2009), and that periods of silence lasting several minutes are not uncommon (Linnenschmidt *et al.* 2012). Research on captive animals shows that porpoise click rates increase during prey capture (DeRuiter *et al.* 2009; Verfuß *et al.* 2009), but that source levels of feeding buzzes are reduced, making them less detectable than other clicks at similar ranges (DeRuiter *et al.* 2009). For many other cetacean species we have only limited information on their vocalisation rates and further research is required.

The EDR results presented here are promising, and can be used in practical assessments of C-POD data and in planning and designing sampling protocols for monitoring studies. Understanding variability in detection probability and effective detection radius is particularly important when using static acoustic monitoring devices for density estimation or monitoring of impacts of anthropogenic disturbance.

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2.7 Appendices

Appendix 2.1: GAMM Result tables for both artificial and real recorded porpoise click playback experiments

Table 2.2 Output of the best GAMM model for playbacks with artificial porpoise clicks.
Each station was modelled separately due to memory size restrictions

		Parametric coefficients				Approximate significance of smooth terms								
Station		**Estimate**	**Std. Error**	**z-value**	**Pr (>|z|)**		**edf**	**Ref.df**	**Chi.sq**	**P-value**	**R-sq. (adj)**	**glmer ML score**	**Scale est**	**n**
2	(Intercept)	-56.124	28.497	-1.969	0.049	s(dist)	5.028	5.028	49.5	0.000	0.476	30030	1	26727
2	as.factor(pod)2B	-0.440	0.082	-5.341	0.000	s(sl)	8.663	8.663	1600.8	<2e-16				
2	as.factor(pod)2C	0.023	0.086	0.268	0.789									
4	(Intercept)	-16.373	2.698	-6.068	0.000	s(dist)	2.659	2.659	33.7	0.000	0.511	17898	1	27544
4	as.factor(pod)4B	0.693	0.098	7.105	0.000	s(sl)	4.663	4.663	1114.8	<2e-16				
4	as.factor(pod)4C	0.923	0.105	8.817	<2e-16									
5	(Intercept)	-14.832	0.870	-7.041	<2e-16	s(dist)	1.000	1.000	133.1	<2e-16	0.400	12185	1	26802
5	as.factor(pod)5B	0.368	0.129	2.853	0.004	s(sl)	4.821	4.821	832.2	<2e-16				
5	as.factor(pod)5C	-0.508	0.147	-3.465	0.001									
CTRL 1	(Intercept)	-9.452	0.772	-12.248	<2e-16	s(dist)	1.000	1.000	102.8	<2e-16	0.534	25819	1	17465
CTRL 2	as.factor(pod)JEM19	-0.362	0.090	-4.033	0.000	s(sl)	4.518	4.518	1430.6	<2e-16				
CTRL 3	as.factor(pod)JEM469	-1.413	0.097	-14.514	<2e-16									

Table 2.3 Output of the best GAMM model for playbacks with recorded porpoise clicks

Parametric coefficients

Station		Estimate	Std. Error	z-value	Pr(>|z|)
	(Intercept)	-2.096	0.725	-2.891	0.004
1	as.factor(pod)1B	1.186	0.795	1.492	0.136
1	as.factor(pod)1C	-0.399	0.840	-0.474	0.635
2	(as.factor(pod)2A	0.400	1.066	0.375	0.707
2	as.factor(pod)2B	0.151	0.957	0.158	0.875
2	as.factor(pod)2C	1.395	0.949	1.470	0.142
3	as.factor(pod)3A	2.621	0.940	1.187	0.235
3	as.factor(pod)3B	2.685	1.063	3.730	0.000
3	as.factor(pod)3C	3.965	0.946	2.770	0.006
4	as.factor(pod)4A	2.685	0.849	3.161	0.002
4	as.factor(pod)4B	2.307	0.842	2.739	0.006
4	as.factor(pod)4C	3.891	0.840	4.633	3.6e-06
CTRL 1	as.factor(pod)JEM1829	1.364	0.764	1.787	0.074
CTRL 2	as.factor(pod)JEM19	-0.254	0.856	-0.296	0.767
CTRL 3	as.factor(pod)JEM469	--0.015	0.861	-0.017	0.986

Approximate significance of smooth terms

	edf	Ref.df	Chi.sq	p-value	R-sq. (adj)	glmer ML score	Scale est	n
s(dist)	1	1	51.23	8.2e-13	0.224	686.96	1	718

Appendix 2.2: Effect of distance from C-POD and signal source level on the detection probability of artificial playback signal depicted by GAMM smoothers

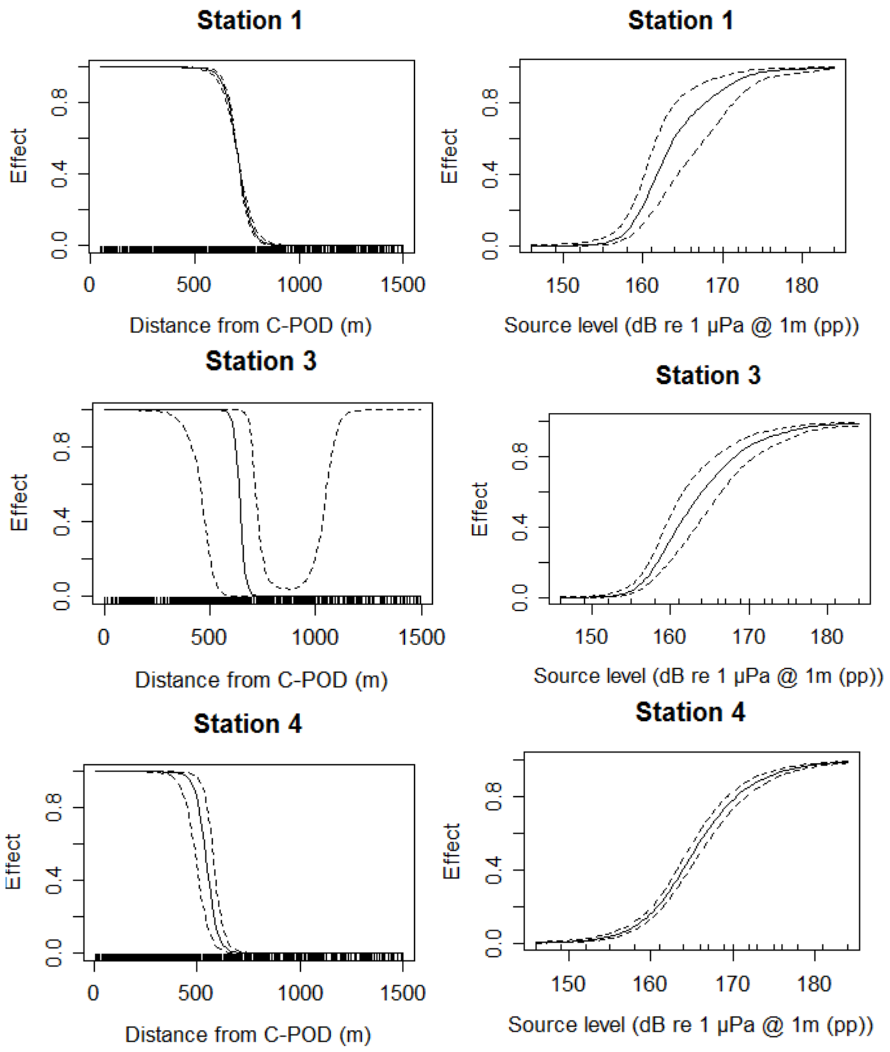
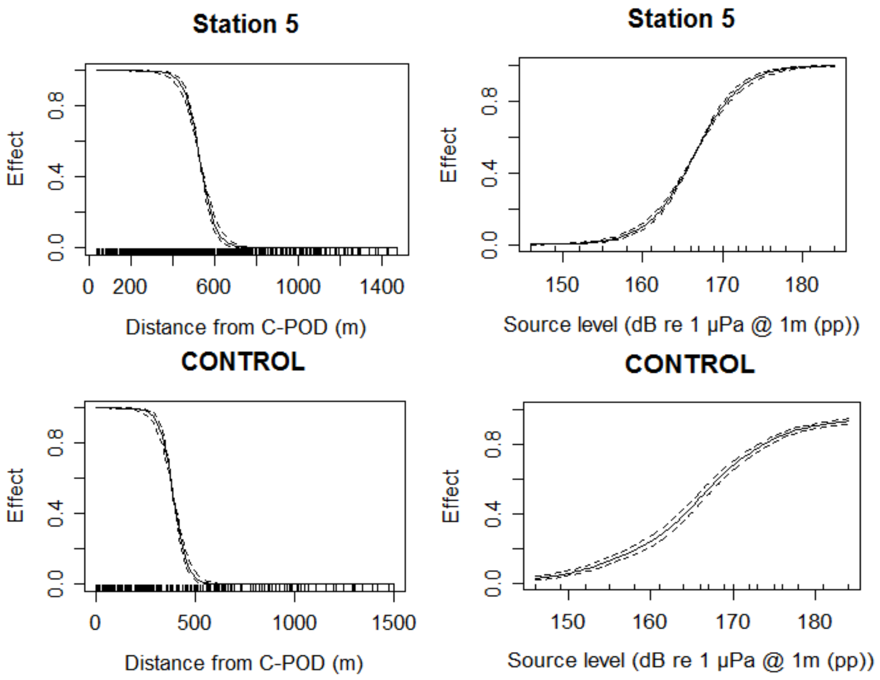


Figure 2.12 Smoothers of the effect of distance from C-POD and signal source level on the detection probability of artificial playback signal as raw clicks (CP1 files) in the GAMM model for all stations. Dashed lines indicate two standard errors; y-axis is transformed to the response variable scale, and the lines on x-axis show the distribution of the values of predictors in the underlying dataset.


Station 5

Station 5

CONTROL

CONTROL

Figure 2.12 Continued from previous page

Appendix 2.3: Effective detection radii and effective detection areas for two source levels for the artificial playback signal

Table 2.4 Effective detection radius and effective detection area with bootstrapped 95% confidence intervals and coefficient of variation (CV) for source level of 184 dB re 1 µPa @ 1m (pp) for the artificial playback signal

POD	SOURCE LEVEL	EDR (m)	2.50%	97.50%	CV	EF. AREA (km^2)	2.50%	97.50%	CV
1A	184	148.0	112.5	181.6	0.12	0.069	0.040	0.104	0.014
1B	184	191.7	161.1	219.9	0.08	0.115	0.082	0.152	0.006
1C	184	150.2	122.6	178.9	0.10	0.071	0.047	0.101	0.009
2A	184	223.5	194.4	254.5	0.07	0.157	0.119	0.204	0.005
2B	184	201.8	174.8	233.4	0.08	0.128	0.096	0.171	0.006
2C	184	225.0	195.9	257.3	0.07	0.159	0.121	0.208	0.005
3A	184	208.7	178.3	240.4	0.08	0.137	0.100	0.181	0.006
3B	184	170.5	140.0	200.7	0.09	0.091	0.062	0.127	0.009
3C	184	192.5	162.9	223.2	0.08	0.116	0.083	0.156	0.007
4A	184	152.2	128.8	174.6	0.08	0.073	0.052	0.096	0.006
4B	184	184.6	160.6	206.1	0.06	0.107	0.081	0.133	0.004
4C	184	189.0	166.1	211.0	0.06	0.112	0.087	0.140	0.004
5A	184	188.0	160.3	213.7	0.07	0.111	0.081	0.143	0.005
5B	184	203.6	180.6	228.1	0.06	0.130	0.102	0.163	0.004
5C	184	170.4	148.1	195.5	0.07	0.091	0.069	0.120	0.005
C1	184	142.3	124.8	162.3	0.07	0.064	0.049	0.083	0.005
C2	184	93.1	76.9	109.4	0.09	0.027	0.019	0.038	0.008
C3	184	131.8	114.5	151.2	0.07	0.055	0.041	0.072	0.005

Table 2.5 Effective detection radius and effective detection area with bootstrapped 95% confidence intervals and coefficient of variation (CV) for source level of 176 re 1 µPa @ 1m (pp), for the artificial playback signal

POD	SOURCE LEVEL	EDR (m)	2.50%	97.50%	CV	EF. AREA (km^2)	2.50%	97.50%	CV
1A	176	103.2	69.7	137.5	0.17	0.033	0.015	0.059	0.029
1B	176	144.6	119.4	170.9	0.09	0.065	0.044	0.092	0.009
1C	176	105.2	81.9	131.5	0.12	0.035	0.021	0.054	0.014
2A	176	145.7	121.7	169.1	0.08	0.066	0.046	0.089	0.007
2B	176	127.2	104.7	151.2	0.09	0.051	0.034	0.072	0.009
2C	176	147	123.6	171.8	0.08	0.068	0.048	0.092	0.007
3A	176	160.9	134.1	192.1	0.09	0.081	0.056	0.116	0.009
3B	176	122.9	94.7	153.5	0.12	0.047	0.028	0.074	0.015
3C	176	144.5	115.5	175.0	0.10	0.065	0.042	0.096	0.011
4A	176	98.57	79.3	119.5	0.11	0.030	0.019	0.045	0.012
4B	176	129.9	108.0	152.7	0.09	0.053	0.036	0.073	0.008
4C	176	134.3	112.1	156.9	0.08	0.056	0.039	0.077	0.007
5A	176	98.87	72.5	124.9	0.1	0.031	0.016	0.049	0.019
5B	176	112.5	86.1	136.5	0.11	0.039	0.023	0.058	0.013
5C	176	84.11	61.9	107.4	0.14	0.022	0.012	0.036	0.019
C1	176	115.7	100.3	132.5	0.07	0.042	0.031	0.055	0.005
C2	176	70.07	57.0	86.0	0.10	0.015	0.010	0.023	0.011
C3	176	105.7	90.28614	122.7823	0.080367	0.035073	0.025609	0.04736	0.0065

Appendix 2.4: Effective detection radii and effective detection areas for the real porpoise playback signal

Table 2.6 Effective detection radius and effective detection area with bootstrapped 95% confidence intervals and coefficient of variation (CV) for the real porpoise sequence for A) Clicks detected (CP1 files), B) Classified trains and C) Trains classified as NBHF (porpoises).

A) Clicks detected (CP1 files)

POD	EDR (m)	2.50%	97.50%	CV	EF. AREA (km2)	2.50%	97.50%	CV
1A	101.0	54.7	170.8	0.30	0.03	0.009	0.092	0.092
1B	158.4	112.6	212.1	0.16	0.08	0.040	0.141	0.026
1C	85.4	52.2	133.1	0.24	0.02	0.009	0.056	0.059
2A	120.8	62.8	214.4	0.31	0.05	0.012	0.144	0.099
2B	107.7	65.2	170.6	0.26	0.04	0.013	0.091	0.067
2C	170.1	109.1	245.7	0.22	0.09	0.037	0.190	0.046
3A	154.7	97.1	214.6	0.20	0.08	0.030	0.145	0.039
3B	326.9	226.8	426.2	0.16	0.34	0.162	0.571	0.024
3C	242.9	173.0	326.4	0.16	0.19	0.094	0.335	0.027
4A	246.8	193.5	310.5	0.12	0.19	0.118	0.303	0.015
4B	223.5	172.1	279.7	0.12	0.16	0.093	0.246	0.015
4C	322.3	259.8	380.2	0.09	0.33	0.212	0.454	0.009
C1	168.3	137.9	205.9	0.10	0.09	0.060	0.133	0.011
C2	100.6	67.8	143.5	0.19	0.03	0.014	0.065	0.036
C3	91.0	63.3	129.6	0.18	0.03	0.013	0.053	0.033

B) Classified trains

POD	EDR (m)	0.0	1.0	CV	EF. AREA (km2)	0.025	0.975	CV
1A	62.0	24.4	138.8	0.47	0.01	0.002	0.060	0.224
1B	116.1	79.3	169.9	0.20	0.04	0.020	0.091	0.040
1C	55.9	31.9	100.7	0.32	0.01	0.003	0.032	0.101
2A	120.5	62.5	201.6	0.30	0.05	0.012	0.128	0.087
2B	58.4	24.4	128.3	0.47	0.01	0.002	0.052	0.221
2C	117.2	72.2	187.6	0.26	0.04	0.016	0.111	0.068
3A	140.2	88.8	212.3	0.22	0.06	0.025	0.142	0.051
3B	227.4	156.0	320.3	0.19	0.16	0.076	0.322	0.035
3C	204.6	140.8	285.5	0.18	0.13	0.062	0.256	0.033
4A	146.5	103.1	210.0	0.19	0.07	0.033	0.139	0.034
4B	65.1	39.0	110.0	0.28	0.01	0.005	0.038	0.077
4C	80.9	50.1	133.6	0.26	0.02	0.008	0.056	0.069
C1	133.4	107.3	173.6	0.13	0.06	0.036	0.095	0.017
C2	49.7	29.2	86.2	0.29	0.01	0.003	0.023	0.086
C3	88.7	61.1	127.5	0.20	0.02	0.012	0.051	0.039

C) Trains classified as NBHF (porpoises)

POD	**EDR (m)**	**0.0**	**1.0**	**CV**	**EF. AREA (km2)**	**0.025**	**0.975**	**CV**
1A	52.9	19.7	127.0	0.52	0.01	0.001	0.051	0.274
1B	60.0	34.6	106.3	0.32	0.01	0.004	0.036	0.103
1C	36.9	19.6	77.8	0.41	0.00	0.001	0.019	0.172
2A	88.3	32.7	184.8	0.45	0.02	0.003	0.107	0.205
2B	55.0	20.6	133.9	0.53	0.01	0.001	0.056	0.283
2C	33.3	8.3	113.2	0.86	0.00	0.000	0.040	0.743
3A	94.6	55.6	167.7	0.31	0.03	0.010	0.088	0.095
3B	101.2	60.3	169.0	0.28	0.03	0.011	0.090	0.078
3C	126.9	79.4	201.6	0.26	0.05	0.020	0.128	0.066
4A	116.2	77.4	187.0	0.24	0.04	0.019	0.110	0.058
4B	39.0	20.6	71.5	0.34	0.00	0.001	0.016	0.119
4C	58.6	34.7	100.1	0.29	0.01	0.004	0.031	0.085
C1	98.4	76.5	138.9	0.17	0.03	0.018	0.061	0.027
C2	42.0	22.6	80.1	0.35	0.01	0.002	0.020	0.123
C3	42.2	23.9	75.1	0.32	0.01	0.002	0.018	0.101

Chapter 3 ACOUSTIC DETECTION PROBABILITY OF BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*), WITH STATIC ACOUSTIC DATA LOGGERS

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Author's contribution

I prepared the fieldwork, collected (with help of volunteers) most of the data and conducted all the analyses and wrote the manuscript. Rhiannon Meier together with volunteers Elisa Girola and Gemma James collected part of the data which was submitted as Rhiannon's MSc thesis in 2010. Nick Tregenza lent the equipment and helped deploy and set the C-PODs.

Len Thomas and Jan Hiddink helped with statistical analysis and R script and improved the structure of manuscript. Jim Bennell conducted side scan analysis of the study area.

All authors proofread the manuscript and offered helpful comments before submission to the Journal.

3.1 Abstract

Acoustic data loggers are widely used for monitoring the occurrence of cetaceans and can play an important role in fulfilling the statutory monitoring requirements of protected species. Although useful for long-term monitoring they are restricted in their spatial coverage and for many devices the effective detection distance is not specified. A generalized additive mixed model (GAMM) was used to investigate the effects of (1) distance from data logger, (2) animal behaviour (feeding and travelling) and (3) group size on the detection probability of bottlenose dolphins (*Tursiops truncatus*) with autonomous data loggers (C-PODs) validated with visual observations. In addition the performance and detection probabilities of single vs. paired data loggers were assessed. The average probability of acoustic detection for minutes with a sighting was 0.59 and the maximum detection distance ranged from 1343-1779 m. Minutes with feeding activity had higher acoustic detection rates and longer average effective detection radius (EDR) than travelling ones. Unexpectedly, the detection probability for single dolphins was significantly higher than for groups, indicating that the acoustic behaviour of single dolphins in the area may differ from those of larger groups, making them more detectable. The C-POD is effective at detecting dolphin presence but the potential effects of behaviour and group size on detectability create challenges for estimating density from detections as higher detection rate of feeding dolphins in comparison to travelling ones could yield erroneously high density estimates in feeding areas.

3.2 Introduction

Monitoring mobile species in the marine environment is challenging because of the difficulty and expense in locating them, especially if they range across many kilometres per day like many cetaceans (Stevick *et al.* 2002). Determining adequate sampling areas and rates for such wide-ranging species poses many problems. Visual surveys, either land or boat based, are restricted to daylight and relatively calm seas (Teilmann 2003) and can be affected by observer variability (Young & Pearce 1999). Cetaceans can easily be missed by visual observers because they swim fast (Akamatsu *et al.* 2008) and spend a large proportion of time underwater. Seasonal ranging patterns of many species mean that both temporal and spatial coverage for sampling is required, but covering large areas is expensive and simultaneous sampling of wide ranges is impractical using visual techniques (Hammond 2001).

Several cetacean species have highly evolved social structures and complex intra-specific communication systems (Tyack 1997) and may travel considerable distances to fulfil high energetic requirements (Bowen *et al.* 2002). Evolutionary adaptations to a marine lifestyle have favoured the development of specialised vocal production and auditory systems (Au 1993; Richardson *et al.* 1998). As a consequence, cetaceans rely on vocalisations to identify conspecifics, communicate, navigate and forage, making acoustic methods one of the most efficient ways to localise and track them. Acoustic surveys, especially those using static data loggers can be conducted 24 hrs a day, regardless of weather and sea state, and can provide a simultaneous cover of large areas (Evans & Hammond 2004).

The bottlenose dolphin (*Tursiops truncatus*) faces threats from many anthropogenic activities such as by-catch, disturbance, marine seismic exploration, and it is listed in the Annex II of the EU Habitats Directive. The directive requires national reporting on the favourable conservation status of threatened species and habitats and the establishment of Special Areas of Conservation (SAC) to ensure their adequate management (European Commission 2006; European Union 2007; Evans 2012). Static acoustic monitoring (SAM) devices have been used in cetacean studies covering long time periods across seasons or years (Verfuß *et al.* 2007; Simon *et al.* 2010) and they show potential to fulfil the statutory monitoring requirements of protected cetaceans in many coastal areas complementing or potentially even replacing some visual surveys (Marques *et al.* 2012). Here the suitability of one type of static acoustic data logger, the C-POD, is assessed as a monitoring tool for bottlenose dolphins.

C-PODs and their predecessors, T-PODs, are static acoustic data loggers that autonomously log times and characteristics of echolocation clicks which the accompanying software identifies as cetacean click trains and classifies into different species groups (Chelonia Ltd 2012a). These click loggers detect echolocation clicks from 9-170 kHz for the T-PODs and 20-160 kHz for the C-PODs, and can be used to monitor many odontocete species. Clicks are logged if they show a sufficiently high peak sound pressure level and a distinct spectral peak in the frequency range covered. Most of the clicks logged are non-cetacean clicks and cetacean detection depends on post-processing to identify coherent trains of clicks among those logged. The first versions of the earlier click detector were tested more than a decade ago (Tregenza 1999), and used to monitor harbour porpoise (*Phocoena phocoena*) and fisheries interactions, and the movements of porpoises around pingers (Cox *et al.* 2001). Since then the T-PODs have been used for monitoring many echolocating cetaceans, such as harbour porpoise, bottlenose dolphin and Hector's dolphin (*Cephalorhynchus hectori*) occurrence in coastal areas (Rayment *et al.* 2009), and their responses to disturbance from marine developments, such as effects of wind farm construction and operation (Carstensen *et al.* 2006; Tougaard *et al.* 2009b; Brandt *et al.* 2011) and various types of fishing gear (Cox *et al.* 2004; Carlström *et al.* 2009). Although the T-POD was first used to monitor harbour porpoises, many studies have since used it to monitor bottlenose dolphin occurrence and habitat use (Bailey *et al.* 2010; Simon *et al.* 2010; Elliott *et al.* 2011a). Dolphins emit frequent and intense clicks within the effective frequency band of both T-PODs and C-PODs (Table 1) for navigation and feeding (Au 1993; Wahlberg *et al.* 2011; Au *et al.* 2012), making them suitable target species for the click loggers.

Table 3.1 Reported echolocation click characteristics of the bottlenose dolphin

Click characteristics	**Reported range**
Mean source level dB re 1 µPa (peak-to-peak) @ 1 m	177-228
Click duration	8-72 µs
Peak frequency	30-150 kHz
Beam width	9-10 °
Sources	(Au *et al.* 1974, 2012; Au & Hastings 2008; Wahlberg *et al.* 2011).

In addition to monitoring population trends and relative abundance, static hydrophones have also been assessed and used for absolute abundance and density estimation (Marques *et al.* 2009; Kyhn *et al.* 2012). The commonly used term, detection function $g(x)$ is the probability of animal detection as a function of a variable such as distance (x) from the data logger (Buckland *et al.* 2001). This can be derived from the predicted values from the statistical and acoustic modelling and gives the probability of detecting a dolphin given it is within distance x of the detector. From the detection function we can integrate distance to attain the effective detection radius (EDR), the distance from the C-POD within which as many animals are missed as are detected at greater distances (Buckland *et al.* 2001). The effective detection area (the circular plot around the data logger) can then be calculated and given sufficient information about detections (such as average group size or the relation between vocalisation rate and animal density), the density for the area can be estimated using equations detailed further below.

While some information exists on the T-POD detection abilities (Rayment *et al.* 2009) detailed information on detection distances, or potential factors influencing dolphin detectability such as vocalisation rates require sea testing for the C-POD. Although bottlenose dolphin echolocation clicks have been studied extensively in captivity (Au 1993) very little is known about how group size or behaviour might influence the click train production rates of wild animals.

The objective of this study was to examine simultaneous visual observations and distances measured with a theodolite and acoustic data logged by the C-PODs to define the maximum acoustic detection range and effective detection radius for bottlenose dolphins. In particular the effect of dolphin group size and behaviour on the detection probability was examined and the performance and detection probabilities of single vs. paired data loggers were assessed. We hypothesised that all variables would have some effect on the dolphin detection probability and that paired data loggers would increase the detectability of visually observed encounters. To our knowledge this is the first study to look at the effect of a combination of biotic factors on the detectability of dolphins, and to describe the effective detection radius and detection probability of bottlenose dolphins with C-PODs, both of which can have potential implications on future monitoring of this protected species.

3.3 Materials and methods

Study Area

The study was conducted within the Cardigan Bay Special Area of Conservation (SAC), Wales between March and July 2010, and consisted of acoustic recordings of dolphin echolocation clicks with C-PODs compared with simultaneous visual observations from a coastal cliff-top monitoring site located at the Old Coastguard Lookout, New Quay (Figure.3.1).

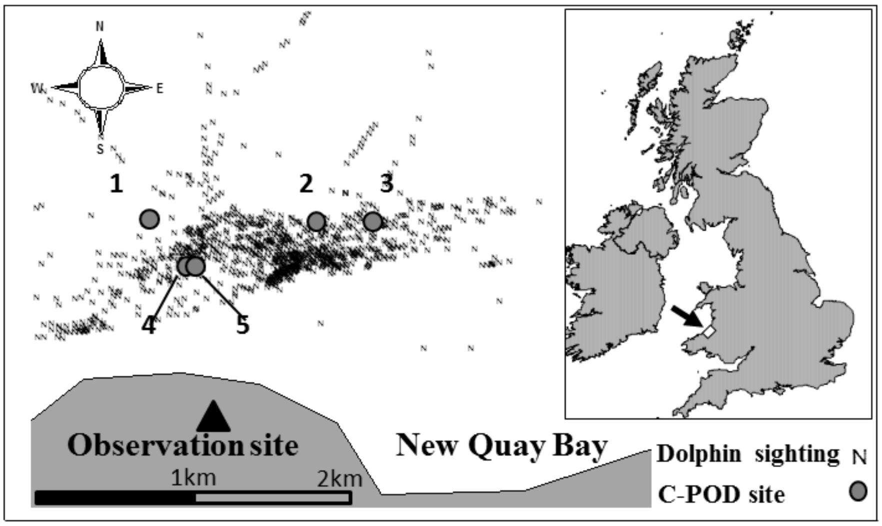

Figure 3.1 Location of the theodolite observation station and the C-POD mooring sites (1-5) for the seven C-PODs deployed in the study (1: C-POD 900; 2: C-POD 885; 3: C-POD 921; 4: C-PODs 840 and 898; 5: C-PODs 901 and 897). Positions of tracked dolphin sightings during the study period marked with *N*.

