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Diurnal variation in harbour porpoise detection — potential implications for management

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ABSTRACT: Robust information on animal distributions and foraging behaviour is required to target management and conservation measures for protected species and populations. Visual survey data are commonly used to model these distributions. However, because visual data can only be collected in daylight, modelled distributions and consequent management actions may fail to identify or protect important nocturnal habitats. We explored this issue using data from the Moray Firth, Scotland, where visual survey data have previously been used to characterise habitat use and distribution patterns of harbour porpoises *Phocoena phocoena*. Marine predators such as harbour porpoises have a widespread distribution, are highly mobile and are known to exhibit behavioural variation in relation to diel cycles. Here, we used long-term passive acoustic data which revealed habitat-specific differences in diel patterns of detection. Harbour porpoises were detected consistently during night and day in sandy areas, with peaks in detection around sunrise and sunset, and at night in muddy areas. Detections also varied with depth, with the greatest proportion of daytime detections recorded in shallower sandy areas, and the most nighttime detections recorded in deeper muddy areas. The proportion of detections with foraging buzzes increased slightly during the night and in muddy habitats. These findings suggest that the importance of muddy habitats could be underestimated when using visual survey data alone. This highlights the value of using a combination of visual and acoustic methods both to characterise species distribution and to support efforts to develop appropriate spatio-temporal management of key habitats.

KEY WORDS: *Phocoena phocoena* · C-POD · Passive acoustic monitoring · Management · Distribution · Modelling

INTRODUCTION

Information on animal distributions is critical to support spatio-temporal management of species and populations (Schipper et al. 2008, Jewell et al. 2012). A thorough understanding of species distributions is important for strategic environmental assessments, marine licensing and consenting for offshore activities, developing appropriate mitigation strategies, identifying and managing protected areas and positioning shipping lanes. A variety of industries and activities can potentially have adverse impacts on marine species if poor management practices are put in place; therefore, it is important to develop appropriate management measures to mitigate these risks. These management actions can have impacts on a variety of industries, including fisheries, shipping, tourism and recreation, oil and gas, renewable energy, mining, marine aggregates, and the military. Therefore, species distribution models, which are often used to inform management, need to be as accurate as possible because the consequences can be far-reaching and costly both for the species and the economic interests of any involved industries.

In this paper, we focus on a single species that has been well studied; however, we illustrate that there is still much to learn which could influence how the species is surveyed and managed. Harbour porpoises

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Phocoena phocoena are the most numerous cetacean in European Atlantic Shelf waters (Hammond et al. 2002, 2013) and are considered to be an important indicator species (Gilles et al. 2016). Harbour porpoises are listed on Annex II and IV of the EU Habitats Directive (EU-COM 1992) and are also listed as a threatened and/or declining species in the Northeast Atlantic by the OSPAR Commission (OSPAR 2008). Harbour porpoises are distributed throughout coastal and shelf waters in areas that are under pressure from human activities such as fishing, oil and gas and renewable energy installations, recreational and commercial ship traffic and also climate change. Harbour porpoises can suffer disturbance, injury or even death from these activities (e.g. Tregenza et al. 1997, Southall et al. 2007, Bailey et al. 2010, Dähne et al. 2013); it is therefore important to understand their distribution so that management measures can be most effective.

Harbour porpoises are small, fast and shy, with nondescript surfacing behaviour which can make visual surveys difficult; however, they echolocate nearly continuously (Au 1993, Akamatsu et al. 2007), making it possible to use passive acoustic detections to monitor their abundance and distribution patterns (Madsen et al. 2006, Marques et al. 2009, Bailey et al. 2010, Kyhn et al. 2012). Passive acoustic monitoring (PAM) offers a complementary method to traditional visual surveys, and, unlike visual surveys, functions both during the day and night. A fundamental limitation of visual surveys is that they must be conducted during daylight hours. Therefore, visual data cannot be used to determine if animal distributions vary between day and night. Indices of detection from PAM have been found to correlate strongly with distribution and relative density estimated from visual surveys (Brookes et al. 2013, Williamson et al. 2016) and have been used to monitor the distribution of cetaceans in a variety of habitats and inform assessments of the impacts of disturbance (e.g. Dähne et al. 2013, Thompson et al. 2013, Wilson et al. 2013).

