

Acoustic detection probability of bottlenose dolphins, *Tursiops truncatus*, with static acoustic dataloggers in Cardigan Bay, Wales

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Acoustic dataloggers are used for monitoring the occurrence of cetaceans and can aid in fulfilling statutory monitoring requirements of protected species. Although useful for long-term monitoring, their spatial coverage is restricted, 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 datalogger, (2) animal behavior (feeding and traveling), and (3) group size on the detection probability of bottlenose dolphins (*Tursiops truncatus*) with autonomous dataloggers (C-PODs) validated with visual observations. 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 traveling ones. The detection probability for single dolphins was significantly higher than for groups, indicating that their acoustic behavior may differ from those of larger groups in the area, making them more detectable. The C-POD is effective at detecting dolphin presence but the effects of behavior and group size on detectability create challenges for estimating density from detections as higher detection rate of feeding dolphins could yield erroneously high density estimates in feeding areas.

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I. INTRODUCTION

Monitoring mobile species in a marine environment is challenging because of the difficulty and expense in locating them, especially if they range across many kilometers 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 and 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 large 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 (Evans and Hammond, 2004).

Several cetacean species have highly evolved social structures and complex intra-specific communication systems (Tyack, 1997) and may travel considerable distances to fulfill high energetic requirements. Evolutionary adaptations to a marine lifestyle have favored the development of specialized vocal production and auditory systems (Au, 1993). As a consequence, cetaceans rely on vocalizations to identify conspecifics, communicate, navigate and forage, making acoustic methods one of the most efficient ways to localize and track them. Acoustic surveys, especially those using static dataloggers can be conducted 24 h a day, regardless of

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weather and sea state, and can provide a simultaneous cover of large areas (Evans and Hammond, 2004).

The bottlenose dolphin (*Tursiops truncatus*) face threats from many anthropogenic activities such as by-catch, disturbance and coastal development and it is listed in the Annex II of the EU Habitats Directive. The directive requires national reporting on the favorable conservation status of threatened species and habitats and the establishment of Special Areas of Conservation (SAC) to ensure their adequate management (European Commission, 2006; Evans, 2012). Static acoustic monitoring (SAM) devices have been used in cetacean studies covering long time periods across seasons or years (Simon *et al.*, 2010; Verfuß *et al.*, 2007) and they show potential to fulfill the statutory monitoring requirements of protected cetaceans in many coastal areas complementing or potentially even replacing visual surveys (Marques *et al.*, 2013). 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 dataloggers 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, 2012). These click loggers detect echolocation clicks from 9 to 170 kHz for the T-PODs and from 20 to 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 harbor porpoise (*Phocoena phocoena*) and fisheries interactions. Since then the T-PODs have been used for monitoring many echolocating cetaceans, such as harbor 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 farms construction and operation (Carstensen *et al.*, 2006) and various types of fishing gear (Cox *et al.*, 2004). Both T-PODs and C-PODs have been used to monitor bottlenose dolphin occurrence and habitat use (Bailey *et al.*, 2010; Elliott *et al.*, 2011; Simon *et al.*, 2010). Dolphins emit frequent and intense click trains and buzzes (very fast click trains) within the effective frequency band of the C-POD (Table I) for navigation and foraging purposes (Au, 1993; Au *et al.*, 2012; Wahlberg *et al.*, 2011), making them suitable target species for the click loggers.

In addition to monitoring population trends and relative abundance, static hydrophones have also been used for absolute abundance and density estimation (Kyhn *et al.*, 2012). The detection function $g(x)$ is the term used for the probability of animal detection as a function of a variable such as distance (x) from the data logger (Buckland *et al.*, 2001). This is derived from the predicted values from the GAMM, and gives the probability of detecting a dolphin given it is within distance x of the detector. From the detection function the

TABLE I. Reported echolocation click characteristics of the bottlenose dolphin.

Click characteristics	Reported range
Mean source level dB re 1 μ Pa (peak-to-peak) @ 1 m	177–228
Click duration	8–72 μ s
Peak frequency	30–150 kHz
–3 dB Beam width	9–10°
Sources	(Au and Hastings, 2008; Au <i>et al.</i> , 2012; Wahlberg <i>et al.</i> , 2011).

effective detection radius (EDR) can be integrated which is the distance from the C-POD within which as many animals are missed as are detected at greater distances (Buckland *et al.* 2001). From this the effective detection area (the circular plot around the data logger) can be calculated and given sufficient information about the detections (such as average group size or the relation between vocalization rate and animal density) the animal density for the area can be estimated using equations detailed 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 vocalization 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 behavior might influence the click train production rates of wild animals. Here, simultaneous visual observations, measured distances and acoustic data logged by the C-PODs were used to define the maximum detection range and effective detection radius for bottlenose dolphins. In particular we examined the effect of dolphin group size and behavior on the detection probability and assessed the performance and detection probabilities of single vs paired data loggers. To our knowledge this is the first study to look at the effect of a combination of biotic factors on 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.