Acoustic Data Collection

A total of seven calibrated C-PODs were set to log clicks within a frequency range of 20-160 kHz. The sensitivity of the units had been standardised when built by rotating the complete instrument in a sound field and adjusted to achieve a radially averaged, temperature corrected, max source pressure level (SPL) reading within 5% of the standard at 130kHz (±0.5 dB). The radial values were taken at 5 degree intervals. Recalibration after the experiment showed that all units were within the original specifications after two years of use and that there were no changes of operational significance. The calibration and standardisation process is described in detail on the manufacturer's website, (www.chelonia.co.uk). Paired loggers were also compared in this study as an additional assessment of uniformity of sensitivity.

The C-POD units were moored over two separate periods in 2010 and were part of a larger experiment including up to 44 C-PODs. The first deployment took place from February to May and consisted of three C-PODs; the second was from June to August with four C-PODs moored in two pairs (Figure 3.1). The moorings were deployed at a site where dolphins are often sighted, and spanned water depths of 17–22 m (chart datum) and distances of 720-1055 m from the visual observation site. The moorings consisted of metal weights, connecting rope, and two pairs of surface buoys on either end of a mooring line, marking the position of the data loggers. The moorings maintained the floating data logger units in a vertical position in the water column, at 1 m above the seabed, which was investigated with a side scan sonar and found to consist of an even mixture of sandy and muddy substrate. Although only five C-PODs were used for the main analysis, during the mid-summer deployment a trial was set up with two additional C-PODs deployed within 1 m of the main device to assess the between-logger variability and to assess the extent to which paired C-PODs (1 and 100 m apart) would increase detection probability.

Visual Observations

Visual observations of dolphins were conducted on 108 days, recording data on the sightings and tracking the animals with a theodolite. Visual scans were conducted by a team of 2-4 trained, experienced observers during daylight hours in sea states ≤ 3 on the Beaufort scale over a visible sea-surface area of approximately 3 km around the C-PODs. 8 x 32 binoculars were used to aid detection and tracking of the study animals. Whilst one observer was tracking the animals with a theodolite, another was dedicated to searching animals outside the tracked group. A dolphin group was defined as ‘a number of dolphins in association with one another, often engaged in the same activity and remaining within approximately 100 m of one another” (Bearzi *et al.* 1997). Once sighted, dolphin groups were tracked using a 30 x magnification Sokkia electronic digital theodolite (DT5A) which provided the horizontal and vertical angles from a GPS-calibrated reference point for each fix, which were later converted to geographical positions and then to distances to the C-POD sites. The theodolite was calibrated daily with set reference points. To ensure that animal positions calculated from theodolite fixes using the equations below were accurate, theodolite fixes of known positions (with GPS coordinates) were taken and the resulting calculations were compared against the GPS generated positions.

Measuring station altitude

The station altitude above sea level was determined with a stadia rod calibration method, following Frankel *et al.* (2009). A 4 m long rod was held vertically on the shore below the monitoring station during low tide, with the bottom of the rod positioned at sea level. From the monitoring station, vertical angles were then recorded to the top and bottom of the rod (n = 20) using the theodolite, and mean (± SE) values of both angles were obtained to reduce measurement error. The reference altitude of the station was then determined using the following equations as described in detail in Meier (2012) (Figure 3.2):

$$A = B - T$$

$$\beta = 180 - B$$

$$\text{Hypotenuse} = \text{Pole Height} \times \sin(T)/\sin(A)$$

$$\text{Station Altitude} = \text{Hypotenuse} \times \cos(\beta)$$

where B is the mean vertical bottom angle of the rod (relative to gravity with 0° = zenith), T is the mean vertical top angle and A the differential angle between B and T.

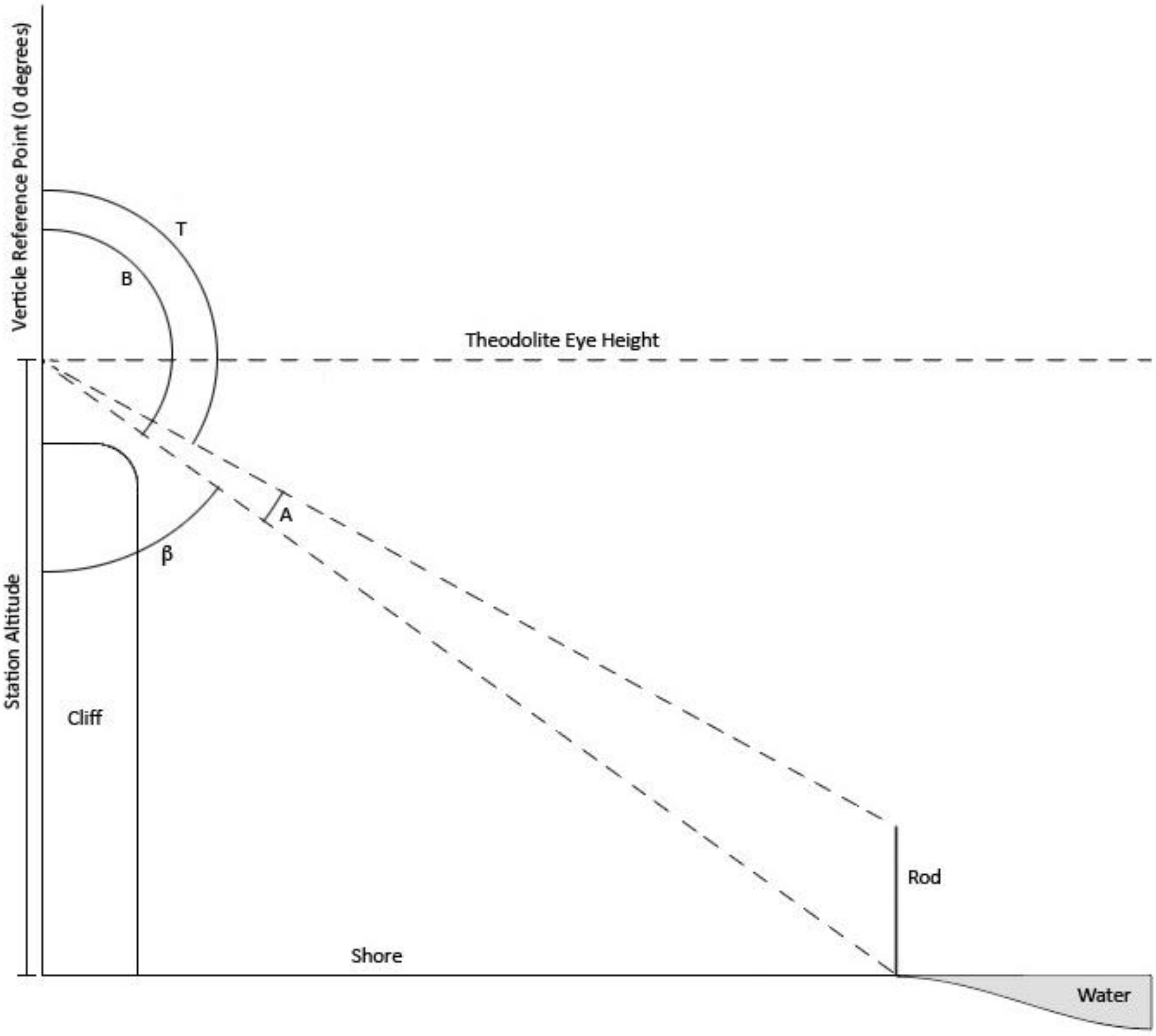

Figure 3.2 Diagram of the rod method (after methodology from Frankel & Yin, 2009) used to determine theodolite station altitude during field studies (reproduced from Meier, 2010).

To account for the effect of tidal height on the elevation of the cliff above sea level during the study, a reference tidal marker (RTM) was painted on an intertidal rock in contact with sea level, at low tide during the spring tidal phase of the lunar cycle. Additional tidal markers were then painted at 0.5 m intervals above the reference tidal marker. This was undertaken at the same time that cliff elevation measurements were recorded to ensure that the station altitude from the reference tidal marker was known. The height of sea level above the reference tidal marker could then be determined from the monitoring station at any point during the tidal cycle. Tidal height measurements were subsequently taken at 15-minute intervals throughout all visual observation periods. The total theodolite height varied between 93.3 – 96.9 m above sea level and was calculated as:

Total Theodolite Height = Reference Station Altitude (RSA) + Theodolite Eye Height –/+ Tidal Height (above/below the RTM)

Dolphin distance from theodolite

The distance of the cetacean(s) from the theodolite (B) was calculated from the measured vertical angle (β) between the animal's position and 'nadir' / 180° from the vertical reference point (0° = zenith), and the known altitude of the theodolite station (A) at the time of the sighting (Figure 3.3). This was calculated using right-angled trigonometry by applying the following equation:

$$B = A \times \tan(\beta)$$

When more than one animal was sighted, theodolite fixes were taken from the animal nearest to the C-PODs at the time of initial sighting and then on every surfacing. Tracking then continued until the animals moved out of view. To ensure that the acoustic and visual data originated from the same group of animals, only those measurements where the focal group was considered to be the only one within the study area were used.

The distance between the animal's position and the C-POD was calculated using the recorded geographical coordinates of the theodolite station and the data loggers (taken with a handheld Garmin GPS device), and the angular measurements recorded with the theodolite.

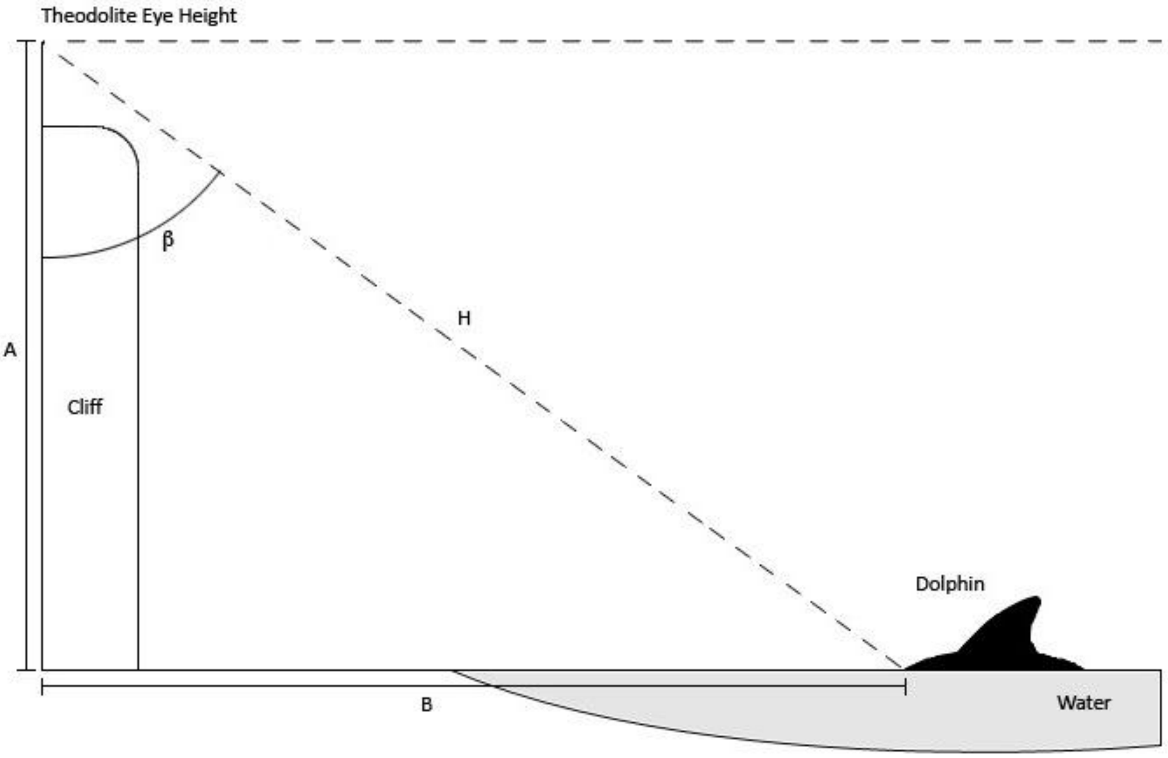

Figure 3.3 Diagram of the trigonometric method used to determine distance of the dolphin(s) and C-POD moorings from the theodolite monitoring station, in the present study. 'A' is the altitude of the theodolite station, 'B' is the base distance between the theodolite and the dolphin(s) or C-POD, and β is the vertical angle between the dolphin's position and nadir (Meier, 2010).

1) Converting geographical coordinates into true bearings

The geographical coordinates of the theodolite station and the horizontal reference point were used to calculate the true bearings (in relation to geographic north) of the horizontal reference point from the theodolite station using the following formula:

$$\theta = \tan^{-1} ((\cos(lat_1) \text{ x } \sin(lat_2) – \sin(lat_1) \text{ x } \cos(lat_2) \text{ x } \cos(long_1 - long_2))/(\sin(long_2 – long_1) \text{ x } \cos(lat_2)))$$

Where lat_1 and lat_2 are the first and second latitude coordinates, and $long_1$ and $long_2$ are the first and second longitude coordinates.

2) Determining the true bearing of the dolphin(s) from the theodolite station

Using a) the determined bearing of the horizontal reference point from the theodolite station (step 1), and b) the measured horizontal angle between the animal, theodolite station and the horizontal reference point (taken from the theodolite), the bearing of the animal(s) from the theodolite station could be determined. The formula used to determine this bearing was dependent on the location of the animal(s) in relation to true north, the horizontal reference point and the theodolite station.

a) Horizontal reference point 1 (coordinates: 52° 13.196’ N, 004° 16.557’ W):

When the animal was to the west:

$A = 360° - (B + C)$

When the animal was to the east:

$A = C – B$

b) Horizontal reference point 2 (coordinates: 52° 12.842’ N, 004° 22.563’ W):

When the animal was to the west:

$A = B + C$

When the animal was is to the east:

$D = 360° - B$

$A = C – D$

Where A is the bearing of the animal(s) from the theodolite station, B is the measured horizontal angle between the animal(s), theodolite and the horizontal reference point, C is the bearing of the horizontal reference point from the theodolite and D is angular difference between B and 360°.

3) Converting theodolite angles into latitude and longitude

The latitude and longitude of the animal(s) position could be calculated, using the calculated distance of the animal(s) from the theodolite station, the geographic coordinates of the theodolite station and the bearing of the animal from the theodolite station (Veness 2010).

The angular distance of the animal(s) (Bd/R) was initially calculated, where Bd is the distance of the animal(s) from the theodolite station and R is the radius of the earth

(6371km). The latitude of the animal (lat_2) was then calculated using the following formula:

$$lat_2 = \sin^{-1}(\sin(lat_1)\ x\ \cos(Bd/R) + \cos(lat_1)\ x\ \sin(Bd/R)\ x\ \cos(\theta))$$

where lat_1 is the latitude of the theodolite station and θ is the true bearing of the animal from the theodolite station.

A similar method was used to calculate the longitude of the animal(s) using the following formula:

$$long_2 = long_1 + \tan^{-1(}(\sin(\theta)\ x\ \sin(Bd/R)\ x\ \cos(lat_1)/ \cos(Bd/R) - \sin(lat_1)\ x\ \sin(lat_2)))$$

where lat_1 and $long_1$ are the latitude and longitude of the theodolite station, lat_2 is the latitude of the animal and θ is the true bearing of the animal from the theodolite station.

4) Determining distance of the animal(s) from the C-POD

With the latitude and longitude of the animal's position (step 1-3), and the latitude and longitude of the C-POD position, the distance between the animal(s) and the C-POD could be determined using the spherical law of cosines as follows:

$$d = \cos^{-1} (\sin(lat_1) .\sin(lat_2) + \cos(lat_1) .\cos(lat_2) .\cos(long_2 - long_1)) .R$$

where lat_1 and lat_2 are the first and second latitude coordinates, $long_1$ and $long_2$ are the first and second longitude coordinates, and R is the mean radius of the earth (6371 km). All angles and coordinates were converted into radians for calculations. All distances determined in this way were then verified using a second methodology following the spherical law of cosines, described in detail in Meier (2010). Formulas were obtained and adapted from http://moveable-type.co.uk/scripts/latlong.html (Veness 2010).

During every theodolite fix, the observers recorded group size, composition and cohesion, travel direction and surface behaviour. Behaviour was defined using the following categories: foraging/feeding (surface foraging, prey pursuit/capture, demersal foraging), socialising (physical contact, synchronised movement, aggression, play), aerial behaviour, travelling, and milling (Shane 1990; Bearzi *et al.* 1999). Due to the low number of observations in some of the categories, only foraging/feeding and travelling categories were used for analysis. Here the terms 'feeding' and 'foraging' are at times used interchangeably to describe both foraging and feeding activities and defined as such if one or more of the following were observed: visible prey in dolphin's mouth or tossed above water surface, feeding birds in the same location as surfacing animals (surface foraging), bursts of high speed swimming with rapid turns in the same area (prey pursuit/capture) and repeated vertical dives in same area with raised tail flukes without consistent travel direction (demersal foraging) (Würsig & Würsig 1979; Shane 1990; Bearzi *et al.* 1999). Travelling was defined as continuous movement in one general direction (Bearzi *et al.* 1999). Environmental data with sea state, swell height, cloud cover, visibility and tidal height were collected at 15-minute intervals to assess the observation conditions so that sightings made during poor sighting conditions would not be used for further analysis. To eliminate observer error, only those sightings in which a single species was present and where the behaviour or group size did not change during the entire encounter were used for the study.

Data Analysis

The data were downloaded using the *C-POD.exe* versions v2.001 and v2.009 and the train detection was conducted with v.2.019. The train detection algorithm identifies click trains (more or less regular series of similar clicks), and estimates their probability of arising by chance from a non-train producing source (like rain or a boat propeller). This probability is determined in part by the Poisson distribution of the prevailing rate of arrival of clicks, the size of the time interval between each click, the regularity of the trains, and the number of clicks in the train. A quality value, 'High', 'Medium', 'Low' or 'Doubtful' quality, is attached to each train to represent the estimated confidence that it arises from a train source, such as a cetacean or boat sonar. A cetacean train is identified as showing variation in temporal spacing of clicks over time, and reduced similarity of the clicks caused by the changing orientation of the animal, propagation effects, and by changes in the click produced, especially in the case of broad-band dolphin clicks. Here only 'High', 'Medium' and 'Low' quality class trains were used, with all 'Doubtful' trains excluded from analysis. Low quality trains were included in the analysis to improve the validity of the data and to incorporate short click trains from animals engaged in behaviors other than foraging (following the manufacturer's recommendation).

The performance of the train detection depends on the level of background noise and interference from other sound sources and the result is a balance of detecting the weakest possible clicks without picking out false detections. Earlier published studies of bottlenose dolphins with T-PODs reported low rates of false acoustic detections during periods when no dolphins were observed visually, (Philpott *et al.* 2007); others described porpoise detections during times when no porpoises were assumed present (Bailey *et al.* 2010) while some chose not to examine their data for false positive detections (Leeney *et al.* 2007; Elliott *et al.* 2011a). Although some false positive detections appear commonplace with dolphin monitoring (Elliott *et al.* 2011b), T-POD studies on harbour porpoises reported very low incidence of false positive detections (Kyhn *et al.* 2012). According to the manufacturer, the C-POD's train detection is now much improved in comparison to the T-POD's, with a very low rate of false positive detections, although there have been no published studies to assess this, with either porpoises or dolphins. To ascertain a false positive rate for a dataset, the manufacturer recommends a visual examination of a sample of classified trains (www.chelonia.co.uk). Additionally one could examine the C-POD click train data from periods when no animals were sighted (although this would then relay on the quality of visual observations) and express the false positive rate as a percentage of total observation time (Kyhn *et al.* 2012). Here both methods were attempted, although visual examination of dolphin clicks is complicated by the fact that dolphin clicks are not as easily defined as the very stereotypical porpoise clicks (Au 1993; Wahlberg *et al.* 2011). Furthermore, attempts to examine false positive detections during periods when no dolphins were sighted are necessarily affected by the potential observer error, as no sightings does not automatically mean that animals were not present, especially with dolphins which can emit clicks of very high intensity. A fast travelling animal, may have ensonified the C-POD and consequently been acoustically detected, whilst being missed by the visual observer. During a 50 day sample (during deployment period 2) of visual observations totalling 147 hours of visual effort time, there were 90 sightings of dolphins, of which 71 were acoustically detected within 5 minutes of the visual sightings, and further six acoustic detections which were not visually detected, totalling 3293 click trains in four C-PODs. The portion of false positive click trains in this sample was considered negligible at 0.0018 % (6 out of 3293). Of the six acoustic encounters without simultaneous visual detections, three were clusters of trains classed as 'moderate' quality, and considered to be actual dolphins missed by observers, whereas three consisted of single 'low' quality click trains and were identified as potential false positives. A further cause for concern with dolphin detections is the potential likelihood of erroneous species classification, especially in areas where both dolphins and porpoises are present. Here we sampled 100 randomly selected click trains which were assigned as dolphins by the train detection algorithm and visually assessed them to identify trains that may have been falsely classified as dolphins when they were actually of non-cetacean origin or from a another species (in this case harbour porpoise). This visual validation was based on known characteristics (Table 1) of dolphin echolocations such as click duration, mean inter-click interval (ICI), modal frequency, bandwidth and amplitude profile represented in CPOD.exe. In cases when more than one of these characteristics was deemed substantially different from the known characteristics, it was categorised as a potential false positive train. The false positive rate for the sample data was 2/100, and in both cases the train was thought to originate from a porpoise. To avoid any further misclassifications of the trains, all encounters with both species present were excluded from the analysis. Other studies have used additional click train criteria in their analyses to minimise the potential for false positive detections (Elliott *et al.* 2011a; Rayment *et al.* 2011).

Comparison of Visual and Acoustic Data

The goal was to examine the acoustic detections on C-PODs during periods of visually confirmed dolphin sightings. A binary code was assigned to indicate whether an acoustic detection occurred during each sample minute of visual detections (1 for detection or 0 for no detection). Visual sightings were used as a ground truth and the overall detection probability was calculated as the fraction of minutes acoustically detected from the total number of minutes with visual sightings. Every minute that a visual sighting occurred was considered a trial if it took place within the truncation distance w, beyond which detection probability is zero. The truncation distance of 1999 m was determined based on detection distances calculated from theodolite tracks. Each trial was examined separately for all the C-PODs. Acoustic detections without simultaneous visual sightings were not included in the analysis. Although a minute is a relatively long time period to assess, it is also one of the most commonly used for analysing C-POD data, which is the reason why it was selected for this study, and the implications this may have for the data is discussed later.

Statistical analysis

The aim of the analysis was to explore the effect of distance, behaviour and group size on the acoustic detection probability and the estimated effective detection radius. The variables used were detection distance, group size and behaviour as well as site of C-POD, the deployment period (and season) and each distinct animal encounter (animal visit to the study site separated by at least 15 minutes of no sightings) to model the detection probability of dolphins as a function of distance from the data logger and to assess the effect of group size and behaviour on the detection probability, as well as residual variation in detectability between encounters not explained by these variables. Each minute of data during an encounter was viewed as a binary trial, and the probability of success (i.e., of acoustic detection) was modelled using generalized additive mixed models (GAMMs), with a logit link function and binomial error distribution. Models were fitted with distance, behaviour and group size as covariates, and model selection was based on Akaike's Information Criterion (AIC) and the deviance explained (from R^2 and McFadden "pseudo R^2") (Crawley 2005; Zuur *et al.* 2010). Adding an interaction term between variables behaviour and group size improved the deviance explained and therefore the model fit. Animal encounter, deployment period and C-*POD* were fitted as random (mixed) variables, to allow for otherwise un-modelled residual variation in detectability between encounters, deployment periods or C-PODs. The intercept values for each random variable were plotted in R to visually inspect this variation and to select the appropriate random variable. Diagnostic plots were inspected to assess overall model fit. All statistical analyses were conducted in R version 2.13.2 (R Development Core Team, 2011) using the packages mgcv and gamm4 (Wood 2011).

Effective detection radius

To arrive at the effective detection radius (EDR, also denoted $\hat{\rho}$), the average probability ($\hat{P}$) of detecting a dolphin when it is within distance w of the data logger was derived from the detection function (Kyhn *et al.* 2012) assuming uniform animal density around the data logger and by integrating out the distance:

$$\hat{P} = \int_0^w \frac{2\pi x g(x) dx}{\pi w^2}$$

$$= \frac{2}{w^2} \int_0^w x g(x) dx \qquad (1)$$

The effective detection radius, $\hat{\rho}$, was then calculated using 1999 m as the truncation distance:

$$\hat{\rho} = \sqrt{\hat{P} w^2} \qquad (2)$$

3.4 Results

After excluding all data from unsuitable conditions or where the group size or behaviour was not distinctly identifiable, a total of 66 dolphin encounters were used for the analyses, consisting of a combined total of 3142 minutes with visual sightings compared with acoustic data from the five C-PODs. Figure 3.4 depicts theodolite fixes obtained from a feeding dolphin and tracks of theodolite positions from a travelling dolphin.

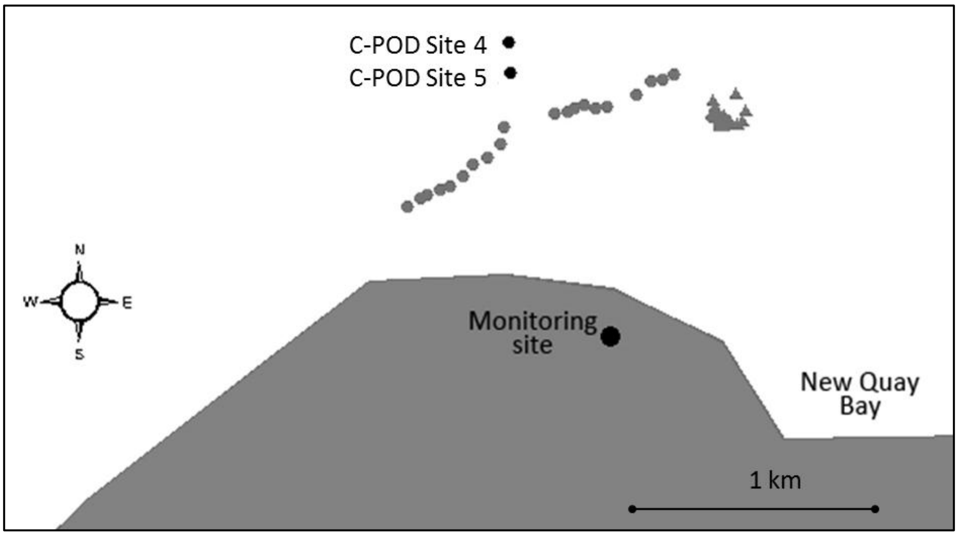

Figure 3.4 Example tracks of a feeding and travelling dolphin observed off of the New Quay Headland during the study. The triangles represent the surface locations of the dolphin classified as feeding, while the circles illustrate surface locations of the dolphin categorised as travelling. C-POD moorings and the theodolite monitoring station are shown on the map by black dots.

Acoustic detections

There were very small differences in number of detections between paired C-PODs, moored 1 m apart, (Figure 3.5), with a high correlation between data from paired C-PODs (Pearson Correlation r=0.995, p<0.0001 and r=0.997, p<0.0001 for the two pairs respectively), which demonstrates the accurate standardisation of these instruments.

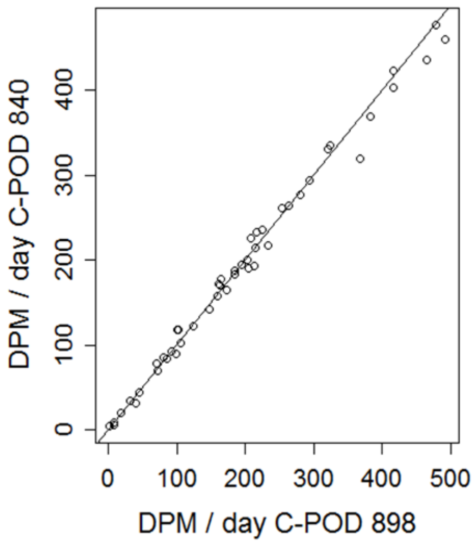

Figure 3.5 Comparison of the number of minutes per day (represented by circles) within which a dolphin was detected for paired C-PODs (898 and 840 and 901 and 897), moored within 1m from each other. DPM =Detection Positive Minutes. Diagonal line of the graph denotes perfect agreement.