The OSPAR Commission (OSPAR 2009) has recommended that acoustic surveys be used as part of the baseline monitoring of harbour porpoises in areas of high density. In particular, they suggest that moored PAM devices (which have increased temporal resolution compared to towed PAM devices) should be used to assess seasonality and fine-scale habitat use and to delineate marine protected areas for harbour porpoises. However, most broad-scale surveys of harbour porpoise distribution to date (e.g. Bailey & Thompson 2009, Booth et al. 2013, Hammond et al. 2013) have been collected using either plane- or boat-based visual surveys or towed acoustic arrays. While repeated visual and towed acoustic surveys in restricted areas can explore the effects of seasonal and tidal cycles (Goodwin 2008, Philpott 2013, IJsseldijk et al. 2015), this is rarely possible for surveys carried out over larger areas due to their restricted temporal coverage.

Differences in harbour porpoise detection with time of day have previously been observed in visual surveys through daylight hours (Scheidat et al. 2012, IJsseldijk et al. 2015). Other studies that used acoustic detections have also reported increases in harbour porpoise echolocation activity at night near structures such as offshore gas installations and bridge pilings (Todd et al. 2009, Brandt et al. 2014), in deep areas (>20 m; Brandt et al. 2014) and reefs (Mikkelsen et al. 2013). However, these studies have not provided the opportunity to investigate larger distributional changes that could take place on a diurnal scale in a wider range of depths and sediment types. Data presented by Todd et al. (2009) were collected in areas with a depth of 40–48 m and in soft clay and sand sediments, while Mikkelsen et al. (2013) studied stony reefs up to a depth of 20 m, and Brandt et al. (2014) collected data from 5–30 m depth but did not report sediment types. Depth was found to be important in these studies, usually with more detections in deeper areas, particularly at night. However, what is considered to be 'deep' has varied between each study. These previous studies suggested that harbour porpoises may target different prey species during night and day, but data on prey in such studies remain elusive.

The objective of the current study was to use moored passive acoustic data to determine if there are habitat-specific patterns of harbour porpoise detection that may reflect diurnal changes in distribution. For simplicity, we restricted the environmental variables under consideration to only depth and sediment type because these are consistently highlighted as important in modelling, and are likely to influence the types of prey available (Brookes et al. 2013, Williamson et al. 2016). We then explored the potential implications of these findings for spatial conservation and management of harbour porpoises.

MATERIALS AND METHODS

Study area

The Moray Firth covers an area of over 6000 km^2 off northeastern Scotland. The water depth varies from 0 to 200 m; however, data for this study were collected at depths ranging from 25 to 74 m. Approximately 15 km offshore is a 15 × 20 km sand bank (Smith Bank) which has depths of 30–40 m at its centre (Fig. 1a). The seabed substrate over most of the Firth is either sand or gravelly sand, although mud and muddy sand are found in a strip along its southern portion (Brookes et al. 2013). Distance to coast has previously been found to be significant when modelling harbour porpoise distribution (e.g. Bailey & Thompson 2009, Booth et al. 2013); however, we did not consider this distance here because it is collinear with depth in this area, which is considered to be a more biologically meaningful covariate (Williamson et al. 2016).