II. MATERIALS AND METHODS

A. Study area and species

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 cliff-top monitoring site located at the old Coastguard lookout, New Quay (Fig. 1). The bottlenose dolphin population is one of the features of the SAC and it has been the target of several years of visual studies (Bristow *et al.* 2001; Pesante *et al.* 2008), as well as being successfully monitored using an array of T-PODs (Simon *et al.* 2010). The dolphins are known to visit the site

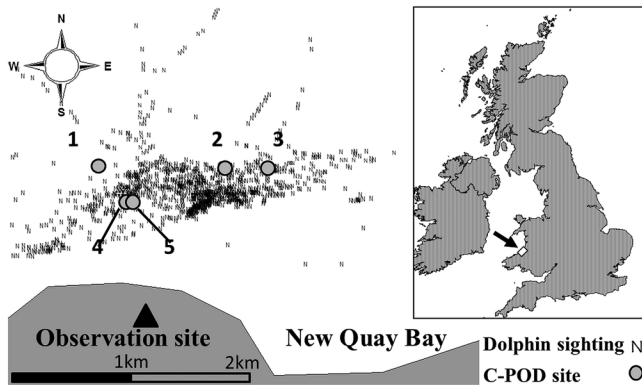


FIG. 1. Location of the theodolite observation station and the C-POD mooring sites (1–5) for the seven C-PODs deployed in the study (1: C-POD 900; 2: C-POD 885; 3: C-POD 921; 4: C-PODs 840 and 898; 5: C-PODs 901 and 897). Positions of tracked dolphin sightings during the study period marked with *N*.

all year round with increased use of the New Quay bay during summer months and daylight hours (Simon *et al.*, 2010).

B. Acoustic data collection

A total of seven calibrated C-PODs were used to log clicks within a frequency range of 20–160 kHz. The sensitivity of the units had been standardized when built by rotating the complete instrument in a sound field and adjusted to achieve a radially averaged, temperature corrected, maximum source pressure level (SPL) reading within 5% of the standard at 130 kHz (± 0.5 dB). The radial values were taken at 5 deg intervals. Recalibration by the manufacturer 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 standardization 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 with a total of 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 (Fig. 1). The moorings were deployed at a site where dolphins are often sighted, and spanned water depths of 17–22 m (chart data) and vertical distances of 720–1055 m from the visual observation site. The moorings consisted of metal weights, a 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.

C. 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 two to four 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. 8×32 binoculars were used to aid detection and tracking of the animals. While one observer was tracking the dolphins with a theodolite, another was dedicated to searching animals outside the tracked group. A dolphin group was defined as “a number of dolphins in close association with one another, often engaged in the same activity and remaining within approximately 100 m of one another” (Bearzi *et al.*, 1999). Once sighted, dolphin groups were tracked using a $30\times$ 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 distances to the C-POD sites (Lerczak and Hobbs, 1998). 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 resulting calculations were compared against the GPS generated positions.

1. Measuring station altitude

The station altitude above sea level was determined with a stadia rod calibration method. 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 (\pm SE) values of both angles were obtained to reduce measurement error. The reference altitude of the station was then determined using standard trigonometric equations described in Frankel *et al.* (2009) where H is the hypotenuse, R is the rod height, S is the station altitude, B is the mean vertical bottom angle of the rod (given relative to gravity with $0^\circ =$ zenith), β is $180 - B$, T is the mean vertical top angle and A is the differential angle between B and T (Fig. 2).

$$H = R \sin(T) \div \sin(A), \quad (1)$$

$$S = H \cos(\beta). \quad (2)$$

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 RTM. This was undertaken at the same time that cliff elevation measurements were recorded to ensure that the station altitude from the RTM was known. The height of sea level above the RTM could then be determined from the monitoring station at any point during the

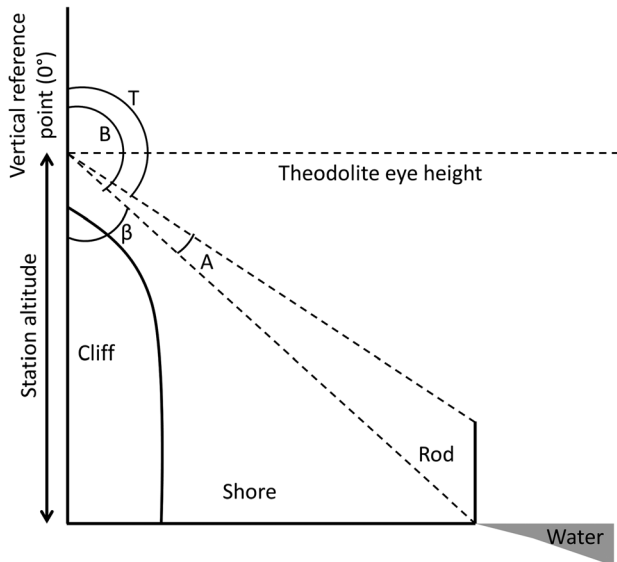


FIG. 2. Diagram of the rod method (Frankel *et al.*, 2009) used to determine theodolite station altitude during field studies (reproduced from Meier, 2010).

tidal cycle. Tidal height measurements were subsequently taken at 15-min intervals throughout all visual observation periods. The total theodolite height varied between 93.3 and 96.9 m above sea level and was calculated as

$$TTH = RSA + EH - / + TH \quad (3)$$

where TTH is the total theodolite height, RSA is the reference station altitude, EH is the observer eye height, and TH the tidal height above/below the RTM.