The maximum detection distances calculated from theodolite tracks for the different C-POD locations varied between 1343 m and 1779 m and the mean maximum distance was 1512 m (95% CI: 1414–1609 m), (Table 3.2). The average detection probability for bottlenose dolphins for all the C-PODs was 0.59 (95% CI: 0.45-0.73). Adding an additional C-POD 1 m and 100 m apart, only slightly increased the probability of detecting more dolphins from an average of 0.72 for single C-PODs to 0.75 for paired 1 m apart and 0.78 paired 100 m apart.

Table 3.2 The maximum and median dolphin detection distance and the overall detection probability (P) for each C-POD. Paired C-PODs during deployment 2 separated by grey lines.

Deployment Period	**C-POD Site**	**C-POD #**	**Max Dist (m)**	**Median Dist (m)**	***P***
1	1	900	1779	729	0.41
1	2	885	1590	535	0.48
1	3	921	1343	668	0.41
2	4	840	1272	462	0.70
2	4	898	1684	465	0.74
2	5	901	1624	539	0.70
2	5	897	1624	541	0.70
1 & 2		Mean	1512	563	0.59

Differences between deployment periods

The detection probability for the second (summer) period was significantly higher than that of the first period (Table 3.2). The mean distance from an observed dolphin to a data logger, the group size and frequency distribution of behaviours differed greatly between the two deployment periods (Figure 3.3). In particular, the average distance between the logger and the sighted animal for sightings was longer and the group sizes larger in the first deployment than in the second. There were also more sightings of travelling dolphins than feeding ones in the first deployment, whereas there were considerably more feeding encounters in the second period (Figure 3.6).

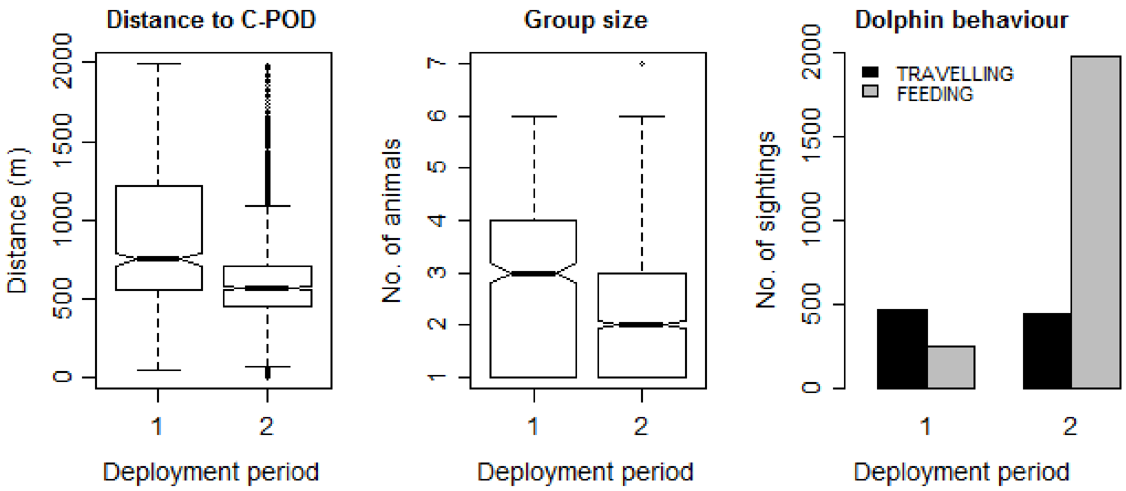

Figure 3.6 Differences between the two C-POD deployment periods for each variable used to explain detection probability. If the notches in box plots do not overlap, the medians are significantly different at the 5% level. Period 1 (Feb to May), n=715 period 2 (June to July), n=2125.

Modelling acoustic detection probability

All variables tested contributed significantly to the model with lowest AIC including the interaction terms (Table 3.3). GAMM with all variables and interactions between group size and behaviour was the model with best fit without false convergence errors and lowest AIC values, despite explaining only 11% (McFadden Pseudo R^2) of the variability in detection probability in the dataset. Of the random variables, the largest effect was found from encounter, judging by the amount of variation introduced to the model. Encounter was thus kept as a random effect in the final model, effectively allowing for the possibility that the outcomes of trials within encounters are more similar than those between encounters. Maintaining the random variable of animal encounter lowered the AIC value (2985), decreased the adjusted R^2 value to 0.11, and increased p-values of all variables, rendering behaviour non-significant (p=0.0543).

The *z*- and *p*-values from the R summary outputs were used to assess the influence of each variable. After distance, the variable group size had consistently the strongest influence on the response variable, followed by interaction between behaviour and group size (Table 3.3).

Table 3.3 Parameter estimates and their statistical significance from the generalized additive mixed model (GAMM) of acoustic detection probability. AC.DET~s(DIST) + GRS * BEH, random=~(1|ENC). The model included as fixed covariates behaviour (BEH, a factor with 2 levels) and group size (GRS, numerical covariate), together with their interaction (GRS*BEH), and a smooth of distance from whale to POD (s(DIST)). Encounter was included as a random effect.

Coefficients	**Estimate**	**Std. error**	**z value**	**Pr(>|z|)**
(Intercept)	-0.5328	-0.804	0.4215	0.4215
BEH	-1.0519	-1.924	0.0543	0.0543
GRS	-0.6483	-2.547	**0.0109**	**0.0109**
GRS* BEH	0.5090	2.016	**0.0438**	**0.0438**
Smooth term	**Effective df**	**Ref.df**	**Chi.sq**	**p-value**
s(DIST)	5.28	135.6	**<2e-16**	

As expected, the detection probability decreased with distance from the data logger, but with a varying effect for two behaviours (Figure 3.7). The number of detected feeding dolphins was significantly higher than that of travelling dolphins (0.17, X^2 =104.9224, df=1, p-value < 2.2e-16) (Figure 3.8), and there was a distinct seasonal difference in the number of animals observed feeding, with a marked increase during the summer months (Figure 3.6).

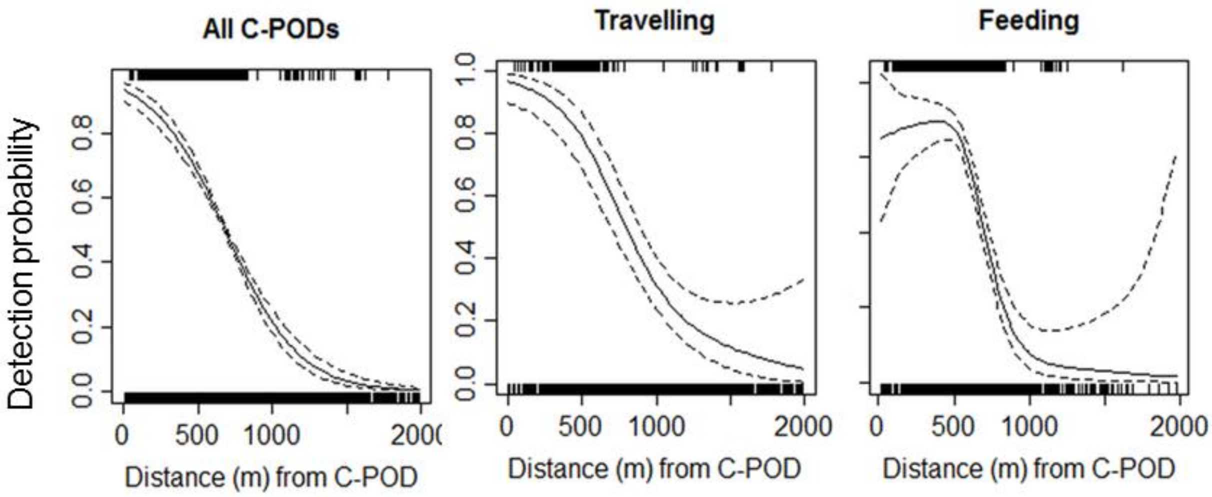

Figure 3.7 Detection probability of dolphin click trains for C-PODs as function of distance from data logger. Solid line is the smoother for distance with GAMM; dotted lines depict the 95% confidence interval.

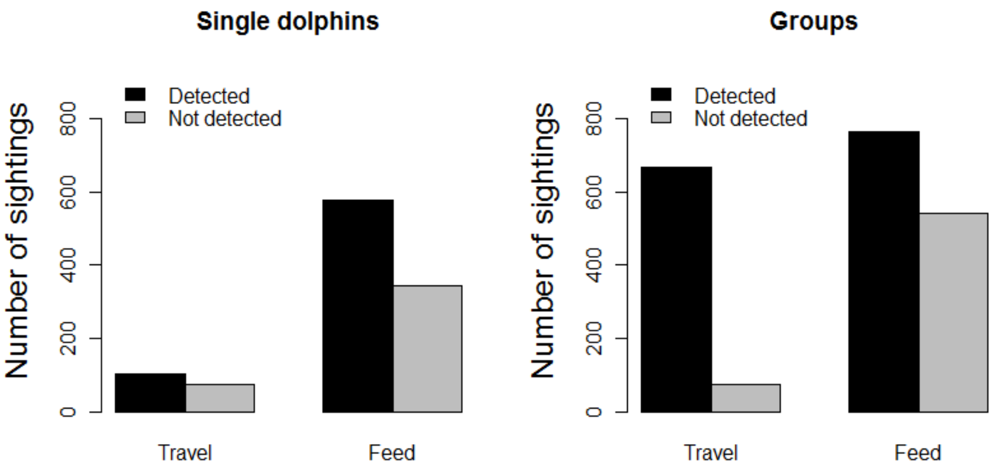

Figure 3.8 The number of visual dolphin sightings with simultaneous acoustic detections (black) and those without matching acoustic detections (grey) in the two behavioural categories for both single animals and groups of dolphins.

The overall detection probability decreased with increasing group size, although for feeding dolphins, an increase in group size increased detectability (Figure 3.9). Furthermore, the detection probability (*P*) for single dolphins was significantly higher than that of groups. For single dolphins, the detection probability of travelling dolphins was higher than for feeding dolphins whereas for groups, the opposite was found (Figure 3.10).

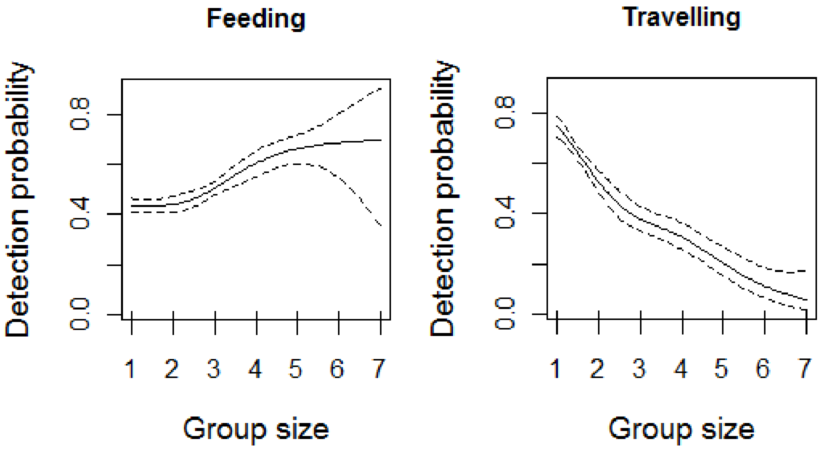

Figure 3.9 The effect of group size on acoustic detection for feeding and travelling dolphins. Solid line is the estimated smoother and the dashed line indicates 95% confidence intervals.

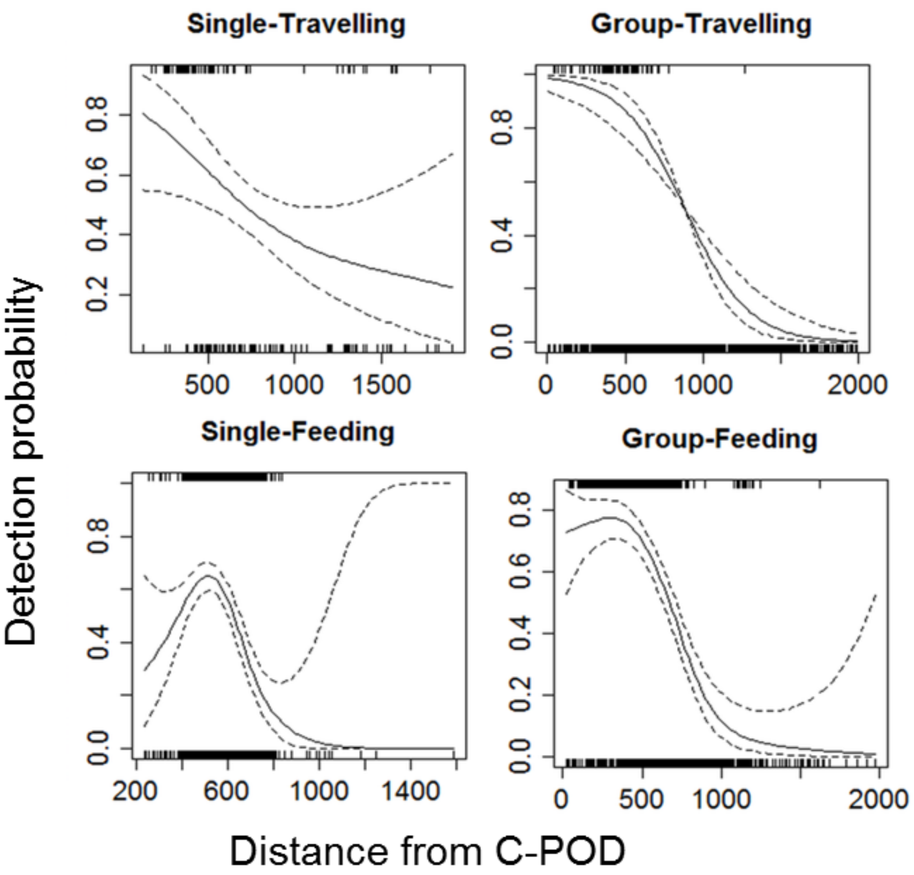

Figure 3.10 The effect of distance (x-axis) on acoustic detection probability (y-axis) for the two different behaviours for single dolphins (n = 1097), and for groups of dolphins (n=1743) obtained using the generalized additive mixed model (GAMM). Dashed lines indicate 95% confidence intervals.

Effective detection radius (EDR)

The average EDR for travelling dolphins was 317 m (95% CI: 211-497 m) and for feeding dolphins, 449 m (95% CI: 280-691 m). The highest EDR was calculated for single travelling dolphins (604 m, 95% CI: 447-785 m). Effective detection area respectively varied from 0.04 km^2 to 1.14 km^2 (travelling) and 0.73 km^2 to 0.55 km^2 (feeding). For travelling dolphins, the EDR decreased considerably with increase in group size (604 m to 113 m), whereas for feeding dolphins the EDR remained relatively constant (481 to 416 m) (Figure 3.11).

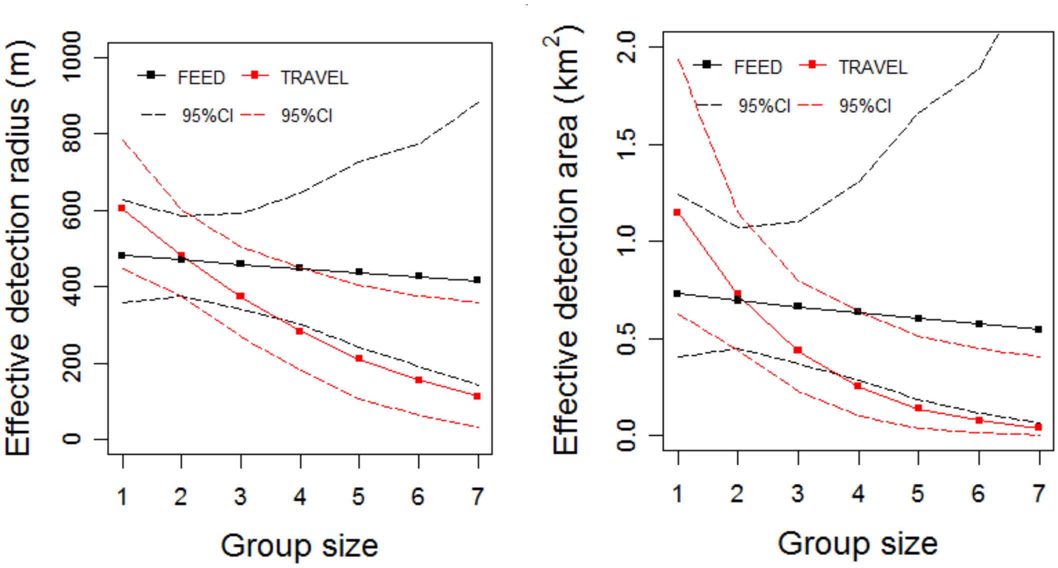

Figure 3.11 Effective detection radii (EDR) and the effective detection area calculated for different behaviours, feeding and travelling, and for all group sizes with non-parametric bootstrapped 95% confidence intervals (CI) (dashed lines).

3.5 Discussion

This study demonstrates the suitability of acoustic monitoring, and in particular that of C-POD to detect presence and absence of bottlenose dolphins. However, the study revealed a notable difference in detection probability for the two visually observed behaviours, and varying results for different group sizes, both of which will have implications on acoustic monitoring studies, posing a particular challenge to future efforts using C-PODs to estimate animal density.

The average effective detection radius was defined at just below 400 m and maximum acoustic detections were recorded 1512 m from the data logger. To our knowledge, this is the first time the effective detection radius (EDR) and maximum detection range have been described using C-PODs for bottlenose dolphins. The values fluctuated between deployments (seasons) as well as between group sizes, reflecting the increased feeding events during the summer period. Based on the estimated EDR, the average effective detection area (a circular plot with EDR as the radius) regardless of animal behaviour would be 0.52km^2– an area for which there is as many dolphins missed inside as are detected outside it.

There were no differences in the two pairs of C-PODs tested, which showed very similar overall detection patterns. Large differences in T-POD sensitivities were seen in previous studies (Kyhn *et al.* 2008) as early T-PODs were not standardised at manufacture. The average acoustical detection probability of each minute when animals were sighted was high, with 59% of all visual minutes also acoustically detected for an area with a diameter of approximately 3000 m. The mean maximum detection range, 1512 m, was higher than previously reported for T-PODs (1246 m (Philpott *et al.* 2007) and 1313 m (Elliott *et al.* 2011a)), which was expected considering the C-POD's improved click detection performance. Although this may seem high, it is in fact lower than theoretically calculated maximum detection distances at typical dolphin frequencies of 75, 100 and 135 kHz and for minimum and maximum measured wild dolphin source levels (SL), 177 and 228 dB re 1 µPa (peak-to-peak) @ 1 m, (Wahlberg *et al.* 2011). Calculating transmission loss based on spherical spreading in shallow water (DeRuiter *et al.* 2010) and sound absorption values measured for sea water at 20°C (Fisher & Simmons 1977), transmission loss (TL) can be calculated as follows:

$TL = 20*\log10(R) + (R)*a$, where R is the distance to the animal in meters and a is the frequency-dependent absorption (~0.04 dB/m at 135 kHz, ~0.03 dB/m at 100 kHz, ~0.02 dB/m at 75 kHz). This equation yields detection distances of clicks at these frequencies for minimum SL as 322 m, 381 m and 415 m and for maximum SL as 1264 m, 1627 m and 2291 m respectively which makes our maximum detection distances entirely plausible. Additionally, distances calculated between animals and the C-PODs depended on the accuracy of the theodolite fixes and the accurate measurement of the theodolite station altitude from the tidal height. However, the maximum estimated error in measuring the tidal height correctly was 50 cm, which would cause a distance error of just over 5 m at distances over 1000 m from the theodolite, which was considered acceptable for the purposes of the study.

In addition to the main effect of distance from the data logger, both behaviour (feeding or travelling) and group size contributed to the final model explaining the detection probability of dolphins. As the model explained only 11% of the variation in the data, it is likely that other factors apart from those examined here may also affect this. Indeed the interpretation of *how* both behaviour and group size affect dolphin detection is by no means straight forward and requires a thorough consideration of other potential affecting factors as well inherent biases and possible errors in the analysis presented here.

The results revealed that in general feeding dolphins were more likely to be detected by C-PODs than travelling ones. This is not surprising, as foraging and feeding dolphins are known to echolocate at high rates, using echolocation clicks to locate and range in on their prey, as well as using buzzes in the final ‘terminal’ phase of prey capture (Jones & Sayigh 2002). Furthermore, feeding animals are likely to be pointing their beam in more directions, increasing the chance of it being picked up by a C-POD. During travelling, animals familiar with the area may not need to echolocate as frequently, and they may also utilise information from each other’s vocalisations without the need to constantly echolocate themselves. As the study period spanned across seasons, it was evident that the previously reported summer peak in dolphin presence (Simon *et al.* 2010) was matched by undocumented behavioural differences whereby the dolphins would spend a much higher proportion of their time feeding in the summer months. As a consequence, the visual sightings of dolphins in the summer lasted longer, were located closer to the shore, and consisted of smaller group sizes than those in the winter. This was reflected in the increased detection rates and EDR for the summer periods – largely due to the seasonal variation in frequency of observed feeding encounters in New Quay Bay probably following increased abundance of prey. Current interpretation of dolphin presence and absence based on C-POD data alone will produce biased results depending on the behavioural budget of the animals, and in particular the time spent foraging near the C-POD deployment site.

When examining group size without the effect of behaviour it was found that increasing group size had a significant negative effect on detectability for travelling dolphins, larger groups being less likely to be detected than smaller ones. This may be due to train detection being impaired by reverberation of a large number of concurrent clicks in shallow water, as this effect can be predicted from the probability assessment of trains described previously, however previous T-POD and C-POD studies reported no difference in acoustic detection from changing group sizes (Philpott *et al.* 2007; Meier 2010). In this study, surprisingly, it was found that single dolphins were significantly more detectable by acoustic means than those in groups. A more detailed picture emerged when assessing the detection probability with an interaction between group size and behaviour. This indicated that detection probability increased slightly for larger group sizes of feeding dolphins, but decreased markedly for travelling animals. Furthermore, it appears that not only are solitary dolphins more detectable than groups, but travelling single dolphins are *more* likely to be detected than single animals feeding in the area. What could explain this? This may be due to foraging animals directing more of their sonar into the sea bed where travelling animals ‘look’ ahead using a louder and more horizontal beam that will be detected by more distant PODs. In groups an increased proportion of animals echo-locating during foraging could outweigh this effect.

In any observational study, observer bias must be taken into account. The observers could have missed single travelling dolphins or simply misclassified dolphin behavior. The accuracy of the visual classification of behaviors is important since the animals only spend a fraction of time on the surface, and despite careful descriptive categories, this classification is inherently subjective (Similä and Ugarte, 1993). Despite our stringent criteria, visual observations can never be perfect, and some animals may well have been missed. However it is unlikely that such an increase in single dolphin detections resulted from numerous (unseen) animals in the area, especially considering the large proportion of single dolphins detected visually and only three minutes which were detected acoustically but not visually. At that rate the overall detection probability would have been reduced by just under 0.2%. With such minor effect this potential error was not taken into account here, but studies with lower vantage point, smaller target species or fewer observers may find missed sightings significantly affecting their calculations.

To avoid issues with potential misclassification of animal behavior, future studies could use an alternative way of determining behavior from the acoustic data, using short inter-click intervals (ICIs) as indicators of foraging activity (DeRuiter et al., 2009; Nowacek 2005). This approach would be particularly beneficial if detection probability was estimated for whole encounters, where the proportion of short ICIs could be assessed for the entire encounter duration, instead of individual minutes like in this study.

The accuracy of the distance calculations is essential for this study. Nevertheless with so many separate calculations, and using manually operated theodolite, some errors are inevitable. In addition, the curvature of the earth was accounted for in all the calculations apart from the first one, which estimated the distance of animal from theodolite. Due to the height of the theodolite station, the fractional error caused from omitting the curvature of the earth in this calculation was small, 0.01 or less for the distances measured below 500 m and 0.05 for distances up to 1750 m (Lerczak & Hobbs, 1998). However, to minimise unnecessary error in distance calculations, this should be accounted for in future studies.

There were more sightings of feeding animals in general, but this does not explain why travelling single dolphins had such a high detection probability. A possibility remains that the vocal behavior of single dolphins differs from that of larger groups. It could be that their vocalisations are louder or less directional – increasing detectability - if they needed to cover a larger area by themselves. Groups of feeding animals may go undetected if the decreased source level of buzzes consequently decreases the detection rate of feeding animals buzzes (Atem *et al.* 2009; Jensen *et al.* 2009b). The decreased detection probability of groups of dolphins may be explained by a theory that echolocation information is shared between group members, and that echolocation production per dolphin decreases with increased group size (Jones and Sayigh, 2002; Quick and Janik, 2008). Similar findings for bottlenose dolphins exist from Sarasota, Florida, where individual dolphins were found to echolocate at a higher rate than groups of dolphins (Nowacek 2005). Quick and Janik (2008) showed that larger dolphin groups produced fewer whistles for some behaviours, potentially engaging in passive listening instead. Alternatively, animals in groups might not need to echolocate to the same extent as single animals if they attain necessary information through whistles instead. The function of echolocation is to create a soundscape that allows animals to identify objects and conspecifics, to navigate through turbid or unknown waters, and to search for, approach and capture prey. Travelling groups may have less need to echolocate continuously, as group cohesion and communication between members by whistling serves as a navigational aid even to those not engaging in vocalisation (Tyack 1997). Furthermore, maximum communication distances by whistles, measured for bottlenose dolphins, range over 5 km (Jensen *et al.* 2012), meaning that groups can easily share information over longer distances than the effective detection distance of the C-PODs. Solitary animals would have to create their own soundscape, and therefore may require more regular echolocation.

Another plausible explanation for the difference in detection rates is if dolphins in this study modified their echolocation strategy depending on the habitat type (water depth, ambient noise, bottom composition, etc.), prey sensitivity and their need to simultaneously communicate with conspecifics, thus varying the click rates, sound intensity and frequency, all of which would affect how the C-POD will record the clicks (Jensen *et al.* 2009b). Similar modification according to environmental factors has been suggested for whistle production (Jones & Sayigh 2002; Acevedo-Gutiérrez & Stienessen 2004; Ansmann *et al.* 2007; Jensen *et al.* 2012). Single dolphins may have different echolocation requirements especially if their feeding tactics or prey targets differ from those of larger groups. For example, if single animals were more likely to feed on dispersed benthic or demersal species they may require more intense or more constant echolocations than groups feeding on large shoals of pelagic prey. Larger groups were seen more frequently in the summer when the waters in the bay are considerably less turbid, and further out to sea away from coastal sediment build-up, facilitating navigation by sight, perhaps reducing the need to echolocate continuously.

Many non-biological factors could also have affected the detection rates measured here, such as equipment sensitivity, water temperature and salinity, location in the water column, bottom topography and composition (Au & Hastings, 2008). Previous studies have demonstrated clear differences in sensitivity between T-PODs (Kyhn et al., 2012; Verfuß et al., 2007) and recommended estimating detection probability for each data logger before embarking on further studies. However, the C-PODs are calibrated to much higher standard than the T-PODs were and the paired C-POD comparison revealed a high similarity between those units that were tested. The C-PODS used in this study were all recalibrated after the experiment by the manufacturer and were all found to be within specification of ±0.5 dB after two years of use.

While it was not possible to control the effects of environmental variables in our experimental set up, we estimated that the potential changes in salinity or water temperature during the short study period would have had only minimal effect on the high frequency sounds (Fisher and Simmons, 1977), especially within the short ranges covered here and it was assumed that any halo-or thermocline presence was relatively constant during the study period (Evans, 1995). The deployment site was selected for its relatively consistent character and each C-POD was moored at the exact same depth from the seabed. Still, ambient noise from recreational activities and coastal development may affect the echolocation frequency range used, causing animals to shift to a frequency less masked by other sounds. It is also important to note that dolphins visit the study area regularly (Baines and Evans, 2012) and it may well be that the echolocation patterns in this area are not applicable for other populations or even other sites within the Cardigan Bay area.