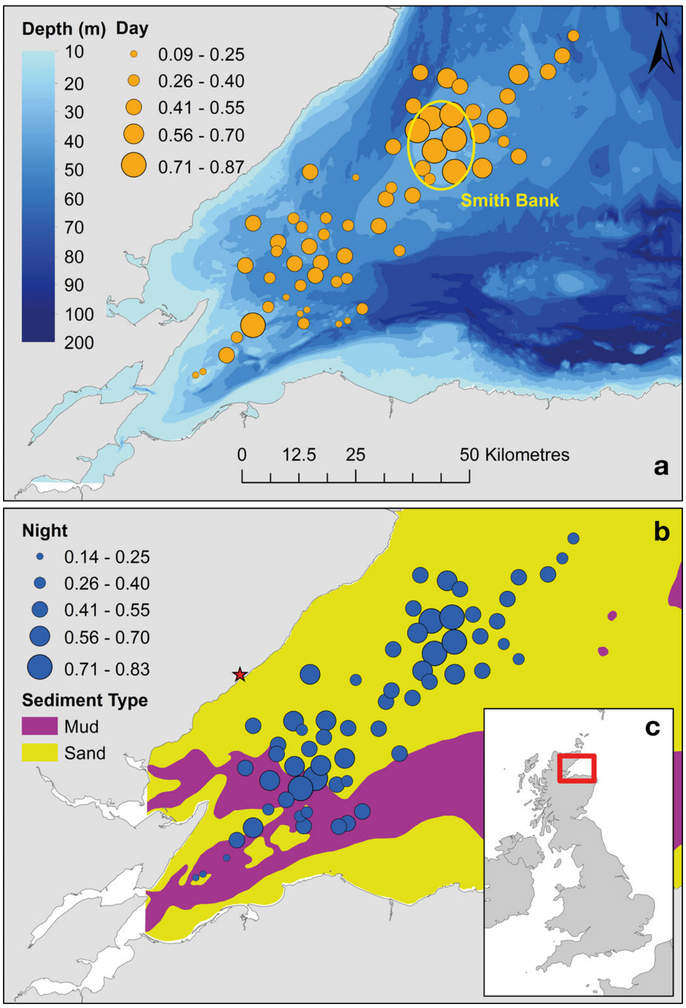

Fig. 1. Locations of C-PODs showing the proportion of hours with detections of harbour porpoises *Phocoena phocoena* during (a) day and (b) night. The background in panel (a) shows the bathymetry of the Moray Firth; Smith Bank is outlined in yellow. Panel (b) shows the 2 sediment types. Helmsdale (the location where sunrise and sunset data were obtained) is illustrated by the star in (b). (c) Location of the Moray Firth (red square) in relation to the British Isles

Data

Polygons of sediment type at a 1:250 000 scale were provided by SeaZone Solutions Ltd (2005). Sediment types were identified using a Folk triangle (Folk 1954). Harbour porpoise distribution has previously been linked to sediment (e.g. Brookes et al. 2013, Williamson et al. 2016), with higher density expected in areas with sandy sediments because one of their primary prey species (sandeel) requires sand to burrow into (Holland et al. 2005). Therefore sediments were classified in 2 groups: sand (including sand, slightly gravelly sand, gravelly sand and sandy gravel) and mud (including muddy sand; Fig. 1b). In sandy sediments, data were collected at depths ranging from 32 to 74 m, and in muddy habitats data collection ranged from 25 to 68 m depth.

The time of sunrise and sunset was obtained from the POLTIPS oceanographic model (NERC National Oceanography Centre, Liverpool, UK) for the port of Helmsdale, in the Moray Firth. This was used to determine which hours occurred during the night and during the day to group the data for analysis. The length of daylight varied from 18 h (with 6 h of night) at the beginning of the study period on 1 July, to 14 h (with 10 h of night) at the end of the study period on 31 August. Hour (0 to 23) was used as a continuous circular variable in the analysis.

Acoustic data collection

Acoustic data were collected in the Moray Firth during July and August 2009 to 2011 at 62 monitoring sites (Fig. 1). The sites were selected to be farther than 5 km from shore to avoid areas with high bottlenose dolphin presence (Thompson et al. 2015), because bottlenose dolphins in this area are known to attack and kill harbour porpoises (Ross & Wilson 1996, Patterson et al. 1998). Therefore, the coastal distribution of porpoises is expected to be influenced by dolphin presence as well as environmental variables.