2. Dolphin distance from theodolite and C-POD

The distance of the dolphin from the theodolite was calculated from the measured vertical angle between the animal's position and "nadir"/180° from the vertical reference point (0° = zenith), and the known altitude of the theodolite station at the time of the sighting using right-angled trigonometry (see the Appendix). 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 possible 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. The geographical coordinates of the theodolite station and the horizontal reference point were first converted into true bearings (in relation to geographic north). Using the determined bearing of the horizontal reference point from the theodolite station and the measured horizontal angles 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. The latitude and longitude of the animal(s) position were then calculated using the 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 (Appendix).

With the latitude and longitude of the animal's position and the latitude and longitude of the C-POD position, the distance between the animals and the C-POD could be determined using the spherical law of cosines as follows.

$$d = \cos^{-1} [\sin(\text{lat}_1) \sin(\text{lat}_2) + \cos(\text{lat}_1) \cos(\text{lat}_2)] \times \cos(\text{long}_1 - \text{long}_2) R, \quad (4)$$

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. Formulas were obtained and adapted from <http://moveable-type.co.uk/scripts/latlong.html> (Veness, 2010). See the Appendix for further details of the triangulation and conversion formulas.

During every theodolite fix, the observers recorded group size, composition and cohesion, travel direction and surface behavior. Behavior was defined using the following categories: foraging/feeding (surface foraging, prey pursuit/capture, demersal foraging), socializing (physical contact, synchronized movement, aggression, and play), aerial behavior, traveling, and milling (Bearzi *et al.*, 1999; Shane, 1990). Due to the low number of behaviors in some of the categories, only foraging/feeding and traveling categories were used for analysis. Here the term "feeding" is used 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) (Bearzi *et al.*, 1999; Shane, 1990). Traveling 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-min intervals to assess the observation conditions so that sightings made during poor sighting conditions would not be used for further analysis. Only those sightings in which a single species was present and the group size did not change during the entire encounter were used for the study. Periods where animal behavior or observed group size was changing between traveling and foraging were excluded from the analysis.

D. 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. This used version 1 of the KERNO train detection algorithm to identify click trains (more or less

regularly spaced series of similar clicks), and estimate 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 a 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. The KERNO train detector uses the amplitude, duration and frequency of clicks to assess similarity and the inter-click intervals to define temporal regularity within the range 0.5–500 ms. The amplitude scale is based on the maximum peak to peak sound pressure level for any cycle within a click. A quality value, “High,” “Medium,” “Low,” or “Doubtful” quality, is assigned to each train to represent the estimated confidence of the click arising 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 broadband dolphin clicks.

Here the “High,” “Medium,” and “Low” quality class trains were used, with all “Doubtful” trains excluded from analysis. When ambient noise is low, the frequency of false positive trains being detected in noise is low and consequently even the lower “quality” trains are more likely to be true positives. Including these will increase the sample size, and improve the validity of the data.

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 (Elliott *et al.*, 2011). Although some false positive detections appear commonplace with dolphin monitoring (Elliott *et al.*, 2013), T-POD studies on harbor porpoises reported very low incidence of false positive detections (Kyhne *et al.*, 2012). According to the manufacturer, the C-PODs train detection is now much improved in comparison to the T-POD, with very low rate of false positive detections, though there have been no published studies to assess this, with 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 are sighted and express the false positive rate as a percentage of total observation time (Kyhne *et al.*, 2012). Here we attempted both methods, 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). Furthermore, attempts to examine false positive detections during periods when no dolphins were sighted are necessarily affected by the potential observer error, as lack of sightings does not automatically mean that animal were

not present, especially with dolphins which can emit clicks of very high intensity, and be acoustically detected from far away. A fast traveling animal, may have ensounded the C-POD and consequently been acoustically detected, while being missed by the visual observer. During a 50 day sample (during deployment period 2) of visual observations totaling 147 h of visual effort time, there were 90 sightings of dolphins, of which 71 were acoustically detected within 5 min of the visual sightings, and further six acoustic detections which were not visually detected, totaling 3293 click trains in five C-PODs. 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. The portion of false positive click trains in this sample was considered negligible at 0.0018 (six out of 3293). A cause for concern with dolphin detections is the potential likelihood of erroneous species classification, especially in areas where both dolphins and porpoises are present. To test this one hundred randomly selected click trains which were assigned as dolphins by the train detection algorithm were visually assessed to identify trains that may have been falsely classified as dolphins when they were actually of non-cetacean origin or from another species (in this case harbor porpoise). This visual validation was based on known characteristics (Table I) 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 these characteristics, it was categorized 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 minimize the potential for false positive detections (Elliott *et al.*, 2011) but here the aim was to rely solely on C-POD algorithm’s classifications.

E. 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 time periods for analyzing C-POD data, which is the reason why it was selected for this study, and the implications this may have for the data are discussed later.

F. Statistical methods

The aim of the analysis was to explore the effect of detection distance, behavior and group size on the acoustic detection probability and the estimated effective detection radius. Other variables used were the C-POD site, the deployment period (and season) and each distinct animal encounter (animal visit to the study site separated by at least 15 min of no sightings). The detection probability of dolphins was modeled as a function of distance from the data logger and the effects of group size and behavior on the detection probability were assessed. The residual variation in detectability between encounters not explained by these variables was also examined. Each minute of data during an encounter was viewed as a binary trial, and probability of success (i.e., of acoustic detection) was modeled using generalized additive mixed models (GAMMs), with a logit link function and binomial error distribution. Models were fitted with distance, behavior 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 ") (Zuur *et al.*, 2010). Adding an interaction term between variables behavior 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-modeled 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).