3.6 Conclusion

Unlike the harbour porpoise, whose vocalisations are extremely stereotyped across time and space (Goodson & Sturtivant 1996), dolphin echolocation clicks are very variable (Wahlberg *et al.* 2011) making it difficult to categorise 'typical' dolphin click characteristics for an automated data classification system, such as the C-POD and creating a challenge when acoustically monitoring dolphins. The results here reveal that detection probability depends on dolphin behaviour and their group size. A higher detection rate of feeding dolphins in comparison to travelling ones could yield erroneously high density estimates in feeding areas. This will pose a serious challenge to density estimation of dolphins with SAM data. Even monitoring dolphin presence may be problematic due to the effects of behaviour and group size on detectability if non-feeding areas are not identified as an important habitat, particularly if the data are used to assess critical areas for protected species like the bottlenose dolphin.

To overcome this issue monitoring programs should conduct preliminary visual studies to obtain an idea of the average group size and behavioural distribution in the area of interest in order to work out the appropriate average EDR (or P) prior to conducting a larger passive acoustic monitoring study. Alternative method would be to use data loggers capable of determining ranges to detected animals, allowing the detection probability to be calculated via distance sampling methods (Marques *et al.* 2012).

3.7 Acknowledgements

This study would not have been possible without the generous input of Michelle Braña Bradin, Lucy Buckingham, Emily Cunningham, Elisa Girola, Gemma James, Line Kyhn, Paula Redman, Julia Sommerfield, Brett Stones, Betty Zocholl, volunteers from Sea Watch Foundation, and the Dennis Crisp Fund of School of Ocean Science at Bangor University.

3.8 Appendices

Appendix 3.1: Details of C-POD deployment settings

Table 3.4 Details of deployment for C-PODs used

Period	POD	Location	Start Date	End Date	Distance from cliff	Filter setting (khz) / Gain
1	885	52.2250 N, 04.3649 W	09/02/2010	20/05/2010	856 m	20 / 133
1	900	52.2250 N, 04.3736 W	09/02/2010	20/05/2010	1053m	20 / 107
1	921	52.2250 N, 04.3619 W	09/02/2010	20/05/2010	874 m	20 / 142
2	840	52.2228 N, 04.3716 W	05/06/2010	30/07/2010	779 m	20 / 173
2	898	52.2228 N, 04.3716 W	05/06/2010	30/07/2010	779 m	20 / 193
2	897	52.2233 N, 04.3717 W	05/06/2010	30/07/2010	828m	20 / 175
2	901	52.2233 N, 04.3717 W	05/06/2010	30/07/2010	828 m	20 / 200
2	909	52.2228 N, 04.3716 W	05/06/2010	30/07/2010	779 m	80 / 127
2	911	52.2233 N, 04.3717 W	05/06/2010	30/07/2010	828 m	80 / 119

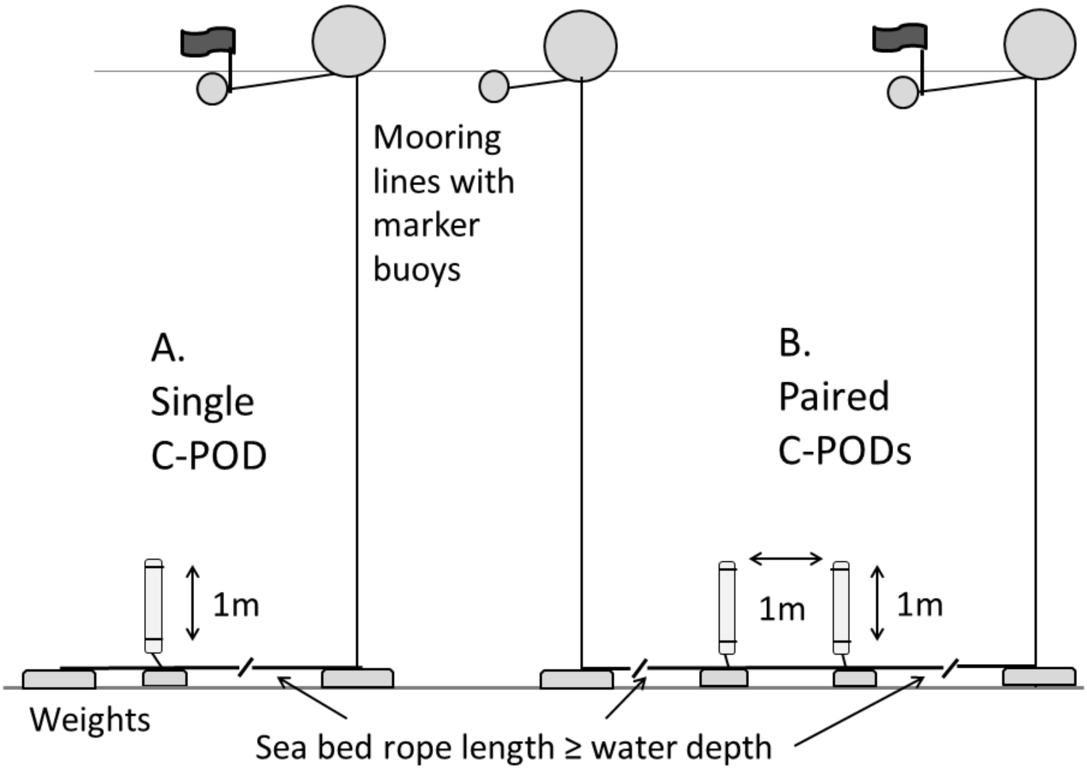

Figure 3.12 Diagram of the C-POD mooring system deployed during the study in A) deployment one (single C-PODs) and B) deployment two (paired C- PODs). Note that seabed rope length not drawn to scale

Appendix 3.2: Inspecting the effect of random variables

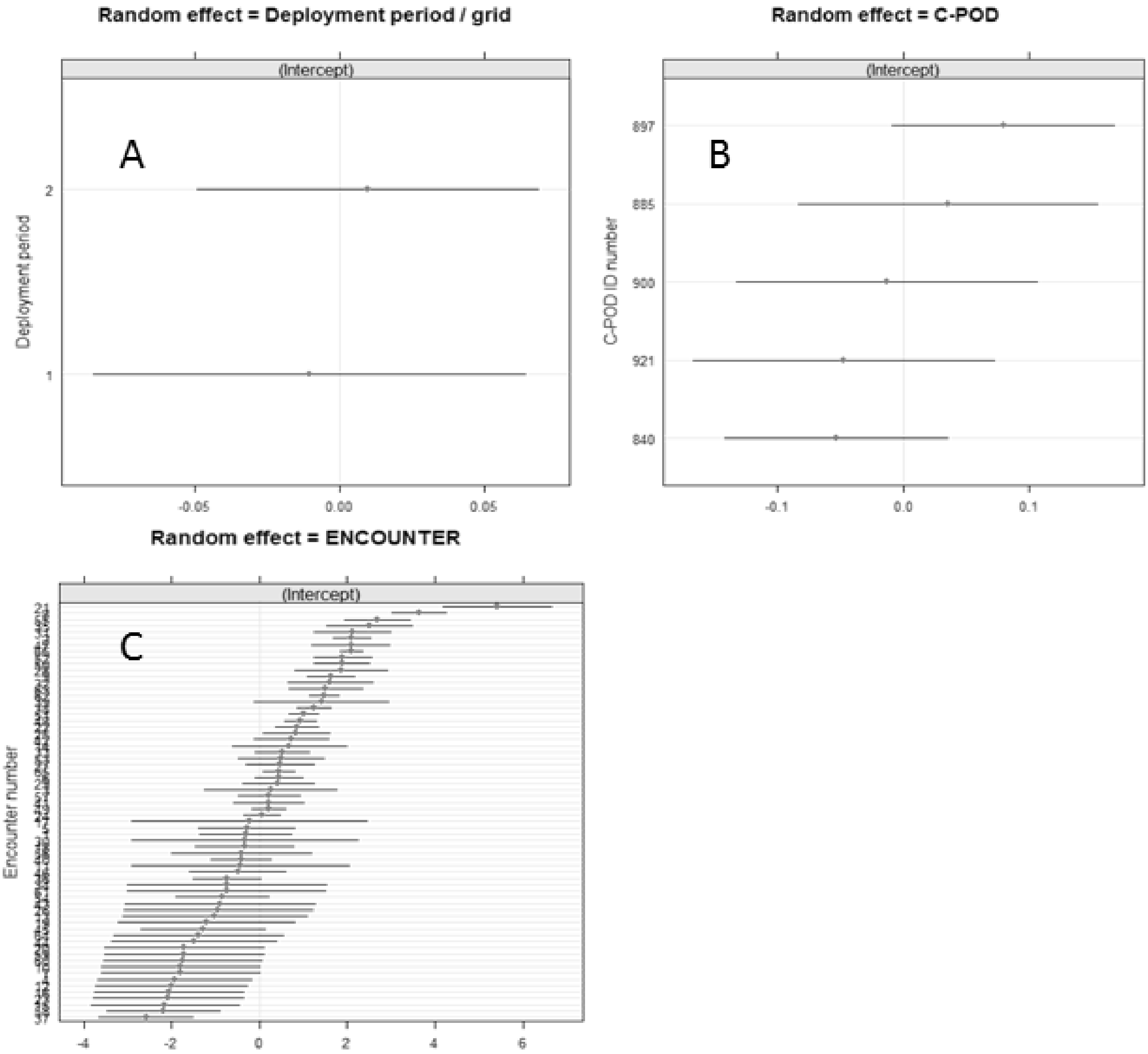

Figure 3.13 Plotting the standard deviations for each level of the random effect around the intercept values from GAMM with a ‘caterpillar’ plot in R. Random effects were: deployment perid (A), C-POD (B) and encounter (C). The larger the difference between intercept values, the bigger the effect on the dataset (as in some encounters) . Overlapping intercept values signify minimal effect from the variables (see deployment period and C-POD). Fitted with ‘lme4’ package in R (Wood 2011).

Chapter 4 COMPARISON OF BROADBAND HYDROPHONE AND C-POD DATA LOGGER RECORDINGS OF WILD BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*) ECHOLOCATION CLICKS

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Author's contribution

This experiment was part of a larger fieldwork organised and funded jointly by the German Oceanographic Museum (GOM) and myself. The idea for the study originated from discussions with various people and would not have been possible without the contribution from Jens Koblitz and Kati Brundiers and others from GOM who designed, built and transported from Germany to Wales an array of hydrophones, several transducers, and all the recording and playback equipment. I managed the day to day logistics of the fieldwork, the two boats used and the research team (including Winnie, Kati and Jens) for land and boat based work. I arranged the deployment of C-PODs, whilst Kati was in charge of setting and maintenance of the C-PODs with help from Winnie. I extracted the information from the hydrophone data with a Matlab script written by Jens. Winnie extracted the C-POD data and conducted initial data handling. I conducted the statistical analyses and wrote the manuscript, which was greatly improved by contributions from both Peter Evans and Jan Hiddink. Jim Bennell and John Turner proof read the manuscript and offered helpful comments before submission to the journal.

4.1 Abstract

Static acoustic data loggers, such as C-PODs, detect echolocation clicks and click trains of cetaceans and have various applications in the monitoring of coastal cetacean populations. Bottlenose dolphins (*Tursiops truncatus)* produce a large range of vocalisations, presenting challenges for the pre-defined C-POD algorithm to accurately identify click trains as dolphins, which can lead to an underestimation of animals detected or an incorrect species classification. As the C-POD has become a popular tool for assessing cetacean presence at sites for coastal development, it is crucial to quantify the detection rate of dolphin vocalisations, and whether click trains with certain characteristics are recognised by the logger's software. Here, we compared simultaneous C-POD recordings of wild bottlenose dolphins to recordings made with a hydrophone with the objective of assessing whether data recorded with the C-POD are comparable to those of concurrent broadband recordings. Earlier work in this thesis indicates that C-PODs may not be able to detect all dolphin feeding buzzes (chapters 3 and 5) and we hypothesise that some click sequences with short ICIs (below 10 ms) may be missed by the C-POD. The total number of clicks recorded, the click rate per minute, and the minimum and maximum inter-click intervals (ICIs) per minute were used for the comparison. The analysis revealed that there was a significant positive correlation between number of clicks logged with the two methods, and that every 1 min sample period with dolphins recorded on the hydrophone had corresponding recordings on the C-POD. However, the hydrophone detected a higher number of clicks per minute. There was a significant difference in the maximum ICI recorded by the two methods ($p < 0.0001$) but no difference in the minimum or mean ICI (at level of $p < 0.05$). Overall, many clicks detected by the hydrophone were not detected with the C-POD, although this did not affect the algorithm's ability to detect dolphin presence since all sampled minutes had dolphins recorded on the C-POD. Contrary to the hypothesis, click sequences with short ICIs (indicating potential feeding events) were identified by the C-PODs despite some not being recorded with the hydrophone, whereas clicks with long ICIs were not classified as dolphin clicks by the current train detection software. C-PODs are capable of identifying bottlenose dolphins, and are suitable for acoustic monitoring, but they do not record their entire vocal repertoire and may not be able to convey full information about vocalisations associated with social context. However, by detecting short feeding buzzes they do have potential to identify

foraging areas, which is critical information for effective management of these protected species.

4.2 Introduction

Echolocation, or biosonar, has evolved as the primary sense for navigation and foraging in odontocetes and bats (Griffin & Galambos 1941; Au *et al.* 1974). Since the discovery of echolocation in dolphins in the 1950s (Kellogg 1958), this sensory system has been under widespread scientific investigation, with much focus amongst cetaceans on bottlenose dolphin *(Tursiops truncatus*) biosonar abilities. The bottlenose dolphin has an exceptionally varied vocal repertoire including burst-pulse sounds and whistles used for communication (Mann *et al.* 2000; Quick & Janik 2008; Janik 2009), and narrowband pulsed sounds like echolocation clicks and buzzes for navigation and foraging (Caldwell *et al.* 1990; Au 1993; Tyack 1997), although clicks probably also have a communicative function (Tyack 1997).

As the majority of the lives of cetaceans is spent underwater, and several species emit frequent vocalisations, acoustic methods provide an important means to study their distribution, abundance and behaviour (Filatova *et al.* 2006; Mellinger *et al.* 2007). One type of static acoustic monitoring (SAM) device is the C-POD, an automated acoustic data logger that records times and frequencies of cetacean clicks. These SAM devices exploit the fact that many odontocetes echolocate regularly (Mellinger *et al.* 2007), and they are capable of recording and storing click data over long periods of time, in most weather conditions, 24 hours a day (Evans & Hammond 2004).

C-PODs and their predecessors T-PODs, have been used to study coastal cetaceans, including the bottlenose dolphin (Philpott *et al.* 2007; Berrow *et al.* 2009; Simon *et al.* 2010), and they can be used to detect trends in seasonal and diel presence (Simon *et al.* 2010; Elliott *et al.* 2011a), assess impacts of coastal developments on habitat use (Leeney *et al.* 2007), or estimate the relative abundance of a population (Kyhn *et al.* 2012). As with any static sampling method, the area surveyed is limited and directly related to the effective detection area, which is around 400 m for bottlenose dolphins (chapter 3).

C-PODs select and log clicks in a frequency band of 20-160 kHz using digital waveform characterisation. They record the time, centre frequency, intensity and bandwidth of cetacean echolocation clicks, and other sounds with similar pure tone properties (www.chelonia.co.uk/design_history.htm, Tregenza (2012)). Logged clicks are stored in the C-POD memory card and downloaded with the accompanying software, *CPOD.exe* for further analysis by the user. These are raw click data stored in CP1 files. The train classification algorithm of the software then assigns these clicks into associated series called click trains and runs a discrimination process to identify the possible source of origin for each train. This produces classified train files, called CP3 files. The trains can be classified as boat sonars or cetaceans, which again are divided into the narrowband high frequency ("NBHF") clicks of porpoises of the family Phocoenidae, and the more broadband generic dolphin clicks, such as those produced by many species of the family Delphinidae (Dudzinski *et al.* 2011). Simultaneously, the software also assigns a 'quality class' to each click train, which represents the probability of the train originating from the said source. Thus each click train will be assigned to a category (boat sonar, NBHF, dolphin, other) and a quality class (High, Mod, Low). Generally, dolphin species are not distinguishable from each other.

Bottlenose dolphins produce highly directional, broad-band echolocation clicks with measured source levels of 177-228 dB re 1 µPa (peak-to-peak) @ 1m, click durations of 8-72 µs, and peak frequencies between 30-150 kHz bandwidth (Au *et al.* 1974; Au & Hastings 2008; Wahlberg *et al.* 2011). Most of the energy within the click is projected out in a directional beam of 9-10^{o} width directly in front of the animal (Au *et al.* 2012). The transmitted beam can be altered in terms of both direction and width, to aid detection of targets slightly off the dolphin's body axis, and the frequency content (Moore *et al.* 2008) can be changed according to ambient noise or other environmental characteristics of particular habitats (Moore & Pawloski 1990; Rendell *et al.* 1999). Echolocation clicks are produced as a series of clicks called trains, which can be further described by their inter-click interval (ICI). ICIs relate to the distance of the echolocation target and the time it takes for the click to reach the target and arrive back at the dolphin, and for the information to be processed (Au 1993). Dolphins decrease their ICIs steadily with decreasing distance to a target (Jensen *et al.* 2009b), and their echolocation rates (the number of clicks or click trains recorded in a time unit) may vary according to different behaviours (Jones & Sayigh 2002). During foraging, they produce shorter and faster clicks, with the shortest ICIs reported for ‘buzzes’ at 3-7 ms duration, emitted immediately before and during prey capture (Wahlberg *et al.* 2011).

Traditionally, recordings of dolphin clicks have been derived from captive studies where the dolphin was trained to remain still and the vocalisations were recorded from directly in front of the animal (Au 1993). Thus most literature on dolphin echolocation focuses upon clicks recorded near to the beam axis, the so called “on-axis” clicks (Madsen & Wahlberg 2007). However, the further from the beam axis the clicks are recorded, the more altered they will be. These “off-axis” clicks have typically lower frequency and amplitude characteristics compared to the on-axis clicks, resulting in a high number of clicks with dominant frequency in the lower part of the frequency range (Au & Hastings 2008). When wild dolphins are being acoustically monitored, the sounds recorded originate from all around the SAM logger, containing a mixture of both on- and off-axis clicks. This can cause a wide variation in the click characteristics recorded, which may be challenging for an automated software to recognise.

With the increased use of C-PODs in acoustic monitoring studies of bottlenose dolphins, the quantification of the efficiency of C-PODs in detecting echolocation clicks is particularly relevant. Practical measures of efficiency are the detection range and probability of detecting dolphins. To assess the acoustic detection probability of dolphins, we need to have a good understanding of the types of vocalisations produced, the context in which they are emitted, and whether different types of vocalisations vary in how they are detected by the C-PODs. SAM studies typically assume that all clicks emitted by the dolphin are detected with equal probability by the logger within the estimated detection radius. Analysis presented in chapter 5 found slightly conflicting evidence for the C-PODs ability to distinguish visually observed feeding behaviour. Here, we hypothesise that some very rapid clicks, with short ICIs, such as those described for feeding buzzes, may be missed by the C-POD’s train detection algorithm, or even not be detected at all. If these types of clicks are less likely to be recorded than others, there will be implications for the application of C-PODs in cetacean monitoring, conservation and protected area management, including the detection of critical foraging areas.

While no survey method is perfect, acoustic methods for marine mammals have advantages over visual techniques with their capability of continuous coverage, automated and potentially less biased data collection, and ability to collect data during conditions that are not suitable for visual surveys. On the other hand, for many species, visual abundance assessment still surpasses acoustic methods despite recent advances in density estimation from acoustic data showing promising results (Marques *et al.* 2009, 2012).

Automated click loggers, like C-PODs, are in some sense at a disadvantage compared to broadband hydrophones because they restrict the accumulated data according to the frequency band they are targeting, therefore missing other information. However, this is also precisely why click loggers are useful, since they limit the data stored, enabling longer deployment periods and reducing observer bias with the automated detection and classification process, providing the devices are calibrated and detector bias eliminated or taken into account.

So whereas C-PODs are designed to miss some data, it is still useful to know what and how much of the data are missed. As C-PODs have gained popularity as a monitoring tool for coastal cetaceans in many areas including the UK, Germany, Denmark and New Zealand assessing and understanding their limitations are crucial to enable future improvements and to assist researchers when drawing conclusions regarding habitat use, acoustic behaviour and activity state, and when estimating relative abundance of dolphins using static data loggers.

This study compares wild bottlenose dolphin echolocation clicks recorded with a broadband hydrophone to simultaneous C-POD recordings, and attempts to assess whether certain click trains may be more detectable than others. To assess this, we used an alternative recording method: a broadband hydrophone with a similar sensitivity and frequency range, deployed simultaneously with the C-POD. The aim was to compare clicks (and click trains) classified with the C-POD’s software algorithm with dolphin clicks extracted from the hydrophone recordings and to examine click characteristics such as minimum, mean and maximum inter-click intervals (ICIs), the total number of clicks recorded and the click rate per minute in both datasets.

4.3 Methods

The study was conducted between 16th April and 5th May 2012 in the near-shore area of New Quay Bay, west Wales (Figure 4.1). This is a shallow bay of 12-25 m water depth, with bottom substrate composed of sand, sandy mud and fine gravel.

Acoustic researchers conducting sound recordings in the field have to cope with environmental and technical challenges, such as generating enough power to drive amplifiers and recording equipment surrounded by seawater, managing engine noise from their own and other boats, accounting for the number of animals and species present and storing the data acquired. This study had its fair share of technical problems as well as being severely constrained by bad weather and a lack of dolphin sightings on suitably calm days. As a consequence, of the three weeks allocated for the recordings, successful recordings were carried out on only two days, and only one day yielded suitable data for the analysis due to a malfunction in the hydrophone recording software. The data used in this study were recorded on 4th May 2012 on a calm day with Beaufort sea state 1 during an hour long encounter with a single feeding bottlenose dolphin.

Three C-PODs were attached together in a triangle formation and deployed from the research vessel, suspended 3 m below the surface, weighed down to keep them in a vertical position. The intention was to compare the data from all three data loggers to the data collected from the hydrophone, which was also suspended from the boat.

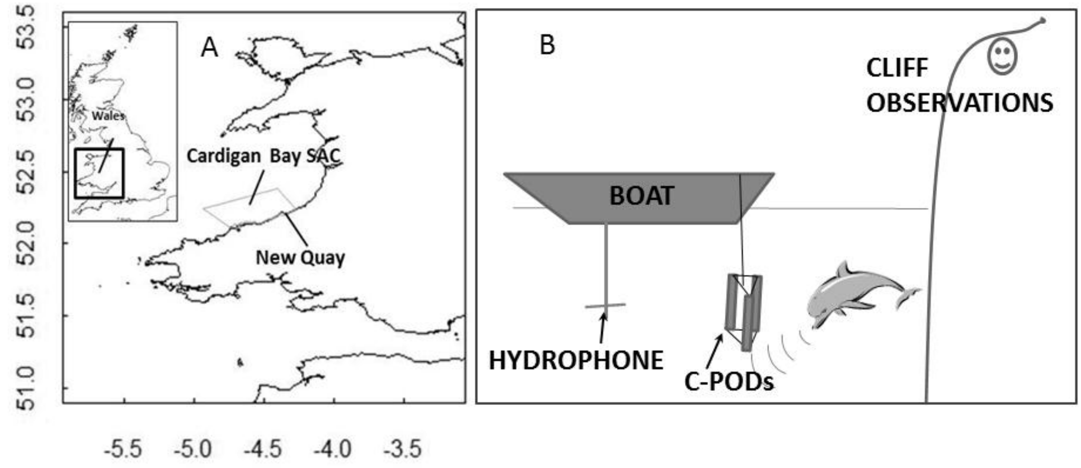

Figure 4.1 Map of the study site (A) and drawing of the recording set up in New Quay bay (B) with a broadband hydrophone and C-PODs suspended from the boat near the

cliff top observation site. Recording position 52° 13.15 N, 004° 21.69W. Not drawn to scale.

Hydrophone recordings were conducted when bottlenose dolphins were sighted within 500 m of the research vessel. The hydrophone used to record dolphin echolocation signals was an omni-directional, Reson TC-4013-5 with 20 m cable, sensitivity: -212 dB re 1V/1uPa at 130 kHz, and a flat frequency response between 110 and 150 kHz. Hydrophone signals were amplified by a custom made 16-channel amplifier by 18 or 38 dB depending on the background noise. Simultaneous A/D conversion was performed by an A/D converter with 16 bit resolution at a sampling rate of 500 kHz per channel (National Instruments PXI-6123). The hydrophone was attached with an aluminium pole to the side of the boat and suspended 3 m below the surface.

The C-POD selects and logs clicks in a frequency band of 20-160 kHz using digital waveform characterisation and duration (5µs resolution), intensity, bandwidth, frequency and envelope criteria to select cetacean clicks. The sensitivity of the C-POD's omni-directional hydrophone varies between -208 and -221 dB re 1V/1µPa, between the entire range of 20 to 160 kHz, with a -208 dB re 1V/1µPa at 130 kHz (www.chelonia.co.uk).

The boat was anchored during the recording period to avoid engine noise and unnecessary movement of the hydrophone set up. A three person cliff-top observation team simultaneously surveyed the area, recording number and behaviour of all cetaceans in the area, ensuring no other species besides bottlenose dolphin were in the vicinity during recordings. The only other cetacean commonly seen in the area is the harbour porpoise (*Phocoena phocoena*), and although porpoise echolocation clicks are very stereotyped and distinct from dolphins, the dolphin clicks can appear similar to porpoise clicks and thus be misclassified by the C-POD software. The aim was to make sure as much as possible, that if porpoise clicks were identified by the software, these would be definite false classifications and not caused by chance encounter of actual porpoises.

Data analysis

With a trained captive dolphin or acoustically tagged dolphin, it would be possible to control or at least monitor the emitted vocalisations and then compare those with recordings from the hydrophone and C-POD. As the study subject was a wild dolphin, it was not possible to compare each emitted vocalisation directly with recorded data, nor could one exactly match the timings of each vocalisation from hydrophone recording to those on the C-POD, although this should be possible with more sophisticated software. To compare the data, the click characteristics were pooled together for one minute blocks across the study period. Data from C-PODs were extracted using *C-POD.exe* software (v.2.026) which classifies clicks into click trains, and compiles various characteristics that researchers can export to analyse the data. The algorithm of the C-POD’s train detection and classification is not available for the public, but some details of the detection process are obtainable from www.chelonia.co.uk. Only click trains classified as dolphins (CP3 files) were used for the analysis, although the raw click data were visually inspected to assess the proportion of dolphin-like clicks not classified as click trains by the algorithm. Click and click train characteristics were then exported for trains classified as High, Moderate and Low quality dolphin clicks, and the mean, maximum and minimum inter-click intervals (ICIs) from each train were compiled.

A Matlab (v2007b) script was used to extract inter-click intervals from dolphin clicks recorded by the hydrophone. The recording software created sound files (*wav* files) of four second duration, and these were grouped together and analysed in segments of 20 seconds due to memory size restrictions of the software used. The waveform of each *wav* file was plotted using time versus intensity of the signal, and a relative intensity threshold value was applied to each 20-second segment to select those echolocation clicks which crossed the threshold value (Figure 4.2). Each 20 s recording was visually inspected to confirm that it contained clicks of the typical dolphin click waveform, although not every click was inspected separately. To avoid echoes in the hydrophone data, a feature was added to the script, which jumped 1250 sampling points (2.5 ms), effectively cutting off any clicks with intervals shorter than 2.5 ms from the previous click. Since some echoes can have longer ICIs than that, all ICIs less than 20 ms were inspected visually, and echoes with opposing waveforms deleted from the dataset. No attempt was made to select specifically on-axis clicks from the hydrophone recordings, so as to ensure that the data analysed from the hydrophone would correspond to the data recorded by the C-PODs.