Data were collected using C-PODs (Chelonia), which include a hydrophone, processor and timing system and can identify and distinguish porpoise and dolphin echolocation clicks in the range of 20–160 kHz at a resolution of 5 µs (Chelonia Ltd. 2014a). The maximum reported detection range for harbour porpoises is 400 m (Chelonia Ltd. 2014a). C-POD sites were selected to conduct studies on the responses of porpoises to seismic surveys (Thompson et al. 2013), and were spaced at least 2 km apart to ensure that individuals were not detected simultaneously. The C-PODs were moored 5 m above the seabed using moorings with either a subsurface acoustic release or a surface buoy. The time of detected echolocation clicks was recorded by the C-POD as well as the centre frequency, frequency trend, duration, intensity and bandwidth of each click (Chelonia Ltd. 2014a). Upon recovery, these data were downloaded and processed using version 2.025 of the cpod.exe software (Chelonia Ltd. 2014b).

Acoustic detection data were analysed on an hourly scale using detection-positive hours per day (DPH) as a metric. DPH has a strong correlation with relative density estimated from visual surveys and minimises the influence of temporal auto-correlation (Brookes et al. 2013, Williamson et al. 2016).

Identifying detection patterns

The C-PODs were grouped by the 2 habitat types with 23, 33 and 25 C-PODs deployed in sand in 2009, 2010 and 2011 respectively, and 9, 9 and 8 in mud (Fig. 2); *t*-tests were used to determine differences between each group of data.

The 2 environmental variables used for analysis in this study (depth and sediment) were selected based on previous research in this area (Brookes et al. 2013, Williamson et al. 2016). To determine whether the combination of depth and sediment influenced detection throughout the day, a GAMM (Generalized Additive Mixed Model) was fitted (using the R package mgcv; Wood 2011) which included harbour porpoise detections as the response variable, and depth, hour and a factor of the 2 sediment types as explanatory variables. A thin plate regression spline was used for the depth covariate, and a cyclic cubic regression spline was used for hour. For both covariates, the number of knots was not specified, as there was no evidence of overfitting. In order to address temporal autocorrelation, this model also included a random effect of the C-POD location, and an autoregressive (AR1) correlation structure that included hour of the day grouped by location and date. This model was fitted using a binomial distribution and maximum likelihood. For visualisation, 2 sets of GAMMs were performed. The first set of GAMMS were fitted to 6 subsets of the data (sand and mud in each of the 3 years) using the same method as above, but using hour as the explanatory variable and detections as the response (Fig. 3). The other set of GAMMs were fitted using 4 subsets of the data (day mud, day sand, night mud and night sand), with depth as the explanatory variable and detection as the response (Fig. 4).

To estimate the proportion of time spent foraging in the different habitats, the duration between clicks (inter-click interval; ICI) was calculated for each detected click, and a mixture model was used to identify peaks in the ICIs (Pirotta et al. 2014). This was done only for hours in which detections were made. Harbour porpoise clicks normally have 3 peaks: the first is generated by buzzes in which there are very short ICIs (usually less than 10 ms; Carlström 2005); the second peak corresponds to normal click trains (Au 1993); and the third peak corresponds to gaps between separate click trains. Sometimes a fourth peak needs to be specified if the proportion of foraging buzzes to normal clicks is very low and the mixture model fails to identify the buzz. If this is the case, the 2 components corresponding to the same click type can be added together after the model is run. The R package mixtools (Benaglia et al. 2009) was used for this analysis.