G. Effective detection radius

To arrive at the 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

$$\hat{P} = \int_0^w \frac{2\pi x g(x) dx}{\pi w^2} \quad (5)$$

$$= \frac{2}{w^2} \int_0^w x g(x) dx. \quad (6)$$

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

$$\hat{\rho} = \sqrt{\hat{P} w^2}. \quad (7)$$

III. RESULTS

After excluding all data from unsuitable conditions or where the group size or behavior was not distinctly identifiable,

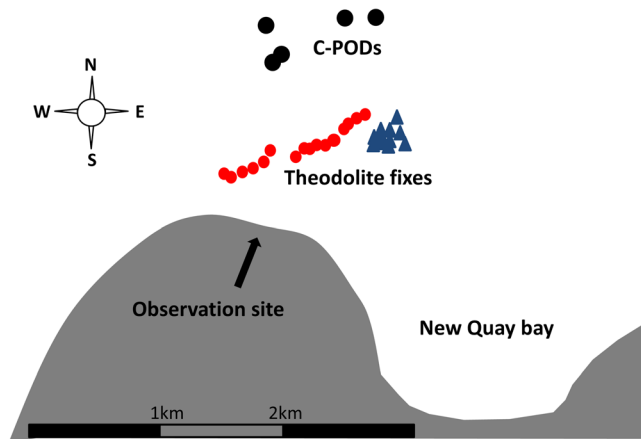


FIG. 3. (Color online) Example tracks of a feeding and traveling dolphin observed off of the New Quay Headland during the study. The triangles represent the surface locations of the dolphin classified as feeding, while the circles illustrate surface locations of the dolphin categorized as traveling. C-POD moorings and the theodolite monitoring station are shown on the map by black dots.

a total of 66 dolphin encounters were used for the analyses, consisting of 3142 min with visual sightings with visual sightings compared with acoustic data from the five C-PODs. Figure 3 depicts theodolite fixes obtained from a feeding dolphin and tracks of theodolite positions from a traveling dolphin.

A. Acoustic detections

There were very small differences in number of detections between paired C-PODs, moored 1 m apart (Fig. 4), 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), demonstrating the accurate standardization of these instruments.

The maximum detection distances calculated from theodolite tracks for the different C-POD locations varied between 1343 and 1779 m (Table II). The average detection probability for bottlenose dolphins for all the C-PODs was 0.59 (95% CI: 0.45–0.73). The mean maximum distance was 1512 m (95% CI: 1414–1609 m). Adding an additional

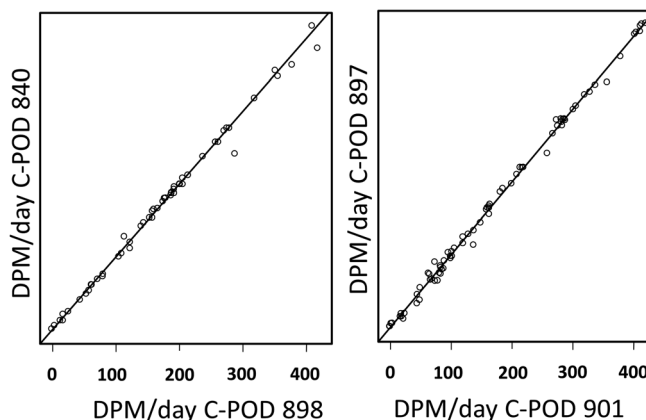


FIG. 4. Comparison of the number of minutes per day within which a dolphin was detected for paired C-PODs (898 and 840 and 901 and 897), moored within 1 m from each other. DPM = detection positive minutes. Diagonal line of the graph denotes perfect agreement.

TABLE II. The maximum and median dolphin detection distance and the overall detection probability (P) for each C-POD. Paired C-PODs separated by gray lines. C-POD sites are marked in the map in Fig. 1.

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

C-POD 1 m and 100m apart, only slightly increased the probability of detecting more dolphins from an average of 0.72 of single C-PODs to 0.75 for paired 1 m apart and 0.78 paired 100 m apart.

B. Differences between deployment periods

As expected the detection probability for the second (summer) period was significantly higher than that of the first period (Table II). The mean distance from an observed dolphin to a data logger, the group size and frequency distribution of behaviors differed greatly between the two deployment periods (Fig. 5). In particular, the average distance between the logger and the sighted animals was higher and the group sizes larger in the first deployment than in the second. There were also more sightings of traveling dolphins than feeding ones in the first deployment, whereas there were considerably more feeding encounters in the second period (Fig. 5).

C. Modeling acoustic detection probability

All variables tested contributed significantly to the model with lowest AIC including the interaction terms (Table III). GAMM with all variables and interactions between group size and behavior 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 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, decreased the adjusted R^2 value to 0.11, and increased p -values of all variables, rendering behavior 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 behavior and group size (Table III).