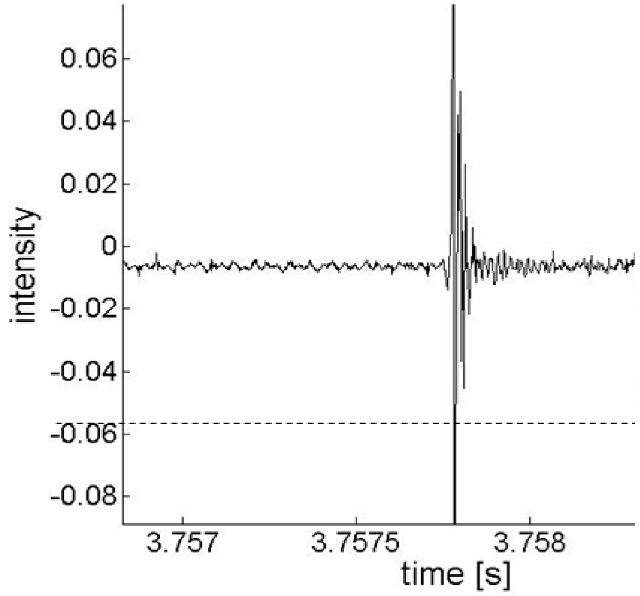

Figure 4.2 Bottlenose dolphin click signal viewed in Matlab as relative intensity against time. The dashed line represents the threshold value that the click intensity has to exceed to be considered a click.

Comparisons of the C-POD and hydrophone recordings were conducted in Excel and R (v.2.13). Data consisted of both counts (click rates) and interval data of ICIs pooled for each minute sample of the dataset. Although pooling data has an effect on the statistical degrees of freedom, it was necessary to cut it to smaller samples to represent the variation in the dolphin vocalisations across the study period.

To investigate the relationship between the click counts from both methods, the non-parametric Spearman’s rank order correlation test was used. To compare the distributions and means of the different click characteristics, we used the non-parametric Kolmogorov-Smirnov test and the Kruskal-Wallis one-way Analysis of Variance by ranks.

The reasoning behind using pooled data for each minute was that it was not feasible to compare the data click by click for the two methods. However, as the hydrophone data were already divided into 20 s long recordings, it was possible to visually compare these snapshot recordings to the continuous C-POD data file, and manually mark those periods of hydrophone recordings which had corresponding detections in the C-POD data. It was then possible to compare the characteristics of those hydrophone recordings which had been detected by the C-POD with those that had not.

4.4 Results

A total of 20 minutes of simultaneous hydrophone and C-POD recordings, when a single dolphin was present, was obtained in the study. This limited amount of data was generated during short single animal encounters in the vicinity of the research vessel in optimum weather conditions. The visual cliff observation team confirmed that no other animal (dolphin or porpoise) was present in the study area and that the animal observed was feeding throughout the recording period. Technical problems with the recording equipment, including data storage and power output on board the research vessel precluded the collection of more extensive recordings. The data covered three separate recording periods of 8 min, 8 min, and 4 min duration with the same animal, all collected from the morning of 4th May 2012.

Despite having deployed three C-PODs suspended from the research vessel, only one of them yielded usable data as one had not started logging due to a faulty SD card (which went unnoticed by the C-POD operator) and the other had switched itself off, probably due to excessive movement from numerous deployments and recoveries to which it was exposed. From the single successfully deployed C-POD, a total of 2219 clicks were acquired for the recording periods, which were automatically classified into dolphin click trains. The data from hydrophone recordings contained a total of 2959 clicks, which were allocated into consecutive click sequences by visual examination of the data. Both methods successfully recorded the dolphin vocalisations for all the minutes when the dolphin was seen in the area. The C-POD’s algorithm classifies clicks into dolphin trains if they fit the predetermined criteria within the algorithm. In our sample, there was only one sequence of clicks that had been identified by the algorithm as a click train but not given a species classification (i.e. one that the algorithm could not place into dolphin or porpoise category), and there were no classifications of porpoises in either dataset. Only classified click trains from CP3 files were used for the analysis, but the visual examination of the raw C-POD click data (CP1 files) revealed that only

73 % of detected clicks matching dolphin click characteristics in frequency and waveform were classified as dolphins by the algorithm.

The number of clicks recorded, and the minimum, mean and maximum ICI values for each minute of successful recordings were compiled for both hydrophone and C-POD data (Figure 4.3). Only those trains that the C-POD's algorithm had classified as dolphins were used for the analysis. The mean ICI and the minimum ICI values from the hydrophone data were very similar for both whereas the maximum ICIs had larger ranges than those extracted from the C-POD data (Figure 4), and the total number of clicks was slightly higher for the hydrophone (in 12 out of 20 samples).

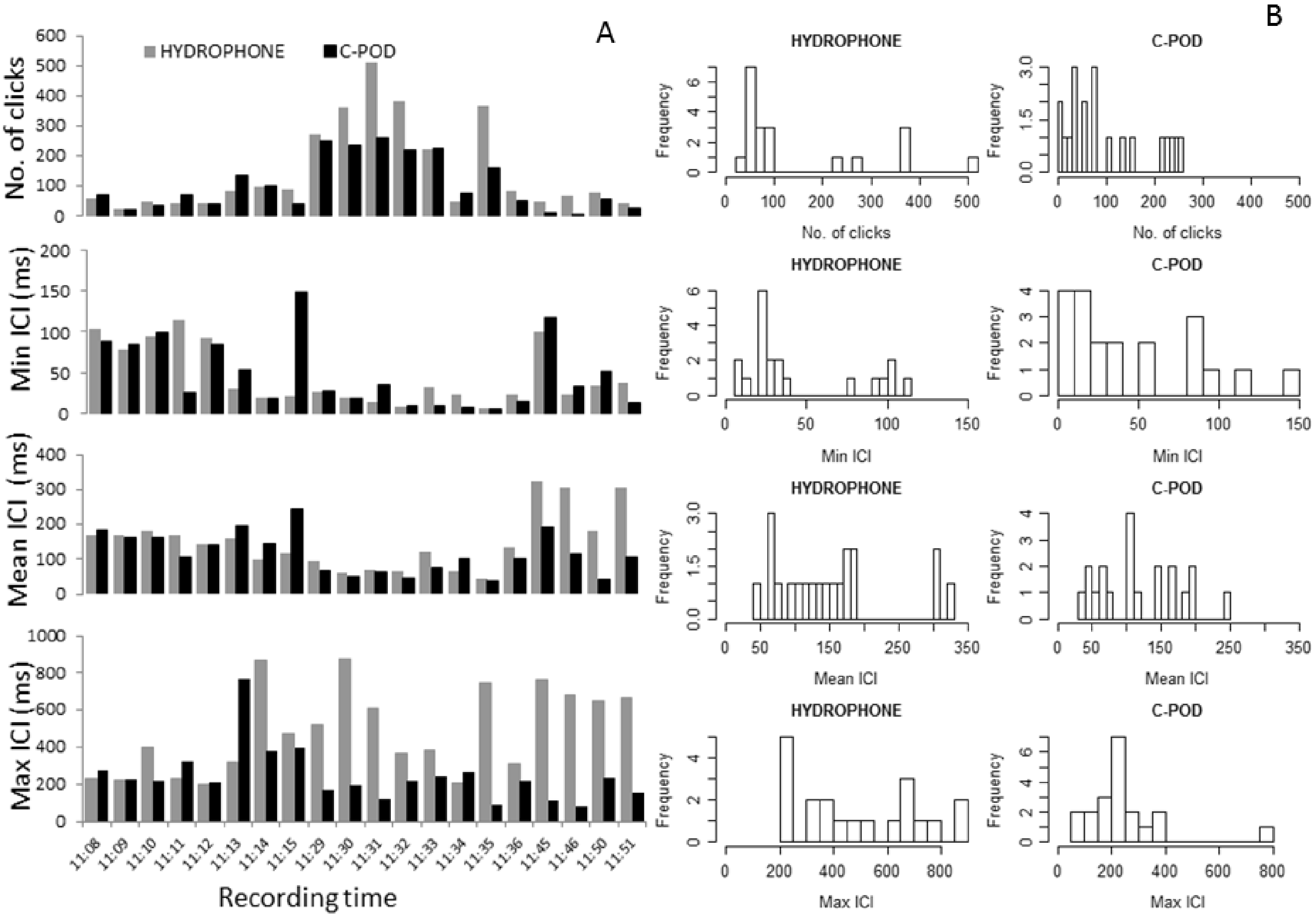

Figure 4.3 The minimum, mean and maximum ICIs for each recorded minute for both C-POD and the hydrophone data (A), and frequency histograms for each variable for both C-POD and the hydrophone (B**).**

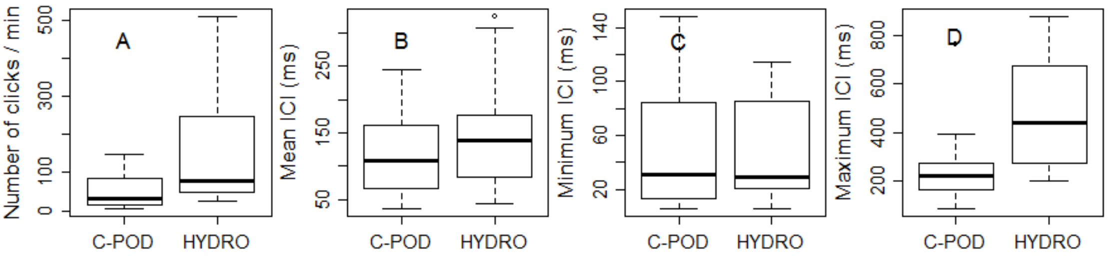

Figure 4.4 Figure 4. Boxplots depicting the distribution of total clicks logged, mean ICI, minimum ICI and maximum ICI for each minute for both hydrophone and C-POD. The thick black line is the median; the upper and lower whiskers represent the interquartile ranges, and circles are outliers.

The click characteristics were compared between the two methods using non-parametric Spearman's rank correlation which revealed significant correlation between C-POD and hydrophone data for *all* click characteristics. As this did not take the outliers into account also Pearson's product moment correlation was conducted, which revealed only the click rate/min and the minimum ICI significantly correlated at level of $p<0.05$ (Figure 4.5). Although the hydrophone detected a higher median value of clicks per minute, the analysis confirmed a significant, strong positive correlation between number of clicks logged with hydrophone and those logged with the C-POD (s = 317.6193, p-value <0.001, $\rho = 0.7612$ (Spearman), t=8.1021, df = 18, p-value <0.001, r = 0.8858 (Pearson)). Similarly the correlation for the minimum ICI test showed a significant positive correlation, albeit not a very strong correlation (s = 610, p-value =0.01505, $\rho = 0.5413$ (Spearman) and t=2.6585, df = 18, p-value = 0.016, r = 0.5309 (Pearson)). The maximum ICI showed a weak negative correlation, although this was not statistically significant (s = 1934, p-value =0.04578, $\rho = -0.4541$ (Spearman) and t=-1.468, df = 18, p-value = 0.1591, r = -0.3271 (Pearson)).

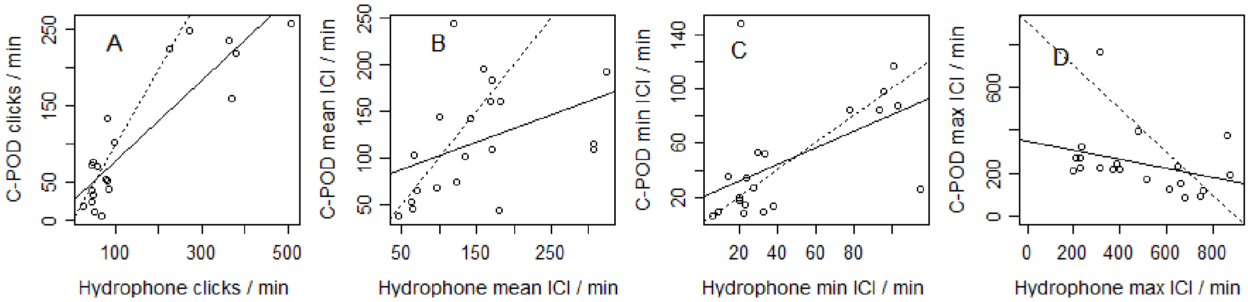

Figure 4.5 Pearson correlation between total dolphin clicks logged/min (A); mean ICI /min (B), minimum ICI/min (C) and maximum ICI/min (D) for the data acquired from the hydrophone and C-POD suspended from boat. Black line is the best fit line from a linear regression, dotted line is the 1:1 line.

Of the four variables examined in this data sample, only the numbers of clicks / min and the maximum ICI / min were found to have statistically significantly different means s, as well as different ratios of variance using the F test in R between the CPOD and the hydrophone (Table 4.1).

Table 4.1 Test statistics and P-values for the Kolmogorov-Smirnov test for differences in mean and the F-test for ratio of variances. Significant p-values in bold.

	K-S Test statistics (D)	K-S P-value	F test statistics (F)	F test P-value
No of clicks/min	0.5238	**0.00629**	9.6566	**4.396e-06**
Mean ICI / min	0.25	0.1963	1.953	0.1535
Min ICI / min	0.25	0.5713	0.7533	0.5468
Max ICI / min	0.555	**0.00396**	2.3946	0.06431

A visual inspection of the hydrophone recordings (n=90), together with the continuous C-POD file, enabled the hydrophone click recordings to be divided into those with and those without corresponding C-POD click train classifications. The proportion of C-POD minutes with ‘raw’ clicks with simultaneous recordings to hydrophone data was 97%, whereas of the classified train data files, only 74% had simultaneous detections with the hydrophone data. The average ICI of those hydrophone recordings without corresponding C-POD recordings was significantly higher at 161 ms than those with simultaneous recordings at 99 ms (Welch Two Sample t-test, t=5.9819, df=292.1, p <0.0001).

4.5 Discussion

Overall, the C-POD performed well by comparison to the hydrophone; every minute of hydrophone recordings were click were detected had corresponding detections on the C-POD, and there was a significant and strong positive correlation in the number of clicks recorded between the two methods. However, significantly fewer clicks (85%) were obtained with the C-POD's train classification method compared to the hydrophone data. Similar comparisons with the C-POD's predecessor, the T-POD, and a broadband hydrophone, revealed even bigger differences in the number of clicks missed by the T-POD (Bailey *et al.* 2010), demonstrating the improved performance of the C-POD compared with its prototype. Of the inter-click interval (ICI) parameters inspected, there was a strong positive correlation with the minimum ICIs recorded but no meaningful correlation found for the mean ICI, and a negative (but non-significant) correlation for maximum ICIs. Despite the fact that no correlation was found for the mean and minimum ICI, they were not significantly different, and the lack of correlation may be due the short time period of recordings presented in the analysis. Of the inter-click interval (ICI) parameters assessed, only the maximum ICI was significantly different between the two datasets. This is probably explained by the fact that the hydrophone click data were visually inspected to identify click sequences, whereas the C-POD data were run with the algorithm that automatically assigns clicks into click trains, which is more conservative and generally does not recognise clicks with very long ICIs as belonging to a train, which may have been classified as such by the visual observers. Therefore, 'single' clicks far apart would be missed by the C-POD. The same reasoning also explains the higher number of clicks in the hydrophone data compared to the C-POD data.

Based on an earlier analysis of C-POD recordings of dolphin and porpoise clicks (see chapter 5 of this thesis), it was hypothesised that the C-POD would miss some of the shortest ICIs because the difference between clicks trains recorded from feeding and travelling dolphins were not very different (although still statistically significant). This could have been caused if some of the fast feeding buzzes were being missed by the C-POD.

The results here did not support such a hypothesis as the minimum ICI values reported correlated well with the hydrophone data. In fact, for some of the samples, the shortest

ICIs recorded were in the C-POD data, although this may be caused by the inability of the C-POD algorithm to accurately pick out from the dataset echoes reflected from the sea surface (Au & Hastings 2008).

To better understand why the C-POD misses some clicks, it is useful to remember that the train detection algorithm was designed to detect cetacean click *trains* with the aim of detecting the occurrence of cetacean vocalisations, and it was never intended to detect every single click produced (Chelonia Ltd 2012b). There will always be individual clicks which are not recognised, due to the trade-off between sensitivity and selectivity and the need to reduce false positive detections. It is therefore expected that the detection rate of the C-POD will be lower than that of the hydrophone. The main potential cause for false detections and for masking the real clicks, is background noise caused by tonal sounds from sediment noise at cetacean frequencies (Thorne 1990). The C-POD's click detection can only detect clicks if they are distinguishable from background noise and therefore will not be able to pick out clicks in very high noise environments. All hydrophones suffer from this, but applying the appropriate high or low-pass filters for the specific location enables better quality recordings to be made. Real-time broadband recordings can assess the noise levels prior to conducting sound recordings, and can better adjust to this problem. With C-POD data, the researcher must assess the quality of the recordings and the level of noise in the data only after the recordings have been made.

In addition to clicks not being detected by the C-POD's hydrophone, they may also not be classified as trains during the post-processing of data by the algorithm, despite having been initially detected. Here, the proportion of C-POD 'raw' clicks with simultaneous detections to hydrophone data was high - 97%, whereas of the classified train data files, only 74% had simultaneous detections with the hydrophone data. To understand why these clicks were not classified into dolphin trains, we examined the ICI characteristics and found that those hydrophone samples that had no corresponding C-POD recordings had significantly larger ICIs. Large ICIs indicate slow clicks, and this type of 'gappy' data are particularly difficult for the algorithm to identify since clicks spaced far apart are not easily recognised as trains (www.chelonia.co.uk). Although these types of 'slow' clicks were uncommon in this dataset it is not known how prevalent such clicks are in dolphin vocalisations. If dolphins produce a lot of spaced out clicks, these will be invariably missed by the C-POD, potentially lowering the logger's ability to detect them.

There were a few instances where fast feeding buzzes were missed by one of the methods, but detected on the other. Feeding buzzes of other species such as harbour porpoises and white beaked dolphins have very short ICIs (down to 1.5 - 2 ms), and are typically lower in intensity than regular clicks. These high repetition rates can make them difficult to detect (Beedholm & Miller 2007; DeRuiter *et al.* 2009). The most likely cause for one equipment missing a click train whilst the other detected it is the high directionality of the clicks (Au *et al.* 2012) combined with the sweeping head movement as the animal scans its surroundings. This would cause the click train to 'ensonify' only one of the instruments. Similarly, dolphin clicks could go undetected if their structure was considerably altered by reverberation (the process of sound decay when echoes and reflections are produced and the sound is subsequently absorbed with each reflection). But if this was the case, one might expect to see altered clicks in both instruments, which was not observed.

Further studies would benefit from feeding the C-POD data through the Matlab script to closely compare the performance of the script with times and number of detections acquired using the C-POD's algorithm. This would allow a closer match with both datasets to see exactly which clicks were detected and which were not (without having to pool the data in to minutes and using average values). The most likely cause of a lower number of clicks recorded in the C-PODs is due to post processing of the C-POD algorithm and the inability of the train algorithm to recognise click sequences with long ICIs and assign these into trains. However, the potential bias introduced in the subjective selection of the intensity threshold of the Matlab script cannot be ruled out. Future studies would benefit from examining received levels and noise levels in both types of recordings to determine directly the detection threshold of the C-POD.

Unfortunately, the algorithm for the C-POD's train detection and classification is not publicly available and so it was not possible to examine more closely why the click sequences with long ICIs are not detected. The manufacturer (Chelonia Ltd) states that the algorithm is so complex that it would not be possible to predict its performance from the algorithm alone, and that it requires intensive testing with real data for empirical validation and to produce a valid and usable transfer function (describing the relation between input and output). Although not within the scope of this study, if the exact system details were available, future researchers could potentially identify areas within the algorithm that could be improved. At present, researchers need to continue to analyse and compare the results of the C-POD studies across different projects to enable them to validate results and interpret them in a sensible way.

Bottlenose dolphin clicks are extremely variable in frequency range, amplitude, length, click rate and inter-click interval, and this poses challenges to any researcher trying to select criteria and parameters with which to identify them. Using automated click loggers and their associated software allows long-term, round the clock monitoring without accumulating excessive data sets, as would be the case with many other acoustic methods. However, the C-POD's algorithm requires distinct parameters in order to recognise dolphin clicks from background noise or from clicks originating from other species such as the harbour porpoise. So far, the different versions of train algorithm from T-PODs to the current C-PODs have steadily improved species detection, which can now identify dolphins and porpoises. Regardless of missing some of the clicks, there were no acoustic events of 30 s or longer on the hydrophone that were missed by the C-POD, and the C-POD data were analysed with considerably less researcher effort than the hydrophone data. However, acoustic detection is not only affected by the instrument, but is very much dependent on animal behaviour and potentially also group size, as demonstrated in chapter 3.

Based upon the results presented here the C-POD is a suitable device for monitoring presence and absence of bottlenose dolphins. It can detect short ICIs that potentially identify foraging events, but besides identifying potential feeding sites, it is not ideal for assessing behaviour without further knowledge on how click rates or ICIs relate to different behavioural states.

The C-POD does not detect *all* clicks emitted and, furthermore, does not classify all these as *trains*. In low density areas, this may be problematic if confirming the presence of dolphins is based on very few detections, whereas in high density areas, missing small proportion of vocalisations would not affect resulting interpretation. C-PODs have the potential to be used in analysis of abundance, click detections serving as cues for animal presence, which can then be converted into abundance estimates using correction factors involving average group size and/or click production rate (Marques *et al*. 2012).

4.6 Acknowledgements

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Chapter 5 IDENTIFYING FEEDING BEHAVIOUR OF WILD BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) AND HARBOUR PORPOISES (*PHOCOENA PHOCOENA*) WITH STATIC ACOUSTIC DATA LOGGERS

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Author's contribution

I organised the data collection (C-POD deployments and pick-up, data extraction and visual observations) with help of volunteers during winter and spring 2010, autumn 2010 and winter 2011. Rhiannon Meier and volunteers collected data in summer of 2010 which was submitted as Rhiannon's MSc thesis in 2010.

I collated the dataset, conducted the analyses and wrote the manuscript. Nick Tregenza lent the equipment and helped deploy and set the C-PODs.

Jan Hiddink helped with statistical analysis and R script and comments from him and Peter Evans and greatly improved the structure of manuscript. Jim Bennell conducted side scan analysis of the study area.

All authors proofread the manuscript and offered helpful comments before submission to the Journal

5.1 Abstract

Sound is the main means of communication for cetaceans and studying their vocal behaviour can reveal important information about their activity patterns. As static acoustic monitoring of whales, dolphins and porpoises becomes more widespread, it is important to understand how data collected with automated click loggers relate to their behaviour. To assess whether behaviour can be inferred from click train data, echolocation click trains of bottlenose dolphins and harbour porpoises recorded by C-PODs were examined with simultaneous visual observations. Recorded click trains from both species had different characteristics for the two observed behavioural categories: travelling and feeding. Foraging click trains for both species were of shorter duration, and had shorter inter-click intervals. The distinction in click trains between the two behaviours was stronger for porpoises. More than one quarter of the porpoise trains represented a distinct group of very fast click trains, or “buzzes”, thought to be associated with foraging, whereas only a small fraction of such trains was found in the dolphin clicks. For both species, the C-PODs showed potential in detecting foraging behaviour and in identifying potential feeding sites and trends in foraging activity.

5.2 Introduction

The protection of a threatened species requires conservation and management of its habitat and the ecosystem upon which it relies. For large, mobile marine mammal species it is not practical to designate their entire habitats as protected areas. Therefore it is essential to identify those areas which, if protected, would be most beneficial to the species’ survival, such as those used for feeding or breeding (Hoyt 2004). To assess impacts of threats on populations, it is important to investigate trends in foraging or breeding success, in addition to monitoring animal abundance (Fiedler & Jain 1992). For marine mammals this typically requires visual observations of behaviour, which can be expensive and often require a lot of manpower, especially when it requires techniques like aerial or boat based surveys, photo-identification or tagging (Evans & Hammond 2004). Many studies of cetaceans rely purely on behavioural observations during surfacing, but behaviour can be difficult to identify accurately from visual observations. Cetaceans are only visible at the surface for between 1-10 % of the time (Tyack & Miller 2002), making classification of animal activity based on their vocalisations more appropriate (Martin & Reeves 2002). Cetaceans echolocate more frequently than they produce other types of sounds, possibly due to the energetic costs of whistles in comparison to clicks (Jensen *et al.* 2012). One method of monitoring echolocation activity is to deploy static acoustic data loggers, such as C-PODs to record the clicks (Dudzinski *et al.* 2011).

The two study species, the bottlenose dolphin (*Tursiops truncatus*) and the harbour porpoise (*Phocoena phocoena*), produce very different vocalisations. The bottlenose dolphin emits sounds in three broad structural categories, burst-pulse sounds, whistles and clicks (Caldwell *et al.* 1990; Tyack 1997). It is thought to use echolocation clicks mainly for navigation and feeding while burst-pulse sounds and whistles are used for communication (Mann *et al.* 2000; Janik 2009), although it is highly likely that clicks also serve a communicative function (Tyack 1997). By contrast the harbour porpoise only produces clicks and is thought to use these for navigation, feeding and communication (Verboom & Kastelein, 2003; Koschinski *et al.* 2008; Verfuß *et al.* 2009). This study focuses on the characteristics of echolocation click trains during different behaviours.

Porpoise clicks have mean source levels ranging from 157-191 dB re 1 µPa (peak-to-peak) @ 1 m, click durations dependent on the click repetition rate between approximately 77 – 300 µs, and a peak frequency around 131 kHz (Au *et al.* 1999; Teilmann *et al.* 2002; Verboom & Kastelein, 2003; Villadsgaard *et al.* 2007). Dolphin clicks are shorter and more varied, with measured source levels of 177-228 dB re 1 µPa (peak-to-peak) @ 1m, click durations of 8-72 µs, and peak frequencies between 30-150 kHz (Au *et al.* 1974; Au & Hastings 2008; Wahlberg *et al.* 2011). Inter-click intervals vary with context for both species. Dolphins steadily decrease their inter-click intervals (ICI) with decreasing distance to a target (Jensen *et al.* 2009b). For porpoises, ICIs of around 50-60 ms have been reported from small data samples during the initial navigation/search phase (Au 1993; Verboom & Kastelein, 2003; Akamatsu *et al.* 2005b; Villadsgaard *et al.* 2007). They are thought to switch to a decreasing ICI only when ‘range locking’ upon the target, and finally end with a terminal buzz with a constant ICI of around 1.5 ms (during maximum click repetition rate) when reaching the target (Villadsgaard *et al.* 2007; Verfuß *et al.* 2009). Both harbour porpoise and bottlenose dolphin are able to adjust the properties of their echolocation signals to allow for varying target range and multiple target selection selection (Jensen et al., 2009b; Wisniewska et al., 2012). Both species project their echolocation clicks in a directional beam with most of the acoustic energy directly in front of the animal, approximately 9-10 ° wide for dolphins (Au *et al.* 2012) and 13° for porpoises (Koblitz *et al.* 2012). Dolphins produce intense, short broadband clicks, whereas porpoises produce only narrowband clicks centred around 130 kHz (Au 1993; Wahlberg *et al.* 2011; Koblitz *et al.* 2012). As higher frequencies are more absorbed by seawater, the higher intensity and lower frequency dolphin clicks travel further than those of porpoises.

Most of the literature describing dolphin or porpoise echolocation focuses only on clicks recorded near to the beam axis, the so called “on-axis” clicks. However, the further away from the beam axis the clicks are recorded, the more altered they become. The “off-axis” clicks from dolphins have lower frequency and amplitude characteristics to the on-axis clicks (Au & Hastings 2008), which results in a high number of clicks with dominant frequency in the lower part of the frequency range, making the dolphin clicks recorded by C-PODs very variable. The quieter, more narrowband, high frequency clicks of the porpoise show very little off-axis click frequency variability and thus are easier to recognise and classify, particularly when using automated algorithms such as those utilised by C-POD’s software. Despite the distinct characteristics of clicks, there are occasions where individual dolphin clicks can seem very similar to porpoise clicks, and this can cause errors in species classification (Simon *et al.* 2010).

Both species alter their vocalisations according to function and behaviour. Dolphins emit different types of vocalisations used for different behaviours (Nowacek 1999, 2005; Acevedo-Gutiérrez & Stienessen 2004; Quick & Janik 2008; Janik 2009; Simard *et al.* 2011). For porpoises which produce only one type of vocalisation (the high frequency click), differences in click train characteristics, particularly the ICI, relate to the behavioural context (Akamatsu *et al.* 1994; Verfuß *et al.* 2009; Clausen *et al.* 2010).

Although echolocation in bottlenose dolphins and harbour porpoises is relatively well studied, few attempts have been made to investigate the influence of behaviour on click train characteristics. Those studies that have examined vocal behaviour in this context have been largely conducted in captivity, and information on wild vocal behaviour involving signal characteristics is generally lacking (Au 1993).