RESULTS

In both sandy and muddy habitats, the proportion of hours that harbour porpoises were detected increased significantly during the night (mean day = 0.44 ± 0.50 [SD], mean night = 0.51 ± 0.50, $t(80902) = -23.28$, $p < 0.01$; Fig. 1). In sand, this increase was slight (sand mean day = 0.50 ± 0.50, sand mean night = 0.53 ± 0.50, $t(61273) = -9.56$, $p < 0.01$; Fig. 3); however, in mud, the increase in detections during the night was greater (mud mean day = 0.28 ± 0.45, mud mean night = 0.46 ± 0.50, $t(18445) = -30.75$, $p < 0.01$; Fig. 3). Porpoise detections also differed in response to depth in the different sediment types during the night and day (Fig. 4). Peaks in detection were observed in sandy habitats around dawn and dusk in 2010 and 2011, with detection during the day and night in sandy habitats in all years being similar, only increasing by a proportion of 0.04. Detections in sand were similar between night and day at different depths, with generally more detections made in shallower areas (the sand bank) where they were detected in ~70% of hours. In contrast, the proportion of hours with acoustic detection in muddy habitats increased during the night by 18%. In muddy areas, detections were greater at night at nearly every depth, but this was particularly apparent in deeper areas (50–60 m), where detections at night were nearly double those during the day (Fig. 4).