As expected with attenuation of sound, the detection probability decreased with distance from the data logger, but

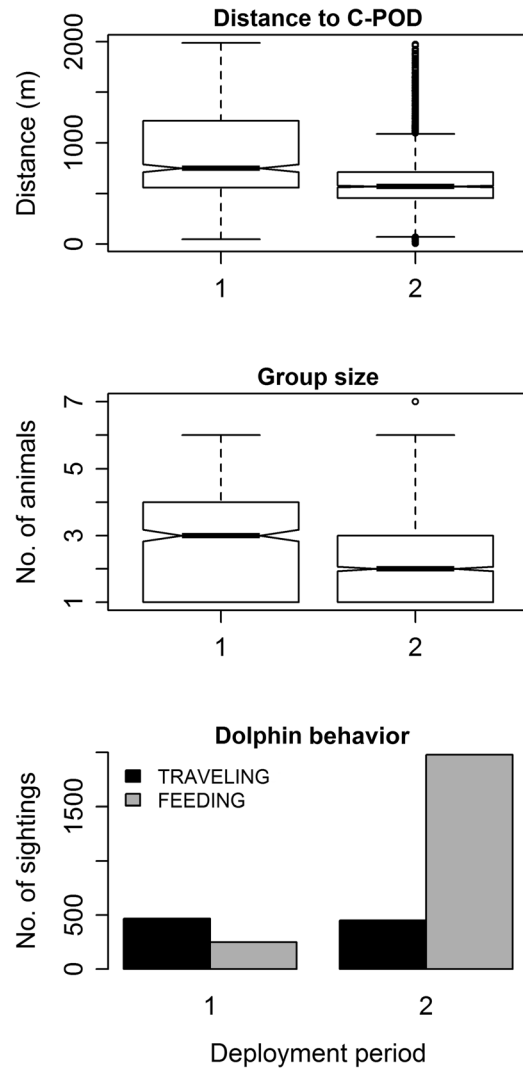


FIG. 5. Differences between the two C-POD deployment periods for each variable used to explain detection probability. If the notches in box plots do not overlap, the medians are significantly different at the 5% level. Period 1 (Feb to May), $n = 715$ period 2 (June to July), $n = 2125$.

with a varying effect for the two behaviors (Fig. 6). The number of detected feeding dolphins was significantly higher than that of traveling dolphins (0.17, $X^2 = 104.9224$, $df = 1$, p -value $< 2.2e-16$) (Fig. 7), and there was a distinct seasonal

TABLE III. Parameter estimates and their statistical significance from generalized additive mixed model of acoustic detection probability. The final model is described as $AC.DET \sim s(DIST) + GRS * BEH$, random = $\sim (1|ENC)$, and included as fixed covariates behavior (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	$< 2e-16$	

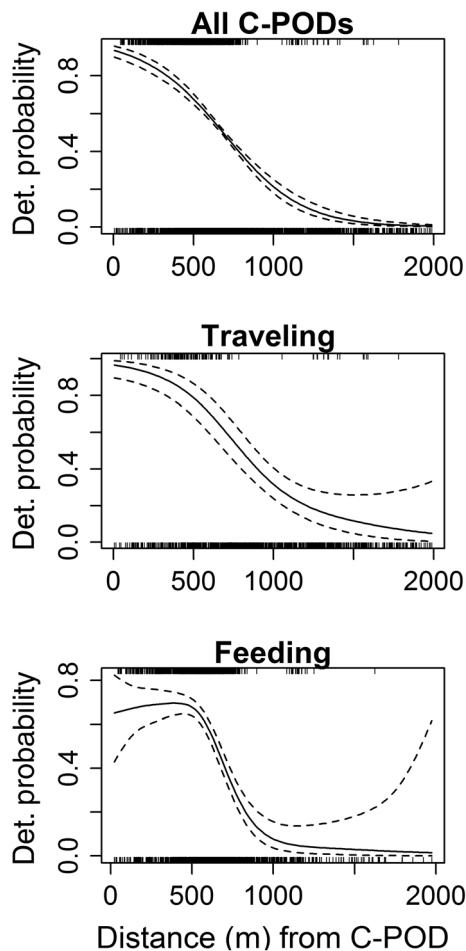


FIG. 6. Detection probability of dolphin click trains for C-PODs as function of distance from data logger. Solid line is the smoother for distance with GAMM; dotted lines depict the 95% confidence interval.

difference in the number of animals observed feeding, with a marked increase during the summer months (Fig. 5).

The overall detection probability decreased with increasing group size, although for feeding dolphins, an increase in group size increased detectability (Fig. 8). Furthermore, the detection probability (P) for single dolphins was significantly higher than that of groups. For single dolphins, the detection probability of traveling dolphins was higher than for feeding dolphins whereas for groups, the opposite was found (Fig. 9).