Previous studies have reported varying porpoise ICIs, with progressively falling ICI during foraging ending in a high rate ‘buzz’ of 300-500 clicks/s, (DeRuiter *et al.* 2009; Miller 2010) with an extremely short ICIs of around 1.5 ms (Verfuß *et al.* 2009) during the final prey capture. For dolphins, studies have shown that echolocation rates (the number of clicks or click trains recorded in a time unit) vary according to different behaviours (Jones & Sayigh 2002) and that during feeding, dolphins produce shorter and faster clicks with the shortest ICIs reported between 3.0 and 7.1 ms (Wahlberg *et al.* 2011).

C-PODs and their predecessors T-PODs are acoustic data loggers developed to record information about odontocete echolocation clicks, and are widely used to monitor cetacean presence (Carstensen *et al.* 2006; Rayment *et al.* 2009; Simon *et al.* 2010). Some studies have also used T-POD data to identify porpoise feeding behaviour (Koschinski *et al.* 2008) and to characterise click train characteristics of feeding and travelling dolphins (Zamudio Reyes 2005; Bond 2006). The use of static click loggers as an alternative to broadband hydrophones with recording gear has its advantages, as they are relatively inexpensive, easy to use with small data storage requirements, have automated train detection and they can be left in situ for several months. The C-POD detects clicks in the 20-160 kHz range and records the time and duration to 5 µs resolution, the dominant frequency, and a range of click characteristics. This selective logging limits the amount of data stored. Continuous broadband recording with 16 bit resolution at 500 kHz sampling rate generates about one terabyte of data every ten days, whereas the C-POD’s four gigabyte memory card can last up to five months.

This study explores the use of C-POD click train data to identify different behavioural states for both bottlenose dolphin and harbour porpoise by comparing click train characteristics and visually observed animal behaviours. Additionally the occurrence of potential feeding buzzes based on ICI criteria is examined for both behavioural categories. We hypothesise that differing click characteristics for the two measured visually observed behaviours, feeding and travelling can be distinguished from C-POD data for the two species.

5.3 Materials and Methods

Data Collection

The study was conducted within the Cardigan Bay Special Area of Conservation (SAC), West Wales from February to July 2010. A total of 33, manufacturer calibrated, C-PODs were deployed near the observation site for 151 days at water depths of 17-22m, each C-POD approximately one meter above the sea bed. During this period, visual observations of the area around the C-PODs were carried out on 72 days for a total of 261 hours from a cliff-top monitoring site on the New Quay Headland within the SAC (Latitude: 52° 13.040 N, Longitude: 04° 21.871 W ± 5 m).

Calibration of C-PODs

The sensitivity of the C-PODs had been tested after manufacturing by rotating each unit in a sound field. The sensitivity of the unit had then been adjusted to achieve a radially averaged, temperature corrected, max source pressure level reading within 5% of the standard at 130 kHz (±0.5 dB). These radial values were taken at 5 degree intervals. After the experiment, the units were sent to the manufacturer for recalibration which showed that all units were within the original specifications after two years of use and that there were no changes of operational significance. This calibration and standardisation procedure is accessible in detail on the manufacturer's website, (www.chelonia.co.uk).

Visual Observations

Visual observations were conducted by two to four observer teams in sea states ≤ 3 over a visible sea-surface area of approximately 3 km around the deployed C-PODs from a cliff top at 93 m from the sea surface. During animal sightings, observers recorded behaviour, group size, travel direction, group composition and group cohesion. Binoculars with magnification of 8x32 and a 30 x magnification Sokkia electronic digital theodolite (DT5A) were used to aid detection and tracking of the study animals. A group of animals was described as 'a number of dolphins or porpoises in close association with one another, often engaged in the same activity and remaining within approximately 100 m of one another" (Shane, 1990; Bearzi et al., 1999). To ensure that the acoustic and visual data originated from the same group of animals all periods with multiple groups were excluded from the analysis. As the effective detection area where porpoises and dolphins are detected with C-PODs is relatively small, approximately 150-200 m for harbour porpoises and around 300-400 m for bottlenose dolphins, depending on behaviour (Chapters 2 and 3, this PhD thesis).

Behaviour was defined using the following categories: foraging/feeding (visible surface foraging and prey pursuit/capture where fish seen fleeing, tossed about or in the dolphins' mouth, feeding birds circling above the dolphins, fish shoals visible under the surface and demersal foraging consisting of repetitive, long feeding dives in the same location), socializing (physical contact, chasing each other, mating, synchronised movement, aggression, and play), aerial behaviour, travelling, and milling, where dolphins are moving in varying directions with no observable surface behaviour (Shane, 1990; Bearzi et al., 1999). Because of the low number of observations in some of the behaviour categories (e.g., only 24 minutes of resting behaviour reported for bottlenose dolphins), only foraging/feeding and travelling categories were used for analysis. Typically, the term "foraging" describes the search for food while "feeding" is the actual event of food intake. Here, the category foraging/feeding comprised both foraging and feeding activities, which for echolocating cetaceans typically involves producing high frequency, echolocation clicks.

"Feeding buzzes" were defined as those clicks with ICIs of less than 10 ms duration that are produced during feeding (Verfuß et al. 2009).. Environmental data with sea state, swell height, cloud cover, visibility and tidal height were collected at 15-minute intervals to assess the observation conditions so that sightings made during poor sighting (e.g., rain, fog or sea state over 3 in the Beaufort scale) would not be used for further analysis.

Acoustic Data

The data were downloaded using the C-POD software (*CPOD.exe*) and the click trains in the acoustic data were identified by the KERNO classifier that is part of the post-processing software. Click trains logged on a static logger are generally only brief fragments of longer trains made by the animal and captured as the animal's sound beam sweeps across the hydrophone. Train duration therefore represents the speed of such sweeping movements and is not a measure of the full duration of trains produced. Click trains (series of clicks) are automatically classified by the KERNO classifier into four quality classes according to their likelihood of being correctly classified as originating from cetaceans. Click trains classified into the three highest quality classes (‘high’, ‘moderate’ and ‘low’) were used in the study, while ‘doubtful’ click trains were disregarded. After consulting the manufacturer, low quality class trains were included in the analysis since the study area has low levels of background noise, and low quality click trains showed a strong temporal association with high and moderate quality click trains. The algorithm also assigns each train to a species class; ‘porpoise’ (also called narrowband high frequency (NBHF)), ‘dolphin’ or ‘boat sonar’. To avoid potential false classification by the algorithm, only data recorded during visual observations of single species were used. Additionally, a visual validation of train identification was carried out using the graphical data presentation in *CPOD.exe* on 100 systematically selected trains of both species. This resulted in one potential false positive porpoise detection and two potential false positives in the dolphin data. For dolphins, both false positives were thought to originate from a porpoise. To avoid problems with erroneous species or behaviour classification, only single species sightings and those periods where behaviour did not change, were included in the analysis. Visual and acoustic data were matched by time and each minute of acoustic data was assigned a behavioural category from the simultaneous visual observations.

A total of 13 different click train characteristics recorded by the C-POD were investigated for both dolphin and porpoise data (Table 5.1). Trains with inter-click intervals of unusually long duration (possibly resulting from solitary clicks which the algorithm grouped together as single trains) were removed.

First the click train characteristics for both species were described for the entire acoustic data. This was then repeated for those minutes that had matching visual observations. The acoustic dataset was then inspected for underlying structure between the characteristics using multi-dimensional scaling (MDS). Patterns in the distribution of ICIs were used to identify distinct groups of trains with similar minimum and average ICIs. Trains were considered as outliers and removed if they had ICIs longer than 250 ms for porpoises and 450 ms for dolphins.

Table 5.1 Echolocation click train characteristics recorded by C-PODs used to compare click trains. Inter-click interval (ICI), sound pressure level (SPL)

Characteristic extracted from C-PODs data	
Train Duration (μs)	Modal Frequency (kHz)
No of Clicks/Train	Mean End Frequency (kHz)
Clicks/s	Minimum Frequency (kHz)
Maximum ICI (μs)	Maximum Frequency (kHz)
Minimum ICI (μs)	Maximum SPL*
Mean ICI (μs)	Mean SPL*
Last ICI in a train units	

*Sound pressure levels (SPL) recorded by C-PODs are on a linear scale that varies with frequency and are the peak-to-peak SPLs of the loudest cycles within the clicks. The data logged on each click are insufficient to calculate a true intensity for the click. At 130 kHz the true SPL is the CPOD scale value / 10 Pascals. The SPL scale upper limit is often exceeded by loud clicks which are then logged as having the highest SPL scale value.

Comparison of Click Trains between Different Behaviours

Click trains recorded during observed foraging/feeding and travelling behaviour were compared to examine for potential differences in train characteristics using Wilcoxon rank sum *W* tests (Mann-Whitney-Wilcoxon). A generalized linear model (GLM) with binomial errors, MDS and an analysis of similarity (ANOSIM) were also used to investigate similarity within predefined groups of click characteristics for the two behaviour categories.

Identifying Feeding Buzzes Based on ICI Criteria

Following previous studies, fast trains with a minimum inter-click interval (MinICI) of < 10 ms were used as a proxy for potential feeding activity and those with minimum ICI more than 10 ms were classed as non-feeding activity (Carlström, 2005; Verfuß et al., 2009). The ratio of these ‘feeding buzzes’ to ‘non-feeding buzzes’ and the total echolocation rate recorded were then calculated for the two different behavioural categories (Todd et al., 2009). Both total number of clicks/min and the number of click trains/min were calculated in order to assess the total amount of vocalisation produced (and recorded) by the C-POD

5.4 Results

During the 151 days of deployment, C-PODs recorded 75,015 minutes of porpoise detections and 42,716 minutes of dolphin detections. There were 88 visual encounters of dolphins and 26 of porpoises. Of these, 139 minutes were considered suitable for further analysis. Only 1106 click trains matched the selected visual observation times, of which 536 were harbour porpoises and 570 bottlenose dolphins.

Entire Acoustic Dataset

Both dolphin and porpoise click train characteristics matched those reported in the literature for frequency range and for average and minimum ICI (Table 5.2). The distribution of inter-click intervals of trains classified as stemming from porpoises had a distinct peak of very short ICIs of less than 2.5 ms, whereas dolphin click trains had three peaks, at less than 2.5 ms, at around 65 ms, and at around 135 ms (Figure 1). The average centre frequency of individual porpoise clicks within a train was concentrated around 130 kHz, whereas the average centre frequency of dolphin trains varied between 25 and 120 kHz. The C-POD records a relative amplitude parameter for the received sound pressure levels of each click (confusingly termed SPLs, but care must be taken not confuse this with the widely used acronym for *source pressure level*). This parameter is shown on a linear scale which varies with frequency and is the peak-to-peak sound pressure level of the loudest cycles within the clicks. The data logged on each click are insufficient to calculate a true intensity for the click. The SPL scale upper limit is often exceeded by loud clicks, which are then logged as having the highest SPL scale value. Here the porpoise clicks showed little SPL variation and relatively low values of below 50 SPL units, whereas the SPL values for dolphin clicks ranged from 10 to 160 units, indicating large differences in the sound pressure levels (Figure 5.2).

Table 5.2 Summary of harbour porpoise (HP) and bottlenose dolphin (BND) echolocation click train characteristics detected by C-PODs during whole of the acoustic deployment period. Mean values (± standard deviation, SD) are shown. Inter-click interval (ICI), sound pressure level (SPL*)

Click Characteristic	**HP medians**	**HP means**	**HP SD**	**BND medians**	**BND means**	**BND SD**
Train Duration (ms)	207.99	371.08	482	1029	1259	1012
No of Clicks/Train	7	10.1	7.4	8	10.7	6.4
Clicks/s	37	102	151	7	20	51.2
Maximum ICI (ms)	33.1	55.9	62.3	169	177	1132
Minimum ICI (ms)	25.3	44.0	49.3	126	134	85
Mean ICI (ms)	27.1	46.2	56.8	138	142	87
Last ICI in a train	30.0	52.4	60	156	169	1155

Modal Frequency (kHz)	129	130	5.5	47	50	19.9
Mean End Frequency (kHz)	126	126.2	5.7	61	63	21.8
Minimum Frequency (kHz)	125	124.4	7.6	37	39	14.0
Maximum Frequency (kHz)	134	134.7	5.4	101	95	33.6
Maximum SPL*	40	68.9	66.1	173	159	80.7
Mean SPL*	28.0	39.9	33.2	68	73	43.1
n	1 376 594			272 317		

* Unreferenced sound pressure level derived from *C-POD* software output. See Table 1.

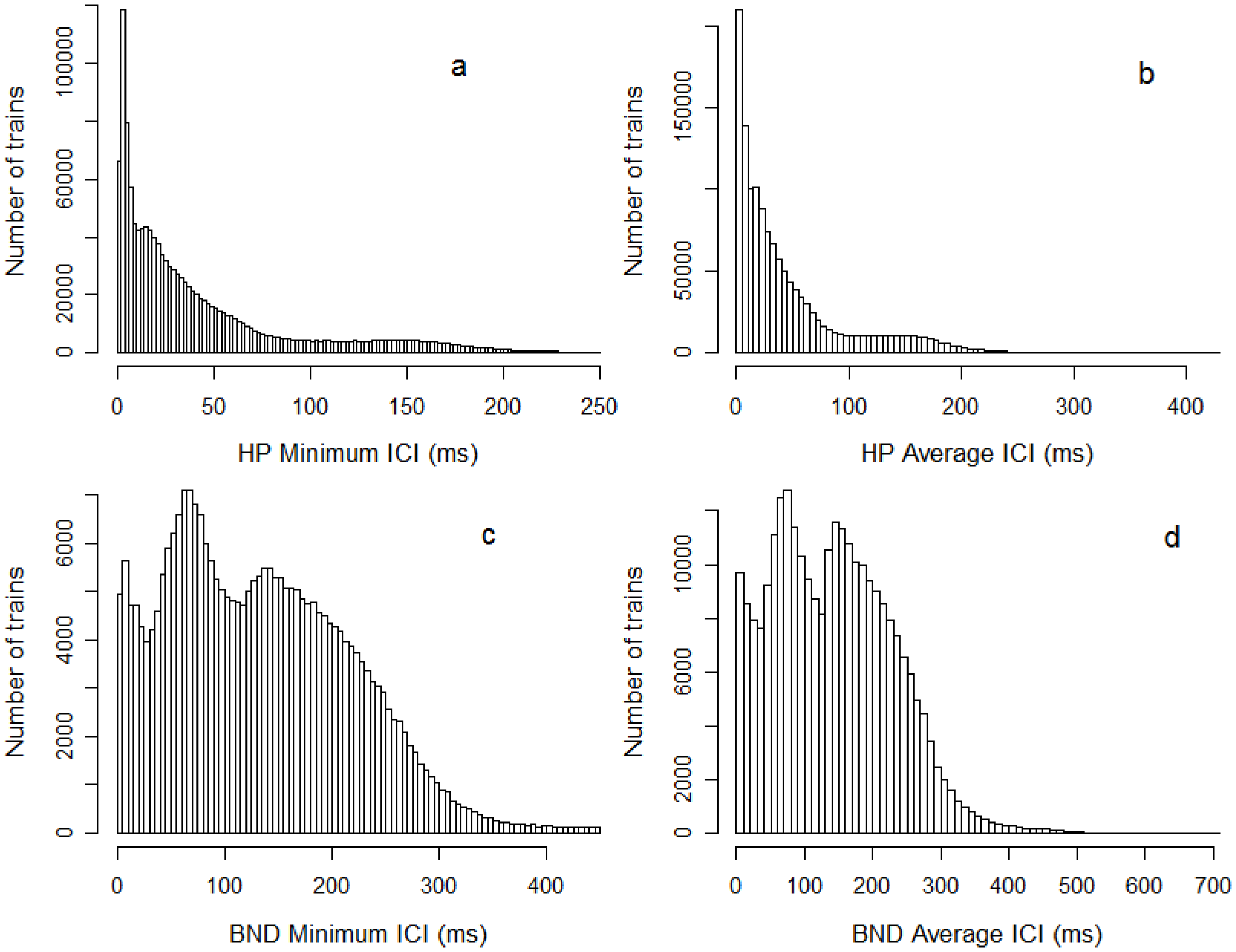

Figure 5.1 Histograms of inter-click minimum and average intervals (ICI) for harbour porpoise (a and b) and bottlenose dolphin (c and d) click trains

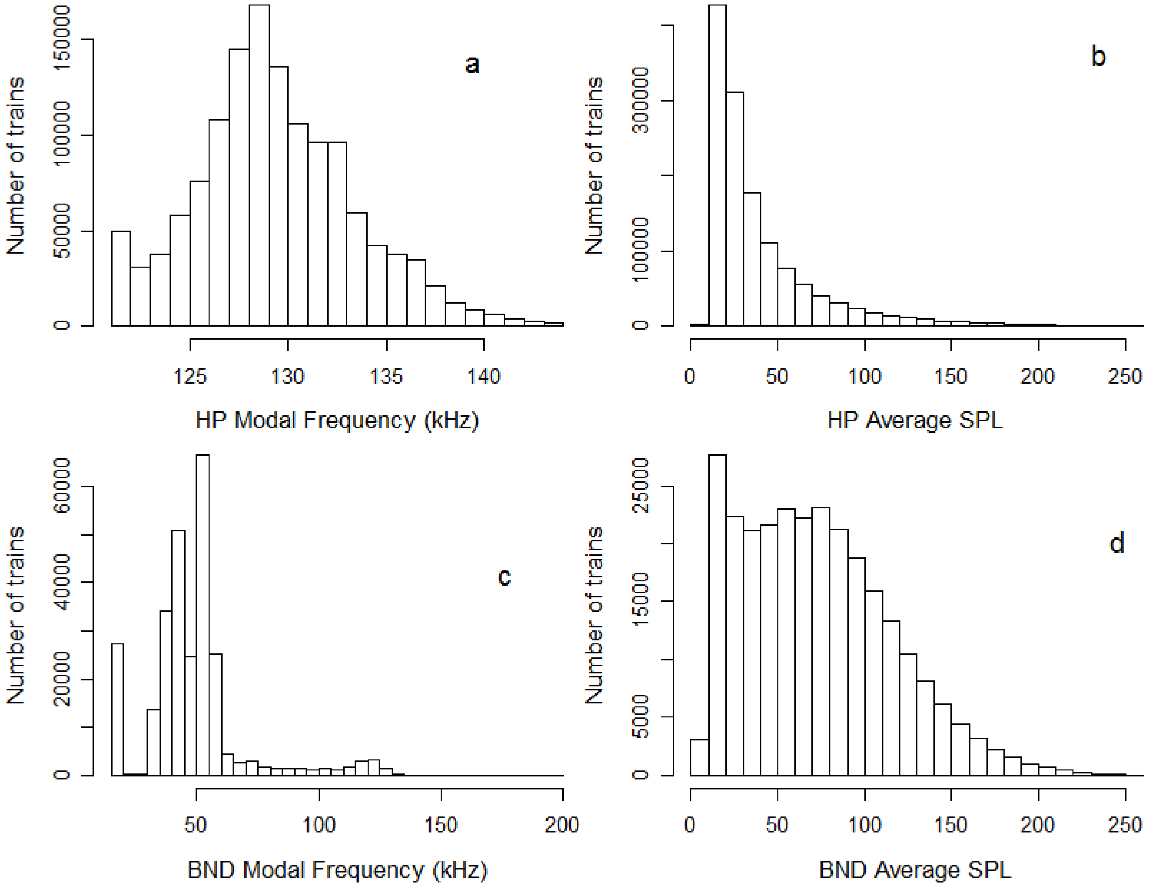

Figure 5.2 Histograms of modal frequency and average received sound pressure levels (SPL) for porpoise (a and b) and bottlenose dolphin (c and d) click trains

There was a positive correlation between train duration and minimum inter-click interval (ICI), shorter click trains being fastest, and having the shortest ICIs (HP: $r = 0.75$, $t = 26.24$, $df = 534$, $p< 0.001$, BND: $r = 0.5521$, $t = 15.78$, $df = 568$, $p < 0.001$).

Differences between Foraging/Feeding and Travelling Trains

Porpoise feeding click trains were shorter in duration, had faster repetition rates, and lower ICIs. Porpoise click trains also had lower frequencies recorded in all frequency categories and lower received maximum sound pressure levels compared to travelling click trains. Similarly, dolphin feeding click trains were shorter and faster, but the differences between the two behaviours were not as obvious as for porpoises (Figure 5.3). According to Wilcoxon rank sum *W* tests, 10 characteristics were significantly different between the two behaviours for harbour porpoise, and six for bottlenose dolphin (Table 5.3).

Table 5.3 Summary of Wilcoxon rank sum *W* tests (Mann Whitney Wilcox) comparing median click train characteristics detected by C-PODs which corresponded to visually observed dolphin (BND) and porpoise (HP) groups engaged in feeding and travelling. Inter-click interval (ICI), sound pressure level (SPL*). Number of click trains analysed: Dolphins: Feeding/foraging, n=424, Travelling, n=146; Porpoises: Feeding/foraging, n=163, Travelling, n=373. Marked in bold are those characteristics that were most influential variables in binomial GLM

Click Characteristics	**HP W test statistic**	**HP P-value**	**BND W test statistic**	**BND P-value**
Train Duration (µs)	11102	< 0.001*	20121	< 0.001*
No of Clicks/Train	20695	0.9718	26199	0.569
Clicks/s	**45605.5**	**1**	**37277.5**	**0.999**
Maximum ICI (µs)	10198	< 0.001*	**19924**	**< 0.001***
Minimum ICI (µs)	9913.5	< 0.001*	20386	< 0.001*
Mean ICI (µs)	10143.5	< 0.001*	20537	< 0.001*
Last ICI in a train	10186.5	< 0.001*	20942	< 0.001*
Modal Frequency (kHz)	**11768**	**< 0.001***	27591	0.863
Mean End Frequency (kHz)	11799	< 0.001*	22482	0.011
Minimum Frequency (kHz)	11526.5	< 0.001*	28470	0.953
Maximum Frequency (kHz)	12466	< 0.001*	19542	< 0.001*
Maximum SPL *	15563.5	< 0.001*	**23879**	**0.086**
Mean SPL *	16502.5	0.03022	**27832**	**0.895**

* Unreferenced sound pressure level derived from *C-POD* software output. See Table 1.

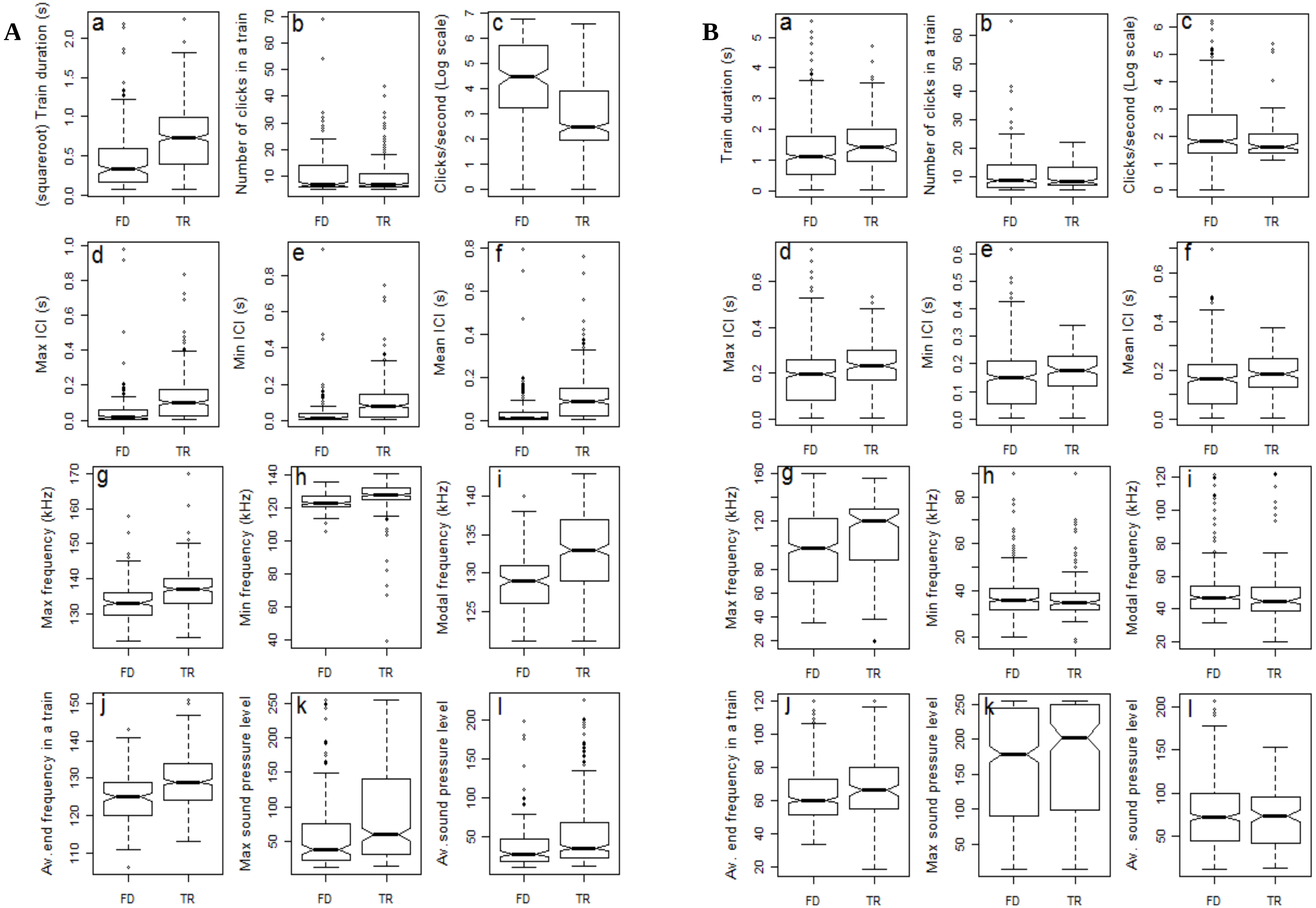

Figure 5.3 Boxplots depicting selected A) harbour porpoise and B) bottlenose dolphin click train characteristics by behaviour: feeding/foraging (FD) and travelling (TR). Characteristics: a) Train duration; b) Number of clicks in a train; c) Clicks/s; d) Maximum ICI; e) Minimum ICI; f) Mean ICI; g) Maximum frequency; h) Minimum frequency; i) Modal frequency; j) Average end frequency; k) Maximum sound pressure level; l) Average sound pressure level. Box represents the interquartile range (IQR), with whiskers extending up to 1.5 x IQR, thick black lines are median values, circles mark outliers, and width of the box indicates sample size. If the notches in box plots don't overlap, the medians are significantly different to the 5% level, $p<0.05$, assuming asymptotic normality around medians and roughly equal sample sizes

Multidimensional Scaling and Analysis of Similarity

ANOSIM within porpoise click characteristics revealed significant differences between click trains recorded during observed feeding and travelling states, (R= 0.2333, p-value < 0.001, 999 permutations). No significant difference was found in dolphin click trains for feeding and travelling animals (R= -0.08403, p=1, 999 permutations). Similarly, no difference in dolphin trains was found from the MDS (Figure 5.4).

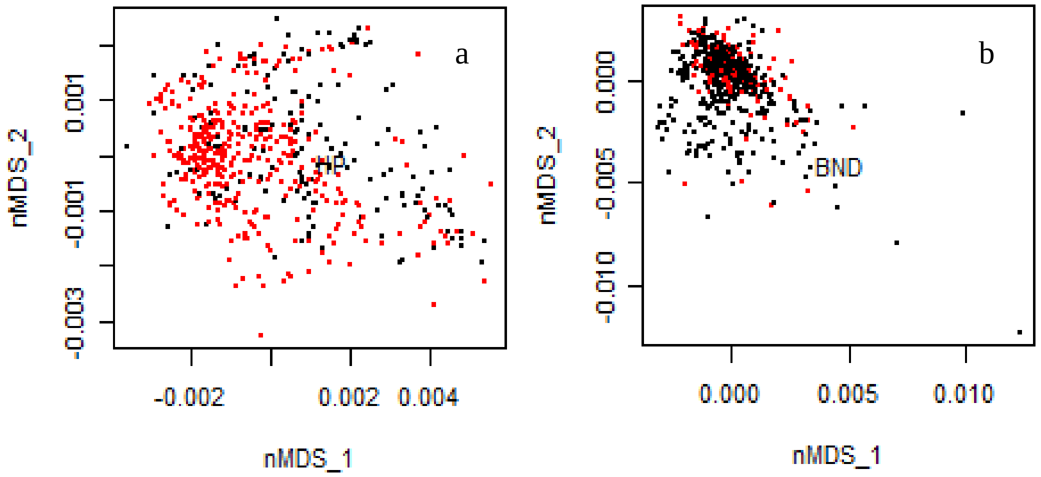

Figure 5.4 Multidimensional scaling (MDS) plots for harbour porpoise (a) and bottlenose dolphins (b) for log transformed click train characteristics by behaviour, feeding/foraging (black) and travelling (red)

Generalized Linear Model

The GLM with binomial errors, conflicted with the ANOSIM analysis, as it indicated that behaviour contributed significantly to explaining the observed differences in click characteristics for *both* study species. For porpoises, modal frequency and clicks/s were the two variables that best explained the difference between feeding and travelling animals (according to AIC model selection). For dolphin data, the selected variables were minimum ICI, average SPL, clicks/s, and maximum frequency. Although clicks/s was not a significant variable, it was nevertheless selected for the best model according to AIC values.

Identifying Foraging/Feeding Click Trains Based on ICI Criteria

For both species, there was a peak of click trains with very short ICIs, indicating possible foraging behaviour (Figure 5.1). This was particularly notable in the porpoise data, with 27.3 % of click trains classified as feeding buzzes with minimum ICIs of <10 ms. Only 3.8 % of the dolphin trains had minimum ICIs under 10 ms. Furthermore, 16.8 % of all porpoise click trains had a minimum ICI of less than 5 ms, whereas only 1.8 % of dolphin data had such short ICIs.

The ratio of these ‘feeding buzzes’ to ‘non-feeding buzzes’ in porpoise data was higher for click trains recorded during observed feeding events in comparison to trains from travelling ones, but there was no such difference in the dolphin data (Figure 5.5). The echolocation rate (for total numbers of clicks produced and number of click trains) was higher for feeding porpoises but lower for feeding dolphins in comparison to travelling animals (Figure 5.5).

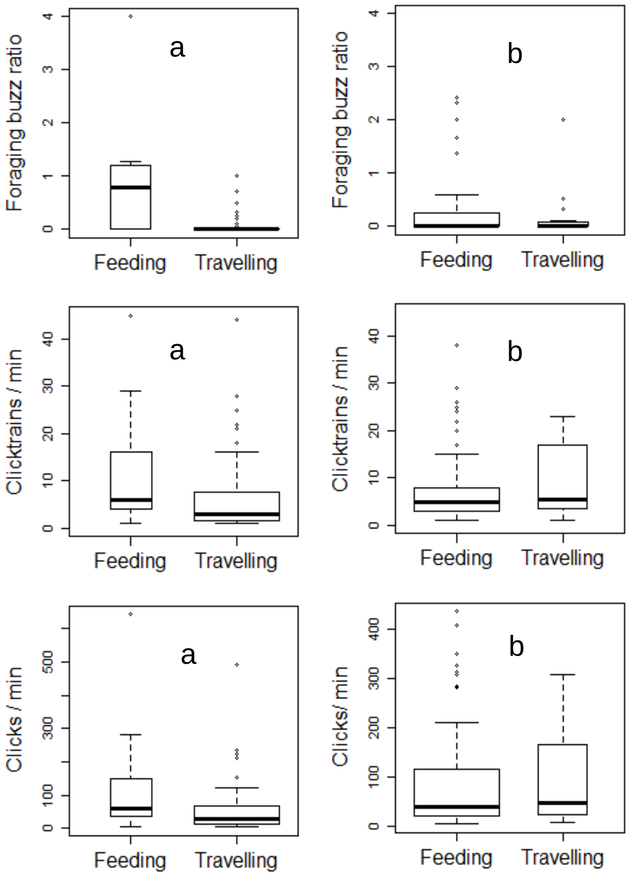

Figure 5.5 Ratio of feeding buzzes (click trains ICIs < 10 ms) to non-feeding buzzes for harbour porpoises (a) and bottlenose dolphins (b) for both behavioural categories (top). Also shown is the echolocation rate in number of trains (middle) and number of clicks recorded per minute (bottom). See Figure 5.3 for explanation.

5.5 Discussion

This study demonstrates that the C-POD click logger together with its associated software is able to identify and distinguish click trains from both bottlenose dolphins and harbour porpoises, and that the resulting click trains have similar characteristics to those described in the literature from direct measurements. The software produces several output characteristics but not all of these are useful for further analysis. Train classification software does not necessarily identify all the clicks of a train with similar probability; and some may go unclassified, while other non-cetacean clicks may be included in the trains. For example, the minimum and maximum frequency characteristics may be affected by these accidental non-cetacean clicks thus obscuring real animal clicks. For this reason, the modal frequency of a train may be more representative of the actual frequency. In cases where there are few detections, or long periods between detections, the software may merge clicks to form trains or alternatively cut trains short, thus causing artificially long or short train durations and potentially erroneous average or minimum inter-click intervals. In fact, train duration is more descriptive of the speed of the animal’s head movement than of the actual vocalisation. Additionally, subsequent trains of very similar characteristics may be of different quality class, in which case the selected quality class, in which case the selected quality class will affect the end results. To avoid these issues, only quality classes high, medium and low were included and trains that had outlier ICI values longer than 250 ms for porpoises and 450 ms for dolphins were discarded.

Minimum ICI and train duration were correlated, so that short trains were also fast trains, indicating that animals sweep their heads from side to side whilst vocalising. Another reason which may cause very short buzzes to be missed by the C-POD, is the lower amplitude levels of buzzes, causing even less of the buzz to be detectable by the C-POD and therefore only partial trains to be recorded.

Trains from porpoises had a distinct peak with a high number of recorded trains containing very short ICIs. Such a peak was not present in the dolphin data which instead had three distinct groupings of ICIs. This could indicate that dolphins use clicks with varied ICIs, producing clicks with short and longer ICIs, whereas porpoises mainly produce clicks with very short ICIs during the last phase of foraging. This might explain why there was a clearer distinction between the two behaviours in the C-POD data from porpoises.

When assessing those trains that were recorded during periods of visual observation, it is evident that both train duration and minimum ICI recorded during observed foraging were shorter than those recorded during travelling. Interestingly, for both species, the trains are of greater intensity (SPL) and of higher frequency in travelling animals. This fits with previous studies where click frequency content was found to correlate with click amplitude (Beedholm, 2010).

This finding is consistent with the theory that travelling animals are interested in interpreting the acoustic scene further ahead, thus requiring more intense clicks with longer ICIs to read echoes from distant targets (Au *et al.* 1985; Atem *et al.* 2009). This is particularly interesting for porpoises as they have so far not been shown to vary their click frequency according to behaviour (Clausen et al., 2010). It must be noted, however, that the SPL of dolphin clicks often exceeds the upper limit of the sound pressure scale of the C-POD and that the sound intensity levels measured from C-POD are not actual source level measurements.

For harbour porpoise data, the difference between feeding and travelling trains was statistically significant using all three methods of analysis (non-parametric Wilcoxon Mann-Whitney, GLM and ANOSIM), whereas the ANOSIM did not indicate statistically significant differences in click trains between the dolphin behaviours. Furthermore, the percentage of click trains which corresponded to the ‘correct’ visually observed behavioural classification was much higher in the porpoise data than in the dolphin data.

There are a number of potential explanations for this: 1) due to the small sample sizes the data may not have been entirely representative of the two behaviours investigated here and the power of the statistical tests was thus reduced; 2) dolphins simply do not produce different clicks for these two behaviours, or 3) the distinction between observed feeding and travelling behaviours was erroneous. The accuracy of the visual classification of behaviour is important since the animals only spend a fraction of time on the surface, and despite careful descriptive categories, this classification is inherently subjective (Similä & Ugarte 1993). Here the observations were carried out only on days with good visibility using visual aids (binoculars and theodolite) and the most experienced observer would confirm the assigned behavioural category depending on his/her judgement of animal movement and speed and any additional information such as feeding birds or visible fish shoals. In order to avoid misclassification, data from encounters where behaviour was frequently changing between the two or where combined feeding and travelling were observed were omitted from the analysis. Additionally, data from encounters of more than one species, and of encounters with several animals engaged in differing behaviours were excluded. Thus, data with observer bias have mostly been excluded from the results. Furthermore, misclassifications would be expected to erode the level of significance of the acoustic discrimination, but as this has proved statistically significant it could be seen as validating the visual classification.

Another explanation for why the data may not be entirely representative of foraging and feeding vocalisations is if some of the dolphin feeding trains (such as trains with very short ICIs) were not recorded by the C-PODs or, even if recorded, they did not fit the algorithm's classification criteria. It is important to note also that C-PODs, like any static acoustic devices are confined to their mooring location and only those clicks which are directed towards the device, and which are produced at the device's detection range are detected. The effective detection radius with C-PODs has been estimated to be around 150-200 m for harbour porpoises and around 300-400 m for bottlenose dolphins, depending on animal behaviour, however C-PODs have been found to detect clicks from over 500 m for porpoises and over 1500 m for dolphins (Chapters 2 and 3, this PhD thesis). Here we used detections from animals up to 1500 m away to maximise our sample size.

Of the trains that were recorded during behavioural observations, over 70 % were during feeding events, and yet only 3.8 % were classified as feeding buzzes with a minimum ICI of less than 10 ms. The comparative absence of fast clicks in the dolphin data could be the result of decreased source levels of the feeding buzzes (Jensen *et al.* 2009b) which would make them less detectable to the C-POD. Alternatively, if they were too similar to porpoise clicks, fast clicks from dolphins might be discarded by the software's train classification process.

Although dolphins are capable of adapting their source levels to suit their surroundings (Jensen et al., 2009b), emitting intense clicks in shallow water can create high levels of reverberation due to sound reflecting from both the surface and seabed (Zimmer, 2011). A single dolphin click in shallow water is thus commonly received as a cluster of many clicks arriving along different pathways. This results in many trains from those animals close to the logger not being identified as trains. C-PODs are designed to detect click trains, and as the C-POD does not log the shortest, most broadband clicks or the lower part of the vocal repertoire (< 20 kHz), and it includes off-axis clicks, the clicks recorded by C-PODs are a relatively inaccurate representation of the actual vocalisations produced. This is likely to be particularly problematic when attempting to classify or characterise dolphin clicks.

The lack of feeding buzzes (clicks with very short ICIs) in the dolphin data would also explain why the echolocation rate for dolphins is actually lower for feeding animals than for travelling animals, contrary to what was expected based on previous studies (Tyack 2000; Nowacek 2005). An alternative explanation could be that if the dolphins considered to be feeding were involved in more complex search behaviour (Bailey & Thompson 2006) and were not producing feeding buzzes until within very close proximity to a fish. Perhaps buzzes are more frequently used on demersal or benthic prey, which are highly camouflaged and lie still on the seabed for the majority of the time (Gibson 2005). This could conceivably make the use of buzzes more necessary than when feeding on fish shoals in the water column. If feeding buzzes are directed towards the seabed, large part of the sound’s energy may be absorbed in the seabed and due to their directional nature, will not be able to ensonify the C-PODs hydrophone and therefore will not be detected.

There were insufficient visual observation data to assess the click characteristics relating to other behavioural categories such as milling, resting or socialising, which also form an important part of these species’ behavioural budgets (Mann *et al.* 2000), and will affect the content and rate of their vocal behaviour. Future studies of wild bottlenose dolphins and harbour porpoises should attempt to assess the vocal behaviour recorded by C-PODs for other visually observable behaviours such as mating and socialising.

Communication trains have been described from porpoises with ICIs as short as those in feeding buzzes (Clausen *et al.* 2010). The extent of the use of such trains is not known, but the data show that, regardless of their actual function, more clicks with short ICIs are produced during feeding than during travelling. It is not possible to distinguish unsuccessful feeding attempts (approaches to a target) from those that end in prey capture, and therefore an increase in feeding buzzes does not necessarily indicate an increase in feeding. However, an increased rate of feeding buzzes should at the very least indicate areas where prey is available and feeding attempts take place, which in itself is critical information for conservation and management purposes.

Regardless of the fact that the C-POD does not record the full vocal repertoire produced by these animals, nor does it select all the recorded clicks for its final train classification, it can reveal valuable behavioural information about its target species by detecting potential foraging events, making C-PODs particularly useful for long-term monitoring studies. These devices can be used to identify important feeding areas, particularly for harbour porpoises but also potentially for bottlenose dolphins. Nevertheless, further studies to extract dolphin feeding buzzes from C-POD data are recommended. Behavioural observations using visual methods are limited to calm seas and daylight hours, typically during summer months. Therefore acoustic monitoring is the only way to acquire detailed information on feeding patterns for animals that are known to forage nocturnally

The C-POD detects and identifies cetacean vocalisations based on complicated algorithm, and its detection capability is dependent on the acoustic properties of the target sound, the surrounding ambient noise and the animal behaviour, as well as the actual sensitivity of the device. Over the recent years many such devices and algorithms have been developed and will hopefully continue to be developed and improved to the benefit of researchers, decision makers and the conservation of coastal cetacean populations. The C-POD, like other similar acoustic devices, is designed for long-term static acoustic monitoring (SAM), and enables researchers to monitor cetacean presence in larger spatial and temporal scales than previously may have been possible. It, as any other method, does have its disadvantages, and due to the nature of its train detection, some individual clicks will always go undetected. It is therefore imperative to recognise that although SAM devices may be very useful in detecting long term trends of presence, or in fact identify feeding areas, they should not be used for analysing vocal behaviour in great detail. Furthermore bias resulting from potential differences between devices, and effects of deployment sites need to accounted for. An important advantage of the static acoustic click logger over traditional acoustic methods is the reduced amount of data incurred and the automated species recognition process, both of which speed up the data analysis. In addition, describing behaviour through acoustic methods removes biases associated with visual descriptions of behaviour, ultimately facilitating comparisons of data between studies and across regions.

5.6 Acknowledgements

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5.7 Appendices

Appendix 5.1: Click train characteristics

Summary of click train characteristics for harbour porpoise (HP) (Table 5.4) and bottlenose dolphin (BND), (Table 5.5) for both feeding and travelling behavioural categories.

Table 5.4 Summary of Wilcoxon rank sum *W* tests (Mann Whitney Wilcox) performed to statistically compare click train characteristics detected by C-PODs during field trials that corresponded to *P. phocoena* groups engaged in foraging/feeding and travelling. Median, mean and standard deviation (SD) values are shown. Inter-click interval (ICI), sound pressure level (SPL)

Characteristic	**HP FD Median**	**HP FD Mean**	**HP FD SD**	**HP Travelling Median**	**HP Travelling Mean**	**HP Travelling SD**	**W test statistic**	**P-value**
Train Duration (ms)	**374.9**	**350.0**	**727.8**	**703.1**	**606.9**	**637.6**	**11102**	**< 0.001***
No of Clicks/Train	10.9	11.1	8.8	9.4	9.6	6.3	20695	0.9718
Clicks/s	198.7	208.3	241.3	54.2	70.7	132.0	27113	1
Max ICI (ms)	**56.2**	**51.9**	**123.7**	**116.1**	**101.8**	**105.8**	**10198**	**< 0.001***
Min ICI (ms)	**43.4**	**39.9**	**100.0**	**94.2**	**83.2**	**92.0**	**9913.5**	**< 0.001***
Mean ICI (ms)	**45.9**	**42.5**	**100.5**	**97.7**	**85.2**	**91.3**	**10143.5**	**< 0.001***
Last ICI in a train	**51.5**	**48.3**	**119.4**	**106.3**	**93.0**	**97.5**	**10186.5**	**< 0.001***
ICI Rising (%)	56.8	56.1	19.1	57.8	57.1	19.4	18245.5	0.3763
Modal Frequency (kHz)	**128.9**	**128.5**	**4.2**	**132.6**	**131.6**	**4.9**	**11768**	**< 0.001***
Mean End Frequency (kHz)	**124.8**	**124.3**	**6.1**	**129.2**	**128.5**	**6.4**	**11799**	**< 0.001***
Minimum Frequency (kHz)	**124.0**	**123.5**	**4.9**	**127.1**	**126.7**	**7.2**	**11526.5**	**< 0.001***
Maximum Frequency (kHz)	**133.5**	**133.3**	**5.9**	**137.2**	**136.5**	**5.9**	**12466**	**< 0.001***
Maximum SPL	**64.6**	**67.9**	**66.3**	**94.8**	**87.7**	**80.0**	**15563.5**	**< 0.001***
Mean SPL	38.3	40.1	32.0	53.8	48.7	40.9	16502.5	0.03022
n	147			253				

* indicates a significant result

Table 5.5 Summary of Wilcoxon rank sum *W* tests (Mann Whitney Wilcox) comparing click train characteristics detected by C-PODs during field trials that corresponded to bottlenose dolphin (BND) groups engaged in feeding and travelling. Median and mean values are shown. Inter-click interval (ICI), sound pressure level (SPL)

	BND Feeding Median	BND Feeding Mean	BND Feeding SD	BND Travelling Median	BND Travelling Mean	BND Travelling SD	W test statistic	P-value
Train Duration (ms)	**1095.8**	**1299.5**	**1003.5**	**1407.3**	**159.7**	**903.8**	**20121**	**< 0.001***
No of Clicks/Train	9	11.2	7.01	9	10.3	4.5	26199	0.5691
Clicks/s	6	24.1	53.8	6	10.9	27.3	27113	1
Maximum ICI (ms)	**192.6**	**185.2**	**128.6**	**226.9**	**229.0**	**101.3**	**19924**	**< 0.001***
Minimum ICI (ms)	**146.4**	**140.6**	**98.3**	**175.3**	**170.6**	**73.3**	**20386**	**< 0.001***
Mean ICI (ms)	**160.5**	**150.1**	**102.9**	**179.4**	**180.4**	**73.9**	**20537**	**< 0.001***
Last ICI in a train	**170.4**	**178.7**	**132.4**	**200.8**	**216.3**	**112.1**	**20942**	**< 0.001***
ICI Rising (%)	60	61.6	17.5	60	60.1	16.5	27327	0.8216
Modal Frequency (kHz)	47	49.1	14.7	45	48.2	18.3	27591	0.8633
Mean End Frequency (kHz)	59	63.3	16.9	65	65.9	20.9	22482	0.01108
Minimum Frequency (kHz)	36	37.9	8.5	35	36.67	10.3	28470	0.9534
Maximum Frequency (kHz)	**98.5**	**96.3**	**29.1**	**121**	**106.9**	**31.6**	**19542**	**< 0.001***
Maximum SPL	181	165.5	80.2	203	172.8	82.1	23879	0.0863
Mean SPL	72	74.7	39.8	70	68.3	34.8	27832	0.895
n	396			131				

* indicates a significant result

Appendix 5.2: GLM output

Results of the Generalized Linear Model (GLM) for harbour porpoise and bottlenose dolphin datasets.

1. Results of the Generalized Linear Model (GLM) for harbour porpoise data

```
glm(formula = HPbeh$Behaviour ~ HPbeh$modalKHz + HPbeh$Clx.s,
   family = binomial, data = HPbeh)
Deviance Residuals:
   Min       1Q   Median       3Q      Max
-2.1333  -0.7571   0.5721   0.7860   1.9221
Coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)    -1.241e+01  3.049e+00  -4.071 4.69e-05 ***
HPbeh$modalKHz  1.042e-01  2.319e-02   4.492 7.06e-06 ***
HPbeh$Clx.s    -3.565e-03  6.733e-04  -5.294 1.20e-07 ***
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
(Dispersion parameter for binomial family taken to be 1)
   Null deviance: 658.53  on 535  degrees of freedom
Residual deviance: 562.79  on 533  degrees of freedom
AIC: 568.79
Number of Fisher Scoring iterations: 4
```

2. Results of the Generalized Linear Model (GLM) for dolphin data

```
glm(formula = BNDbeh$Behaviour ~ BNDbeh$MinICI_us + BNDbeh$avSPL +
   BNDbeh$Clx.s + BNDbeh$MaxF, family = binomial, data = HPbeh)
Deviance Residuals:
   Min       1Q   Median       3Q      Max
-1.3514  -0.8096  -0.6428   1.2144   2.4574
Coefficients:
                Estimate Std. Error z value Pr(>|z|)
(Intercept)      -2.203e+00  4.686e-01  -4.702 2.57e-06 ***
BNDbeh$MinICI_us  2.625e-06  1.284e-06   2.045   0.0408 *
BNDbeh$avSPL     -8.596e-03  2.844e-03  -3.023   0.0025 **
BNDbeh$Clx.s     -8.991e-03  5.585e-03  -1.610   0.1074
BNDbeh$MaxF       1.449e-02  3.697e-03   3.918 8.93e-05 ***
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
(Dispersion parameter for binomial family taken to be 1)
   Null deviance: 648.64  on 569  degrees of freedom
Residual deviance: 610.99  on 565  degrees of freedom
AIC: 620.99
Number of Fisher Scoring iterations: 5
```

Chapter 6 DISCUSSION AND CONCLUSIONS

The goal of this research was to assess the suitability of the C-POD for acoustic monitoring studies of bottlenose dolphins and harbour porpoises, with a particular regard to density estimation. My intention was to quantify the detection probability of harbour porpoises and bottlenose dolphins using C-PODs and how source level, and animal behaviour and group size affect this, by assessing the performance of both the click detection and the train classification algorithm of the device. I aimed to examine these aspects in more detail than previous studies, in particular for the bottlenose dolphin, for which the information on the detection probability was still lacking. The overall hypothesis was that C-PODs are capable of detecting the echolocation clicks of both bottlenose dolphins and harbour porpoises but that their detection probability is affected by distance from the data logger, animal behaviour and group size, and the results of chapter 2 and 3 confirm this. I also hypothesised that although C-PODs probably do not detect *all* echolocation clicks emitted they are still able to record enough detail to enable feeding and foraging behaviour to be distinguished and the results obtained in chapters 4 and 5 support this hypothesis. Here, the main results of each chapter are summarised and placed in the broader context of static acoustic monitoring and the statutory monitoring requirements for bottlenose dolphins and harbour porpoises. The suitability of the C-POD as a monitoring tool and particularly as an instrument to estimate animal density is assessed. The limitations of the study are explored, and recommendations made for future efforts of acoustic monitoring of the two species.

6.1 Detection probability of harbour porpoises

Click detectors have thus far been used successfully to identify and monitor local trends in the presence of cetaceans in specific areas, as well as in studies revealing patterns of population trends more widely, and identifying seasonal feeding strategies for coastal species (Verfuß *et al.* 2007; Elliott *et al.* 2011a). The latest challenge in static acoustic monitoring (SAM) is to develop statistical methods for density estimation based on acoustic cues. To facilitate this, it is essential that factors affecting acoustic detection rates and vocal behaviour are reviewed (Küsel *et al.* 2011; Kyhn *et al.* 2012; Marques *et* *al.* 2012). In chapter 2, I estimated the detection probability of harbour porpoises as a function of increasing distance from the data logger and decreasing source level with an extensive field experiment using artificial and actual recorded porpoise clicks. Furthermore, this detection function was modelled for both clicks detected (CP1 files) and classified click trains (CP3), including those correctly classified as harbour porpoise click trains. The results of the playback study were used to calculate the effective detection radius (EDR) and area for the data loggers in this area, for different source levels potentially used by the porpoise. A 20 dB reduction in the source level of the artificial playback signal reduced the EDR by 42% from 187 m to 107 m, highlighting the importance of identifying the mean source levels used in a particular study area, which is likely to depend on the level of ambient noise (Au *et al.* 1985). The stereotypical vocalisations of the harbour porpoise (Villadsgaard *et al.* 2007; Koblitz *et al.* 2012) were easily picked up by the C-POD, but the decreased detection probability of the click trains by comparison to the raw clicks shows that many clicks are being excluded from the train classification process.

The detection probability decreased progressively from detected clicks to classified trains, and further to correctly classified species. Although the raw click files (CP1) had high detection rates of porpoise clicks and maximum detection distances close to what is theoretically possible, the detection rates of the correctly classified click trains were greatly reduced by comparison. The challenge remains for the developers of the software to improve the train classification algorithm to match the click detection abilities of the device, which would greatly increase its effective detection area. However, it is unlikely that this can be achieved at all, since more complicated signal (trains and species classification) will always require more information (more intense clicks and larger number of them) than just detecting a click – and therefore the detection probability of click trains will always lower than that of clicks.

These findings contribute to the current knowledge of the capabilities of the C-POD, and the effective detection areas estimated in this study will help design effective and useful monitoring studies for harbour porpoises and other species with similar behaviour and vocalisation characteristics. Although these results are site and context dependent, they can be used as guidelines in other studies where such an expensive and time-consuming experiment is not possible. The results highlight the need for future research on the effect of emitted source levels and possible modification due to variations in ambient noise levels which will affect the detection probability of porpoises with any SAM device. Further study is also needed to define how changes in behaviour or number of animals may affect the vocal behaviour and click production rate of the porpoise – both of which are crucial for achieving accurate density estimations (Marques *et al.* 2012).

6.2 Detection probability of bottlenose dolphins

With the growing interest in developing adequate and cost-effective acoustic monitoring methods for bottlenose dolphins and recent changes in the C-POD's train detection algorithm which have improved its ability to classify dolphin echolocation clicks (Chelonia Ltd 2012b), the C-POD has potential to complement visual survey techniques in monitoring efforts of this Annex II listed species (Evans & Thomas 2011). The main problems facing the acoustic monitoring of dolphins are the large range of vocalisations produced which can frequently be behaviour-dependent, (Janik & Slater 1998; Acevedo-Gutiérrez & Stienessen 2004), the lack of stereotypical echolocation clicks (Au 1993; Wahlberg *et al.* 2011), and their highly varied group size and composition in the region and elsewhere (Connor *et al.* 2000; Baines & Evans 2012; Veneruso & Evans 2012). To address these problems, chapter 3 explored the C-POD detection probability of bottlenose dolphins with regards to effects of distance from the data logger, animal behaviour and group size and defined the effective detection radius (EDR) and area for these parameters. Results confirmed that as well as distance from the C-POD, both group size and behaviour play an important part in the detectability of dolphins by click loggers. The results revealed that, in general, feeding dolphins were more likely to be detected by C-PODs than travelling ones, but that single dolphins have an unexpectedly high detection probability, especially so when travelling.

The study highlighted a distinct difference in detection probability for the two visually observed behaviours, with varying results for different group sizes, both findings of which will have implications on acoustic monitoring studies, posing a particular challenge to future efforts to use C-PODs to estimate animal density. Higher detection rates of feeding dolphins in comparison to travelling ones could yield erroneously high density estimates in feeding areas and vice versa. Current interpretation of dolphin presence and absence based on C-POD data alone will produce biased results depending on the behavioural budget of the animals, and, in particular, the time spent foraging near the C-POD deployment site.

Only two distinct behaviours were examined: feeding and travelling. Since other activity states and behaviours are also likely to affect vocal behaviour, for example the production rate or types of vocalisations emitted, further research in this area is required, focusing both on types and rates of vocalisations produced.

6.3 Comparison of C-POD data with broadband hydrophone recordings

One of the main gaps in our knowledge of the ability of C-PODs to detect and classify cetacean trains, is a quantitative assessment of the proportion of clicks undetected by the logger. Chapter 2 approached this question by comparing the detection probability of porpoise clicks to the actual trains classified by the algorithm and found that many clicks were not assigned to trains, markedly decreasing the effective detection area of the C-PODs.

In chapter 4, a selection of wild bottlenose dolphin click data recorded with a broadband hydrophone was compared with simultaneous C-POD recordings. Here I inspected the number of actual clicks missed by the combined click detection and train classification process, and assess the temporal characteristics of identified click trains to define whether clicks with certain inter-click intervals (ICIs) may be more likely to be missed than others. In particular, I hypothesised that click trains with very short ICIs, such as those present in feeding buzzes (Verfuß *et al.* 2009; Miller 2010), would not be detected by the C-PODs nor classified into click trains as often as would slower clicks. Interestingly, the analysis gave a result counter to the proposed hypothesis – in this sample dataset, the C-POD was able to identify click trains with short ICIs and, consequently, to describe feeding buzzes. This is encouraging for monitoring studies that are planning to use C-PODs to identify feeding sites or quantify feeding activity based on detected vocalisations. However, a considerable portion of dolphin clicks remained unclassified by the train detection algorithm, similar to the results presented for (playback) porpoise clicks in chapter 2. The sample size was relatively small, based on one encounter with a single dolphin, and the analysis of the hydrophone recordings was based on semi-objective threshold definition of clicks, so the results are not conclusive. Further work describing vocalisations recorded by SAM devices for both bottlenose dolphin and harbour porpoise is recommended to enable a better interpretation of SAM data.