D. Effective detection radius (EDR)

The average EDR for traveling 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 traveling dolphins (604 m, 95% CI: 447–785 m). Effective detection area respectively varied from 0.04 km² to 1.14 km² (traveling) and 0.73 km² to 0.55 km² (feeding). For traveling dolphins, the EDR decreased considerably with an increase in group size (604–113 m), whereas for feeding dolphins the EDR remained relatively constant (481–416 m) for all group sizes (Fig. 10). It must be noted that the EDRs were integrated from the detection function assuming uniform around the dataloggers. The animal locations however were concentrated within a potential travel

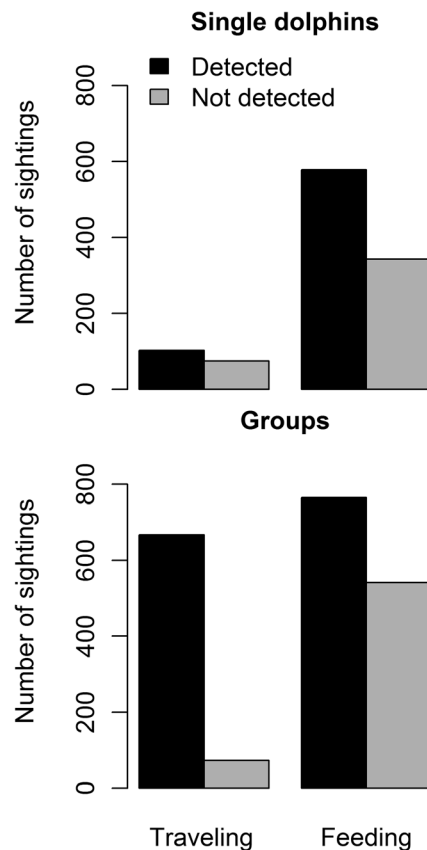


FIG. 7. The number of visual dolphin sightings with simultaneous acoustic detections (black) and those without matching acoustic detections (gray) in the two behavioral categories for both single animals and groups of dolphins.

corridor following the coastline (Fig. 2) and it is not clear how much this would have affected the calculations. To avoid this, future studies with high enough sample size could systematically sample their dataset ensuring a uniform distribution of distances.

IV. DISCUSSION

This study demonstrates the suitability of acoustic monitoring, and in particular the 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 behaviors, 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 just below 400 m although detections were recorded over 1512 m from the data logger. To our knowledge, this is the first time the 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 behavior would be 0.52 km²—an area where there are as many dolphins missed inside as are detected outside it.

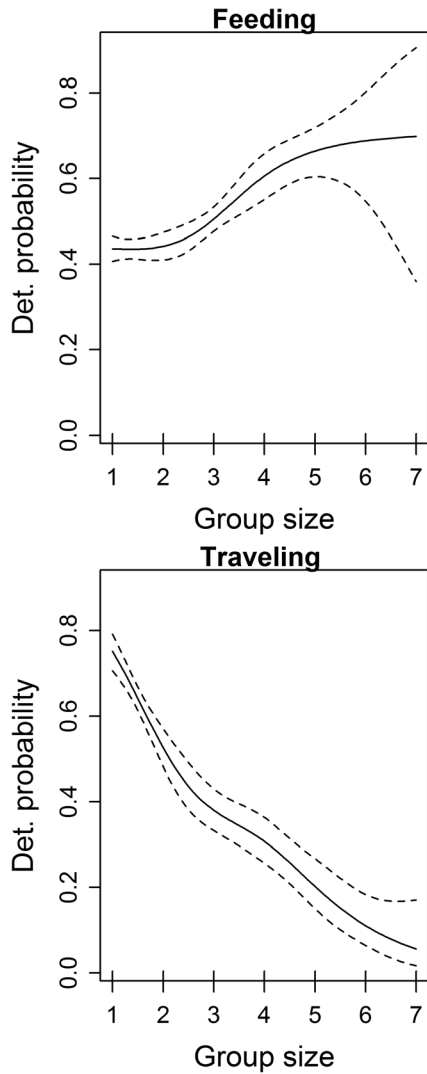


FIG. 8. The effect of group size on acoustic detection for feeding and traveling dolphins. Solid line is the estimated smoother and the dashed line indicates 95% confidence intervals.

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 (Kyhne *et al.*, 2008) as early T-PODs were not standardized 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.*, 2011), which was likely due to C-POD's improved click detection performance. Although this may seem high, it is within calculated theoretical maximum detection distances of a pure tone at typical dolphin frequencies (75–135 kHz) for minimum and maximum measured wild dolphin source levels (SL), 177 and 228 dB re 1 μ Pa (peak-to-peak) @ 1 m, (Wahlberg *et al.*, 2011) using the minimum received level of 120 dB re 1 μ Pa for the C-POD (J. Loveridge, Chelonia, personal communication) (Table IV). Using transmission loss based on spherical spreading in ideal conditions in shallow

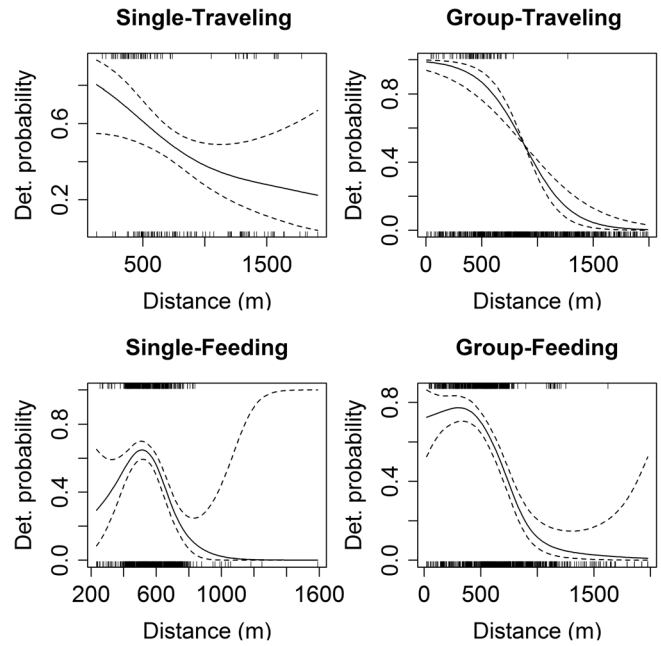


FIG. 9. The effect of distance (x axis) on acoustic detection probability (y axis) for the two different behaviors for single dolphins ($n = 1097$), and for groups of dolphins ($n = 1743$) obtained using generalized additive mixed model (GAMM). Dashed lines indicate 95% confidence intervals.