6.4 Identifying animal behaviour from C-POD data

Recent advances in statistical methods to estimate density from passive acoustic data have emphasised the importance of understanding how acoustic behaviour and vocalisation rate relate to the actual behaviour of target species (Mellinger *et al.* 2007; Küsel *et al.* 2011; Marques *et al.* 2012). Previous studies with T-PODs have attempted to identify feeding events of free living harbour porpoises (Carlström 2005; Koschinski *et al.* 2008; Todd *et al.* 2009), but these studies did not conduct visual validation for their behavioural classifications. Earlier, I demonstrated that behaviour, together with group size, will significantly affect the detection probability of bottlenose dolphins, and consequently the effective detection area and any density estimates derived from this (see chapter 3). To address this problem in the context of SAM, conclusive information on the behavioural budget of the study species is needed, together with the ability to distinguish different behaviours from acoustic monitoring results.

In chapter 5, I examined the latter solution and inspected C-POD data in comparison with visual observations of dolphin and porpoise behaviour, to assess whether SAM data can be used to discern behavioural information of target species. The resulting click trains of both species had similar characteristics to those described in the literature (detailed in chapters 1 and 5). The results showed that there was a clear difference between travelling and feeding click trains recorded by the C-POD – indicating that C-POD data could be used to characterise feeding events and thus identify potential feeding areas. This finding was more evident in the harbour porpoise data since in bottlenose dolphins, the result varied between the analytical methods. A number of explanations were proposed to explain the lack of statistical difference between vocal characteristics for the two different dolphin behaviours, including an inadequate sample size, an actual absence of distinct vocalisations produced by the dolphins, and potentially erroneous behavioural classifications by the observers, all of which are discussed in detail in chapter 5.

The key finding of this study was that C-POD data record enough of the vocal repertoire to represent different behaviours, although these results were restricted to only two distinct behaviours, feeding and travelling. Distinguishing the behavioural state of the target species allows for more in-depth analysis of the habitat use of the target population studied and is crucial in estimating density from acoustic data (Marques *et al.* 2012), since differences in behaviour can significantly alter vocal detections and consequently density estimation by acoustic means. Additional studies defining the relationship between behaviour and vocalisations are strongly recommended for both species.

6.5 Summary of key findings

Based on the results presented here, I can conclude that the C-PODs are capable of detecting both harbour porpoise and bottlenose dolphin echolocation clicks, and accurately distinguishing and correctly classifying them. The effective detection area of the bottlenose dolphin was much larger than that of the harbour porpoise, most likely due to the more intense clicks emitted by the dolphin. The C-POD detected clicks well but the train detection algorithm was found to be conservative and, as a consequence, many clicks were not assigned to click trains. The reduced number of train detections considerably decreased the effective detection area (EDR), in comparison to that obtained for the click detections, as was shown in the harbour porpoise playback experiment. In areas of low background noise and only single species present – where species classification is not required, the raw click files could be used to detect cetaceans and increase the area monitored. Despite the C-POD missing some echolocation clicks, and the conservative selection process of the click trains, the resulting data were still informative enough to identify foraging sites, when using short inter-click interval (ICI) as an indicator of potential feeding behaviour. However, behaviour and group size were shown to affect dolphin detection and consequently the effective detection area. It is likely that porpoise detection is also affected by behaviour, since their vocal behaviour during feeding was distinguishable from travelling. These factors make density estimates based on SAM data challenging. Furthermore, when attempting to distinguish foraging from other behaviours, or to specifically identify foraging sites, it is important to note that the foraging and/or feeding *will* be detected from further away. This has implications on how far away from the data logger the each identified behavioural activity can be extrapolated to.

6.6 Limitations of the study

Study site and sample sizes

All the experiments described in this thesis were conducted in New Quay, Ceredigion, where the height of the headland near a well-known feeding site for both species allowed prolonged visual observations to take place. Additionally, the site had weak tidal currents, a low number of commercially operating fishing boats, no ferry or shipping activities, and only a small recreational harbour nearby, and thus a minimal risk of losing equipment. Most importantly, in New Quay I had easy access to a suitable commercial boat to deploy and pick-up C-PODs, and to service moorings when required. However, the results obtained here are based on one geographical location and in the future would be useful to compare them to those obtained elsewhere to see whether site-specific differences will significantly affect the estimated effective area.

Approach to detection threshold

The approach taken here was to use distance and source level of detections to estimate the detection probability of C-PODs. Another, perhaps more universal approach would have been to assess C-PODs detection probability by using ambient noise levels and estimated transmission loss together with known source levels to examine received levels and to characterise the C-PODs detection threshold.

Equipment

Many technological and weather related constraints limited the amount of data collected, especially the number of usable visual observations, despite extensive observation periods. The broadband recordings in particular (described in chapter 4), suffered from an unprecedented and prolonged period of bad weather during April 2012, as well as multiple equipment related issues. The limited amount of data collected was due to very short single animal encounters in the vicinity of the research vessel in optimum weather conditions, as well as technical problems with the recording equipment (both hydrophones and C-PODs), and issues with data storage and power output on board the research vessel. Importantly the highest source levels used for the omnidirectional playback experiment in chapter 2, have been found to contain some irregularities, since the analysis was conducted. The resulting dataset has since been modified for publication and only the lower source levels up to 168 dB re 1 µPa @ 1 m have been retained in the analysis.

Many studies have reported problems with C-PODs not starting or stopping in the middle of deployment (Chelonia Ltd 2012a), and this was also experienced in this study (See chapter 4). Some of the problems could have been avoided by more stringent operator protocol to ensure that each C-POD had indeed started logging. However, no obvious explanation could be found for the failure of one of the devices during the study. The only way to have discovered this would have been to download the experimental data on a daily basis – which is not practical for a monitoring study. This is an issue that the manufacturer clearly needs to address before these data loggers can be used in wider monitoring studies.

Statistical significance

In this thesis, I attempted to avoid setting strict null hypotheses and testing their statistical significance with P-values as such practice has many inherent weaknesses (Ioannidis 2005; Gerrodette 2011), especially since descriptive statistics can often produce more ecologically meaningful conclusions than simple significance testing (Beninger *et al.* 2012). Most of the results presented here can be confirmed from careful visual examination of the range and distribution of the data, although I have still used traditional statistical tests to compare means and variances of my samples, particularly in chapters 4 and 5. Significance values do not conclusively confirm the existence or the absence of real biological difference or effect. The datasets used here were not extensive, and small studies often report non-significance even when important real effects may have been detected by a large study (type II error). Equally, statistical significance does not necessarily mean that the described effect is real (type I error), or biologically significant, and confidence intervals can reveal much more about the importance of the finding (Ioannidis 2005).

In chapters 2 and 3, I used a combination of an information-theoretic approach together with significance testing (Anderson *et al.* 2000; Beninger *et al.* 2012) when applying

Generalized Linear Models (GLM) and Generalized Additive Mixed Models (GAMM) to the data. Put simply, in this approach, different models are compared according to the principle of parsimony, which implies that the model that best represents the data is the one with fewest possible parameters. Consequently, there is always a trade-off between model fit (likelihood) and model complexity. The measure used in this study to apply the principle of parsimony was Akaike's Information Criterion, AIC (Beninger *et al.* 2012). Other possible approaches for statistical analysis, which are more informative than simple P-values, are based on maximum likelihood ratios and Bayesian inference methods. All these methods can produce varying results, and ideally should be used in combination with visual data inspection and descriptive statistics for improved statistical inference and meaningful ecological interpretation (Gerrodette 2011).

Software versions

The software (*CPOD.exe*) used for the extraction of data from the click loggers has undergone some developments during the last three years, and as a consequence some of the earlier analyses were conducted twice. In general, the updates in the software have not affected the analyses, although it must be noted that there is now a newer addition in the latest software (GENENC train classifier), which allows for more accurate detection on dolphin type click trains with fewer false positives (www.chelonia.co.uk). I was not in a position to re-run the entire raw data with this latest classifier, although an initial comparison of part of my dataset was conducted with it. Fortunately, due to the nature of the dataset from Cardigan Bay which has very low levels of background noise in the recorded C-POD data, there was scarcely any difference between the 'old' dataset and the data run with the new classifier, particularly due to the fact that I had used all three train quality classes ('High', 'Mod' and 'Low'). Therefore, I am confident that the results presented here would not be very different had I been able to use the latest train classifier. In more noisy surroundings the C-POD's train classifier is likely to miss more clicks, and therefore the EDR estimated here would be overly optimistic for those environments.

6.7 Recommendations for static acoustic monitoring programmes and suggested areas of future research

Despite recent advances in SAM technology and associated statistical approaches, acoustic data loggers have many shortcomings and limitations that need to be addressed in order to conduct meaningful monitoring programmes. Many of these were considered here but some remain unanswered and require further research. Here I attempt to address these with proposed practical solutions for the ideal research project.

Vocal behaviour

The main limitation of any acoustic method is simultaneously its greatest asset - its reliance on vocalising animals. Only vocally active animals will be detected and animals that are silent for long periods will be missed, making certain species more suitable for acoustic monitoring – e.g. the harbour porpoise, which echolocates almost continuously (Akamatsu *et al.* 2007). Several species-specific factors including the frequency range, vocalisation rate and emitted source levels of the target species, as shown for porpoises in chapter 2, need to be taken into account when deciding whether SAM is the appropriate survey method (Kyhn *et al.* 2009).

Recommended solutions: Describe the full vocal repertoire of the monitored species including their frequency range and source levels, and evaluate the proportion of silent or vocally inactive periods within an animal's behaviour budget to assess whether it is suitable for acoustic monitoring. For example, if the animal only vocalised during foraging, or at night time, placing data loggers near foraging sites would be the best option to assess animal presence in the area. Describing source levels requires using expensive hydrophone arrays or attaching acoustic tags on the animals themselves, but is necessary to effectively define EDR and effective area, as demonstrated in chapter 2.

Effect of behaviour and group size on vocalisations

As described in detail above, one of the main drawbacks of acoustic monitoring methods is the variability of vocalisations depending on the behavioural context and group size of the target species, although both of these factors affect visual surveys in equal measure. The effect of behaviour and group size on detection rates was clearly established for bottlenose dolphins in chapter 3. It is therefore crucial to define the relationship between different behaviours and group sizes with vocalisations and rate of sound production of the target species since all these can significantly affect the detection probability with SAM devices. (Janik 2000; Johnson *et al.* 2006; Verfuß *et al.* 2009).

Recommended solutions: Assess the variability of vocalisations and their production rate for different behaviours and how this may be influenced by group size. One way to do this would be to conduct an experiment on detection probability using visual validation to examine the effect of these variables on detection probability, as described in chapter 3.

Species discrimination

Although considerable effort has been spent to discriminate different species based on their vocalisations (Rendell *et al.* 1999; Bearzi 2005), there are still large gaps in our knowledge in this field. In particular, this applies to our ability to distinguish species based on their click characteristics alone, which is obviously relevant to click detectors such as the C-POD and the T-POD (Simon *et al.* 2010). The harbour porpoises and bottlenose dolphins are relatively easy to identify based on their vocal behaviour, as demonstrated in chapters 3 and 4. However, even for those species that we can distinguish acoustically, overlap exists in parts of their vocal repertoire creating challenges to automated systems to accurately distinguish them from each other. Although the C-POD has improved its performance in this field by comparison to the T-POD, with a much reduced number of false positives, many clicks are simply discarded to avoid misclassification (See chapters 4 and 5).

Recommended solutions: As above – invest in further research to describe the full range of vocal repertoire of target species to design a more accurate species discrimination algorithm based on echolocation characteristic so that C-PODs or other SAM data loggers could be used in locations where multiple cetacean species are present. Assess the variability of vocal production and characteristics during multi-species encounters and during inter-specific interaction to discover whether animals adjust their vocal behaviour to avoid producing overlapping signals. More in-depth knowledge of vocal production during multi-species encounters would greatly facilitate the use of C-POD to assess presence and absence and to infer relative or absolute abundance.

Detection thresholds and ambient noise

As mentioned above, another factor that limits a SAM's ability to detect cetaceans is ambient noise. In noisy environments such as shipping lanes or areas with high tidal flow (Hamilton *et al.* 1956) any vocalisations with low source levels will be masked by the ambient noise and only detectable at close range to the hydrophone (Akamatsu *et al.* 2008). To combat this animals may alter their vocalisations, including frequency range and emitted source level (Au *et al.* 1985; Ansmann *et al.* 2007) which may be problematic to automated detection algorithms, which have been set to detect species based on set parameters. Studies attempting to monitor cetaceans in proposed tidal energy extraction sites may experience difficulties in discerning cetaceans from such noisy backgrounds, regardless of the acoustic method used, and should seek alternative ways to monitor a buffer site surrounding the proposed development sites, and combine visual and acoustic methods to achieve reliable estimates of habitat use and abundance.

Recommended solution: To reliably use acoustic devices, such as C-PODs we really need to understand their detection threshold and how this varies with ambient noise of different frequencies. Measuring ambient noise as part of the acoustic monitoring study is essential to correctly assess the signal to noise ratio in given period and to identify periods when recorded data may not be reliable.

Moorings and deployment techniques

A recent study by Dudzinski *et al.* (2010) collated useful information about moorings for static acoustic monitoring gear for both shallow and deep water applications, listing the various constraints to be taken into account when deploying expensive and delicate equipment in the marine environment. For this study, moorings were developed with local fishermen over several years and this collaboration proved fruitful – the only losses of equipment incurred from deliberate or accidental interactions (entanglement) with leisure craft or fishermen, the actual mooring design used here was robust and reliable (Appendix 3.1, Figure 3.12) for the conditions in Cardigan Bay. Elsewhere, strong tides and currents, storm damage and shipping have created a lot of problems for SAM deployments (Dudzinski *et al.* 2010). An anchoring and marking system should be developed with plenty of local knowledge to fully appreciate prevailing sea conditions and take into account other sea users. Mooring systems could also introduce a bias to the study, especially when recording animals at close ranges. Large, conspicuous moorings may attract or repel both cetaceans and their prey, or alter the acoustic conditions of the study area. Chains and other additional fixtures may create unwanted noise and large anchor blocks may cause acoustic shadows or refractions. Large marker buoys will be dragged by the tide and currents, and if attached to the same connection line as the data logger, they can physically affect it by pulling or from vibrations. Apart from the physical effects of the mooring, it may also be that due to species-specific behavioural differences, prey availability or general foraging preferences the monitored animals may spend proportionally more time either near the bottom (if feeding on benthic prey), or in the water column or near the surface (if feeding on pelagic prey).

Recommended solutions: Collaborate with local sea users, fishermen and other researchers that deploy SAM devices under similar environmental conditions to gain information about the most reliable and practical deployment and anchoring methods. Conduct a pilot study to test the effect of mooring type and C-POD deployment depth on detection probability of target species.

Automated detection and train classification

The automated click detection and species classification enable large amounts of data to be processed without excessive time and staff costs, and can be much more reliable than subjective observer based analysis (Marques *et al.* 2012) as well as more comparable over time periods and across regions. However, as demonstrated in chapter 2 for porpoises and chapter 3 and 4 for dolphins, many factors affect the final output of an automated system, such as animal behaviour and environmental factors to equipment sensitivity and the detection algorithms. Further affecting factors are user defined settings such as time scale used and frequency filter options when exporting data from the C-POD. As discussed in chapter 4, one of the drawbacks of the C-POD is that the train detection is not openly available to the public. Although such algorithms may not be useful to most people using C-PODs for acoustic monitoring, it means that it can be difficult to validate the data recorded and to assess potential faults in the data collection methods. Figure 6.1 illustrates the many factors and processes affecting detection, classification and data analysis of echolocation clicks with C-PODs, as described in this thesis.

Recommended solution: Familiarise yourself with both the click detection process and the train detection algorithm (from data available on the manufacturer's website) and most crucially with the data handling and analysis options of the C-POD software before deploying your equipment.

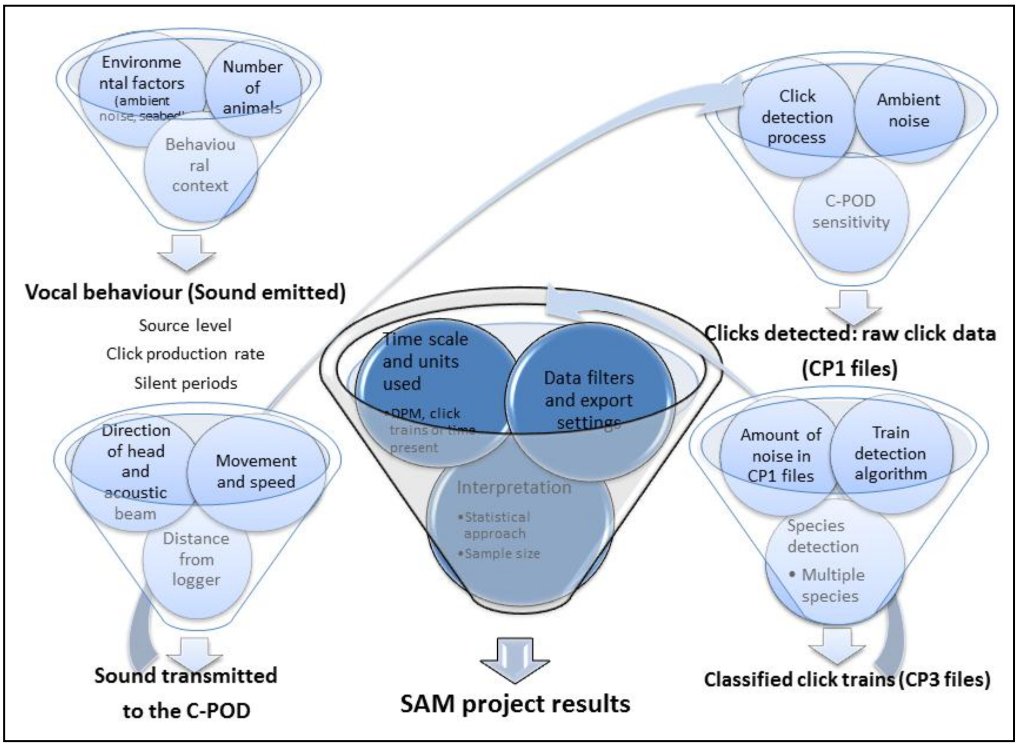

Figure 6.1 Illustration of the processes affecting detection, classification and data analysis of cetacean sounds with C-PODs as described in this thesis

Research design

In order to produce useful and accurate information with C-PODs one must assess the suitability of the logger for the target species, evaluating factors such as device thresholds against known animal source levels and click characteristics. In chapter 2 I show that decreased source level of harbour porpoise significantly decreases the effective detection area. In chapter 3 I demonstrate how feeding dolphins are more likely to be detected than travelling dolphins. Therefore, the researcher must be knowledgeable about vocal behaviour and movement patterns of the target species, to be able to estimate the effective detection area of the devices and to ensure that the C-PODs are places in the most appropriate place. He/She should also investigate the physical characteristics of the study areas as well potential logistical constraints for moorings, deployment and pick-up and interactions with local stakeholders.

Attaining 100% acoustic detections

Based on results from chapter 2, and a mean EDR of 72 m, nine C-PODs would be required to achieve 100% detection in an area of 1 km^2, and 61 C-PODs (!) would be required to ensure detection and correct classification of all porpoise click trains. However, this is actually not entirely useful as overlapping detections could not be ruled out considering that porpoise click trains were detected up to 265 m away and the mean maximum detection distance across C-PODs in this study was 163 m (95% CI: 132-194). Furthermore, recent studies with T-PODs have shown that even just a few SAM devices, acoustic detection rates correlated well with visual sightings rates (Goulton, 2012, MSc Thesis).

Avoiding simultaneous detections with highest possible cover

To exclude the possibility of simultaneous recording whilst still achieving the best possible coverage and to enable a rectangular survey design (instead of overlapping circles), C-PODs would need to be deployed far enough apart to exceed their maximum detection range. Allowing 250 m between each C-POD would satisfy these criteria but would require a total of 16 C-PODs to cover an area of 1km^2. The narrowband nature of the porpoise's echolocation click means that it will be unlikely to cause simultaneous detections with the same click trains more than 54 m apart, based on a beam width of 12.25° at 250 m from the C-POD. Obviously any additional side-to-side head movement would increase this. For example, if the porpoise head side-to-side movement is 45° with a beam width of 12.25°, the beam at 250 m from the animal would cover a maximum range of 388 m – although as seen from the maximum detection ranges, at these distances there is insufficient information to arrive at the C-POD to allow for effective detection of porpoise click trains.

Avoiding the effect of animal movement

Considerations for research design should also include the potential swim speed of the animals. Using a maximum swim speed of 2m/s (Westgate *et al.* 1995; Otani *et al.* 2001), the porpoise might cover a distance of 120 m in a minute. If the C-PODs are deployed over 250 m apart (to ensure no simultaneous detections) and the data are sampled in no longer than one minute periods (to ensure that the animal does not move into the EDR of another C-POD), it will be possible to arrive at a crude density estimate for a series of consecutive sampling snapshots in the study area, providing the average group size in the area is known (or estimated) from visual observations.

Obviously, a typical sampling design would not aim to cover the entire area such as an SAC, because of its size and costs involved, but rather to represent conceivable variation in the study area (such as depth or bottom substrate) in a systematic manner to account for the effect of this variation on animal distribution and behaviour. Hence the amount of sampling points required will depend on the nature of the area of interest, the target species, and the research question asked. Areas where only bottlenose dolphins are present, fewer C-PODs will allow for covering larger areas than those were also porpoises are present, due to the larger effective detection area of the dolphins. When both species are being simultaneously monitored the different EDRs of the two species must be taken into account, preferably aiming for an effective coverage of porpoises with lower EDR and accounting for potential overlap of dolphin detections in the data.

6.8 The future of static acoustic monitoring and C-PODs

Static acoustic methods are widely used in several locations, and click loggers such as T-PODs and C-PODs have gained popularity in monitoring coastal cetaceans, particularly in the UK, other parts of Europe and in New Zealand (Simon *et al.* 2010; Elliott *et al.* 2011a; Rayment *et al.* 2011; Brandt *et al.* 2011). Current developments in the statistical methods to enable the use of SAM data for density estimation (Marques *et al.* 2010, 2012; Küsel *et al.* 2011; Kyhn *et al.* 2012) have further increased the potential application of such devices.

Monitoring coastal areas is more necessary than ever, considering increased anthropogenic threats on coastal areas due to population growth, increased coastal tourism and recreational use of coastal sea areas with expanding populations in many developing countries with more disposable income (Evans *et al.* 2007; Reynolds, III *et al.* 2009). The pressure on inshore fishermen who need to work harder to make ends meet with decreasing fishing stocks place an extra burden on those coastal areas where cetaceans and humans co-exist (Evans & Hintner 2010). Furthermore, there is an increased demand to develop techniques to extract marine renewable energy, whether in wave, wind or tidal form, and many of the areas earmarked for such developments coincide with important cetacean habitats, with potentially negative consequences (Carstensen *et al.* 2006; Evans 2008; Dolman & Simmonds 2010; Simmonds & Brown 2010; Brandt *et al.* 2011). In addition, we are also dealing with potentially fluctuating climate where the consequences of future changes on the marine realm and its inhabitants remain poorly understood (Alter *et al.* 2010).

All these pressures will require increased monitoring efforts to ensure that a balance remains between human developments and the marine environment, and to fulfil the reporting and monitoring requirements defined for EU Habitats Directive Annex II species. It is highly likely that static acoustic monitoring will be one of the ways to achieve these so long as limitations to its use are acknowledged and resolved (Mellinger *et al.* 2007; Marques *et al.* 2012). SAM devices will be able to provide long-term coverage, complementing visual surveys and information acquired from satellite tagging studies (Read & Westgate 1997; Sveegaard *et al.* 2011b). Acoustic surveys using mobile hydrophone arrays have produced comparable density estimates to visual surveys and identified key habitats (Gillespie *et al.* 2005; Sveegaard *et al.* 2011a). However, despite their popularity, SAM methods and particularly T-PODs and C-PODs, are still some way from being able to deliver clearly interpretable data on animal abundance.

In this study I set out to describe and seek solutions to some of those shortcomings, and to increase our knowledge of the efficacy of the C-POD in particular. Using playback studies and visual observations, I defined the effective detection area for detection for both harbour porpoises and bottlenose dolphins, and found that source level greatly influences the detection probability of porpoises whilst behaviour and group size have a significant effect on the detection rates of dolphins. In fact, current interpretation of dolphin presence and absence based on C-POD data alone will produce biased results depending on the behavioural budget of the animals, whereby feeding dolphins will be more likely to be detected than travelling ones and the proximity of a regular feeding site near a monitoring location will increase detections.

After assessing the vocalisations produced during visually observed feeding and travelling behaviours, I found that whereas resulting data were distinctly different for the two behaviours, it was more obvious within porpoise data. Currently the C-POD cannot be used to distinguish a variety of behaviours, only as an indicator for potential feeding and /or foraging. Although I first thought that this could result from the C-POD's inability to detect very fast feeding buzzes, this does not seem to be the case. Additional comparison with broadband data and more in-depth analyses of different behaviours and corresponding vocalisations are needed to enable C-POD data to be used to distinguish behavioural states from click data alone, particularly for the bottlenose dolphin.

By no means have I managed to conclusively define the feasibility of the C-POD as a monitoring tool, nor have I been able to address all the limitations of the method, or to develop alternatives and solutions for each. Nonetheless I have shown that SAM in general has much potential and that the shortcomings of static acoustic methods only mean that we have a challenging task ahead to resolve them.

The advantage of any automated SAM device is the ability to decrease or eliminate observer bias present in visual surveys, and provide the ideal detection probability with minimal responsive movement towards the observer (Marques *et al.* 2012). This is also the case with C-PODs. Automated analysis, and in particular species discrimination, allows for large datasets to be analysed with reduced observer variation, saving staff time and decreasing costs. In addition, due to the automated detection process, and providing any unit specific variation is accounted for, static data loggers can produce results that are comparable over wide areas and time scales. Long term monitoring enables SAM to measure small trends in abundance, even for low density areas (Verfuß *et al.* 2007; Rayment *et al.* 2011) which can be challenging for visual surveys. Notably, the ASCOBANS (The Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas) Advisory Committee has acknowledged in its recent reports that static acoustic monitoring has proven valuable in small scale monitoring, and that it will be essential for assessing effectiveness of recovery efforts for many small cetaceans (Evans & Teilmann 2009; ASCOBANS 2011).

The C-POD's train detection algorithm has limitations (as does any survey method), and the resulting output of the train classification is affected by various factors. However, this does not hinder the device's current use as a practical tool for long-term monitoring and environmental impact assessments of several cetacean species, as well as identifying trends and patterns in cetacean occurrence for areas and species that previously had very little (if any) monitoring effort (Leeney *et al.* 2011; Rayment *et al.*

2011). Neither should be seen as an obstacle to future efforts to develop and refine its click detection and train classifying algorithm. Furthermore, using visual and acoustic methods simultaneously may help reduce the impact of inherent biases of these respective methods. More research is required on the capabilities of the C-POD, namely the detection threshold, and the vocal behaviour of its target species to be able to adjust results and correct for biases such as reduced detection probability in noisy environments or the variability in vocalisations according to behaviour. Future studies of cetacean acoustics, defining species-specific vocal repertoires, developing species discrimination algorithms and assessing behaviour and density specific vocalisation rates, will further enable the advancement of SAM methods and increase the feasibility of using loggers like C-PODs as a density estimation tool.

Given the recent advances in statistical methods to estimate animal density from static acoustic monitoring devices (Marques *et al.* 2012), and the growing requirement for reliable estimates of population sizes for many protected species, the results of this thesis provide necessary information to increase our understanding of how click loggers can and cannot be utilised to detect two of the most common, coastally occurring, cetacean species in the UK and the Atlantic coastline of northern Europe. The results should assist those implementing monitoring guidelines to design effective acoustic strategies, as well as aid in interpreting existing datasets collected using SAM devices, particularly C-PODs, thus encouraging future research in cetacean acoustic methods.

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