water (DeRuiter *et al.*, 2010) and sound absorption values measured for sea water at 20 °C (Fisher and Simmons, 1977), transmission loss (TL) can be calculated as follows:

$$TL = 20 \log_{10} R + (R - 1)a, \quad (8)$$

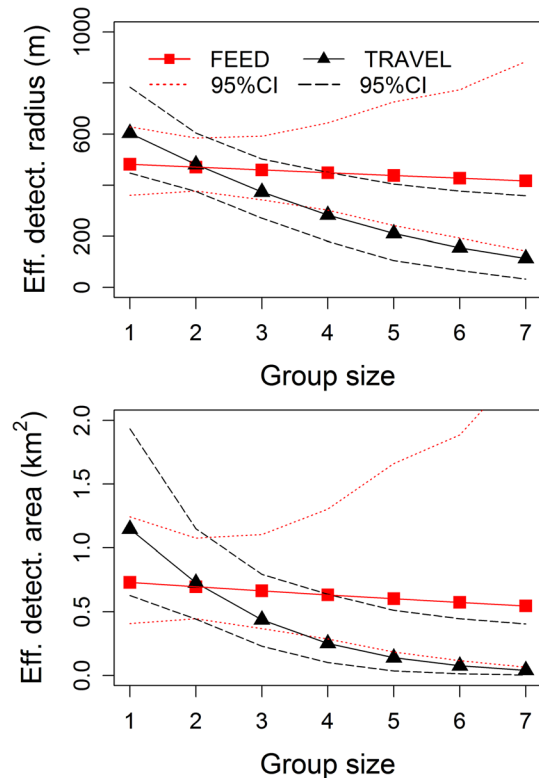


FIG. 10. (Color online) EDR and the effective detection area calculated for different behaviors, feeding and traveling, and for all group sizes with non-parametric bootstrapped 95% confidence intervals (CI) (dashed lines).

TABLE IV. Theoretical C-POD detection distances for a 75, 100, and 135 kHz tone at for minimum and maximum measured wild dolphin source levels (SL), where a is the frequency-dependent absorption rate and the minimum received level for C-POD is 120 dB re 1 μ Pa.

kHz	a (dB/m)	Detection distance (m)	
		SL = 177 dB re 1 μ Pa	SL = 228 dB re 1 μ Pa
135	0.04	238	1167
100	0.03	275	1486
75	0.02	331	2082

where R is the distance to the animal in meters and a is the frequency-dependent absorption rate.

The theoretical detection distances were calculated for a simple tone without estimates for noise level at these frequencies as no ambient noise measurements were conducted on the study site. In reality there will always be noise present and the broadband, off-axis, overlapping dolphin clicks arriving at differing angles will behave in a very complex way, making shallow water transmission loss and its effect on signal detection difficult to quantify. It is therefore very challenging to accurately model dolphin train detection, although theoretical estimates such as those presented here can be used to indicate potential maximum detection areas and to assess plausibility of study results.

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. The maximum estimated error in measuring the tidal height correctly was 50 cm, which would have caused 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 behavior (feeding or traveling) 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 behavior 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 traveling 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 and Sayigh, 2002). During traveling, animals familiar with the area may not need to echolocate as frequently, and they may also utilize information from each other’s vocalizations 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 behavioral differences whereby the dolphins would spend a much higher proportion of their time in the area 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 the 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 behavioral 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 behavior we found that increasing group size had a significant negative effect on detectability for traveling dolphins, larger groups being less likely to be detected than smaller ones. This may be due to train detection being impaired by reverberation 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 (Meier, 2010; Philpott *et al.*, 2007). In this study, surprisingly, 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 behavior. This indicated that detection probability increases slightly for larger group sizes of feeding dolphins, but decreases markedly for traveling animals. Furthermore, it appears that not only are solitary dolphins more detectable than groups, but traveling single dolphins are more likely to be detected than single animals feeding in the area. This may be due to foraging animals directing more of their sonar into the sea bed where traveling 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 echolocating during foraging could outweigh this effect. Furthermore the train detector seeks coherent trains and has an inherent bias against trains with irregular spacing of click. Overlapping of trains (from multiple animals) may reduce this coherence and make overlapping trains less likely to be detected.

In any observational study, observer bias must be taken into account. The observers could have missed single traveling 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.

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 and Hobbs, 1998). However, to minimize unnecessary error in distance calculations, this should be accounted for in future studies.

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 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.

A possibility remains that the vocal behavior of single dolphins differs from that of larger groups. It could be that their vocalizations are louder or less directional—increasing detectability—if 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. 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, FL, 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 behaviors, 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. Traveling groups may have a reduced need to echolocate continuously, as group cohesion and communication between members by whistling serves as a navigational aid even to those not engaging in vocalization (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.*, 2009). Similar modification according to environmental factors has been suggested for whistle production (Jensen *et al.*, 2012; Jones and Sayigh, 2002). 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 including water temperature and salinity, location in the water column, bottom topography and composition (Au and Hastings, 2008), and importantly the equipment sensitivity, or the amplitude threshold which the signal needs to exceed to be detected. The C-POD threshold is derived from empirical studies of how often “chance trains” are detected in a diverse set of real deployments in cetacean-free environments. The train detection thresholds have been adjusted to bring these sources of false positive to low levels that are lowest for “High” quality trains and highest for “Doubtful” trains (N. Tregenza, personal communication). 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. The C-PODs are now 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 setup, 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 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 and hence estimated detection ranges and probabilities from this study are not applicable for other populations or even other sites within the Cardigan Bay area.

V. CONCLUSION

Unlike the harbor porpoise, whose vocalizations are extremely stereotyped across time and space, dolphin echolocation clicks are very variable (Wahlberg *et al.*, 2011) making it difficult to categorize “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 behavior and their group size. Higher detection rate of feeding dolphins in comparison to traveling ones could yield erroneously high density estimates in feeding areas and vice versa. 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 behavior 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 behavioral distribution in the area of interest in order to work out the appropriate average EDR (or P) prior to conducting a larger 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.*, 2013).

Static acoustic monitoring devices, like the C-POD, can provide a potentially cost effective and practical solution to fulfilling the statutory long-term monitoring requirements of protected coastal cetacean species providing the recorded data is consistently accurate and the knowledge exists to correctly interpret resulting data. These findings emphasize the importance of prior knowledge of the behavioral patterns and vocal characteristics of the target animals for developing appropriate experimental design, effective placement of data loggers and a meaningful analysis of the data for acoustic monitoring studies in the future.

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APPENDIX: CALCULATION OF ANIMAL DISTANCE FROM THE C-POD

1. 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 ($0^\circ = \text{zenith}$), and the known altitude of the theodolite station (A) at the time of the sighting (Fig. 3). This was calculated using right-angled trigonometry by applying the following equation:

$$B = A \tan \beta. \quad (\text{A1})$$

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 possible 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 (see Fig. 11).

2. 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:

$$\theta = \tan^{-1} \left[\frac{(\cos \text{lat}_1 \sin \text{lat}_2 - \sin \text{lat}_1 \cos \text{lat}_2) \times \cos(\text{long}_1 - \text{long}_2)}{[\sin(\text{long}_2 - \text{long}_1) \cos \text{lat}_2]} \right], \quad (\text{A2})$$

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.

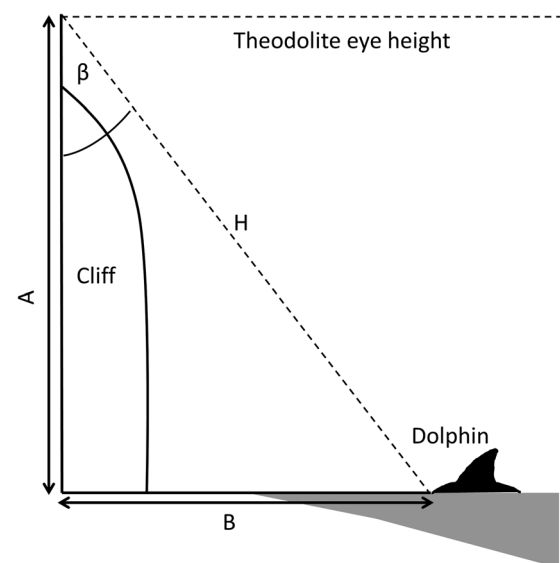


FIG. 11. Diagram of the trigonometric method used to determine distance of the dolphin(s) and C-POD moorings from the theodolite monitoring station, in the present study. “A” is the altitude of the theodolite station, “B” is the base distance between the theodolite and the dolphin(s) or C-POD, and β is the vertical angle between the dolphin’s position and nadir (Meier, 2010).

3. 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.

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

When the animal was to the west:

$$A = 360^\circ - (B + C). \quad (A3)$$

When the animal was to the east:

$$A = C - B. \quad (A4)$$

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

When the animal was to the west:

$$A = B + C. \quad (A5)$$

When the animal was to the east:

$$D = 360^\circ - B, \quad (A6)$$

$$A = C - D, \quad (A7)$$

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 the angular difference between B and 360° .

4. 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.

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

$$lat_2 = \sin^{-1}(\sin lat_1 \cos Bd/R + \cos lat_1 \sin Bd/R \cos \theta), \quad (A8)$$

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:

$$long_2 = long_1 + \tan^{-1}(\sin \theta \sin Bd/R \cos lat_1 / \cos Bd/R - \sin lat_1 \sin lat_2), \quad (A9)$$

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.

5. 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:

$$d = \cos^{-1}[\sin lat_1 \sin lat_2 + \cos lat_1 \cos lat_2 \times \cos(long_2 - long_1)]R, \quad (A10)$$

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. Formulas were obtained and adapted from <http://moveable-type.co.uk/scripts/latlong.html> (Veness, 2010).

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