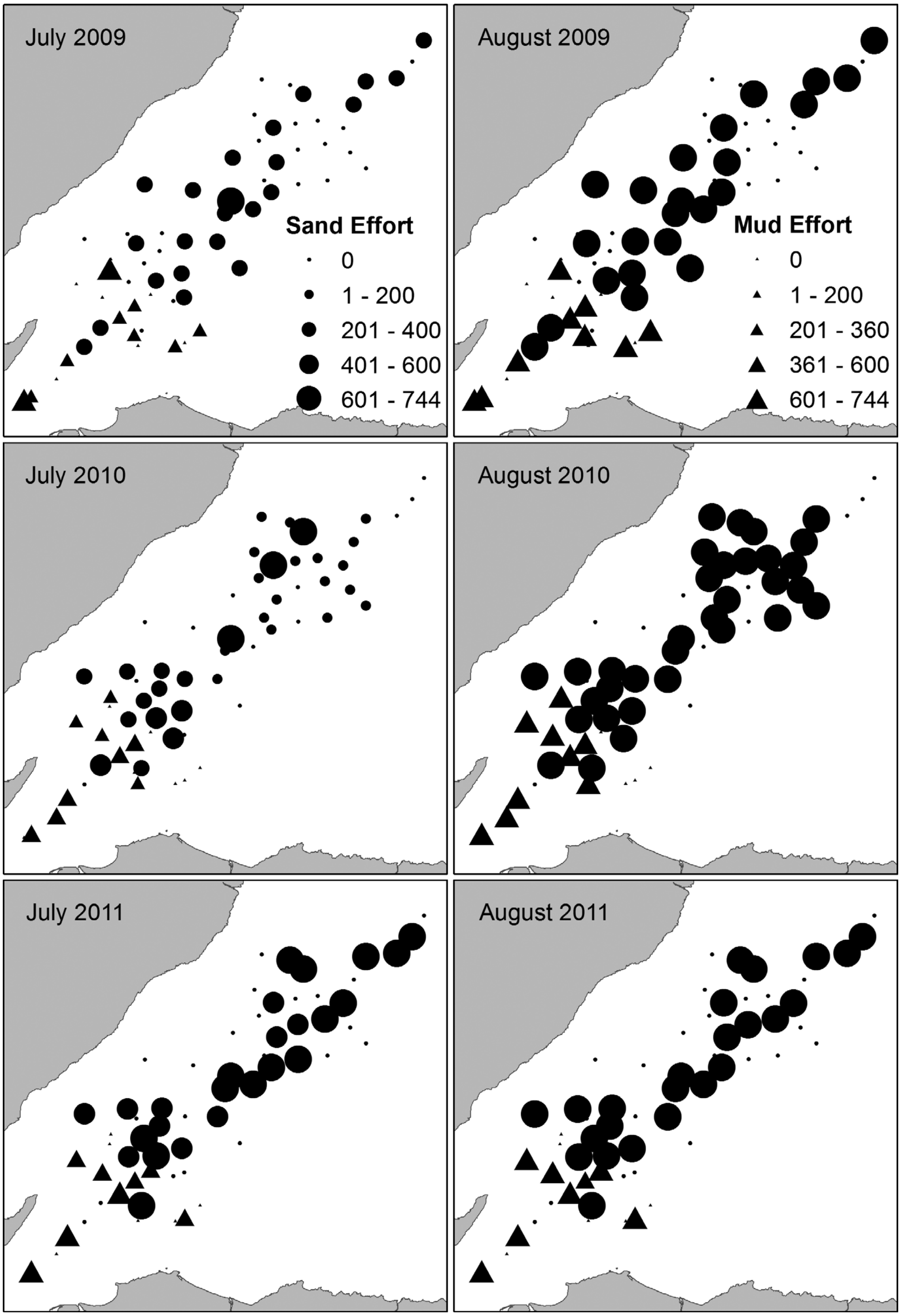

Fig. 2. Number of hours that C-PODs recorded data (effort) at each location in July and August 2009 to 2011 in areas with sandy (circles) and muddy (triangles) sediments

In the full model which included detection modelled as a function of depth, hour and sediment type, only sediment and hour were significant (ANOVA: sediment $F = 13.59$ $p < 0.01$, hour $F = 74.69$ $p < 0.01$, depth $F = 2.87$, $p = 0.09$). However, when the data were split up by sediment, depth and hour were both significant in the 2 sediment types (muddy sediment: hour $F = 101.18$, $p < 0.01$, depth $F = 4.10$, $p = 0.04$; sandy sediment: hour $F = 33.31$, $p < 0.01$, depth $F = 8.74$, $p < 0.01$).

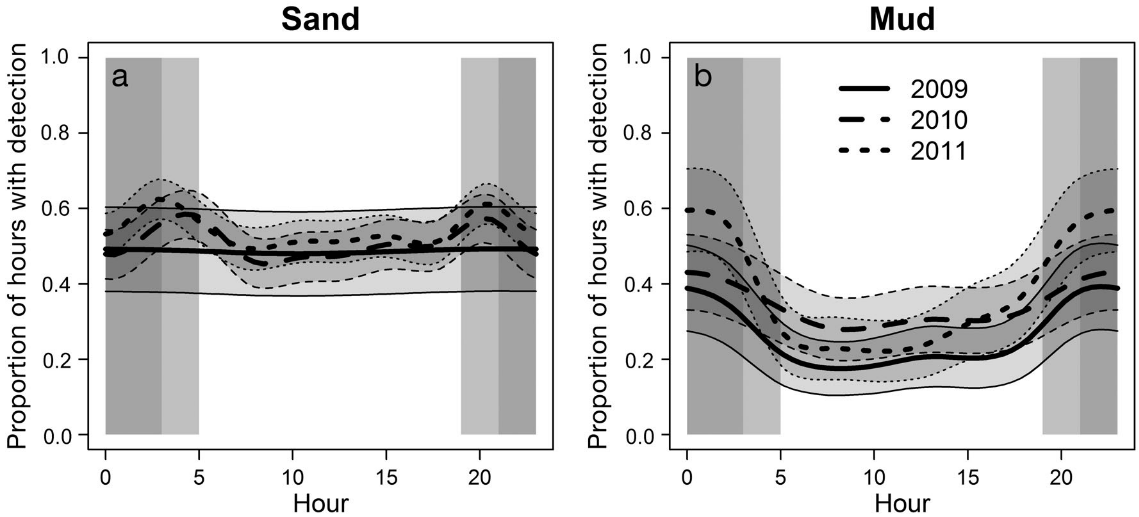

Fig. 3. Proportion of hours that harbour porpoises *Phocoena phocoena* were detected in July and August in (a) sandy and (b) muddy areas in 2009 to 2011 against hour of day. The 95% confidence interval is also shown as the shaded region around each line. The dark grey bars represent hours that were night throughout the entire study period, and light grey represents the hours that shifted from light to dark as the study progressed from 1 July to 31 August in each year

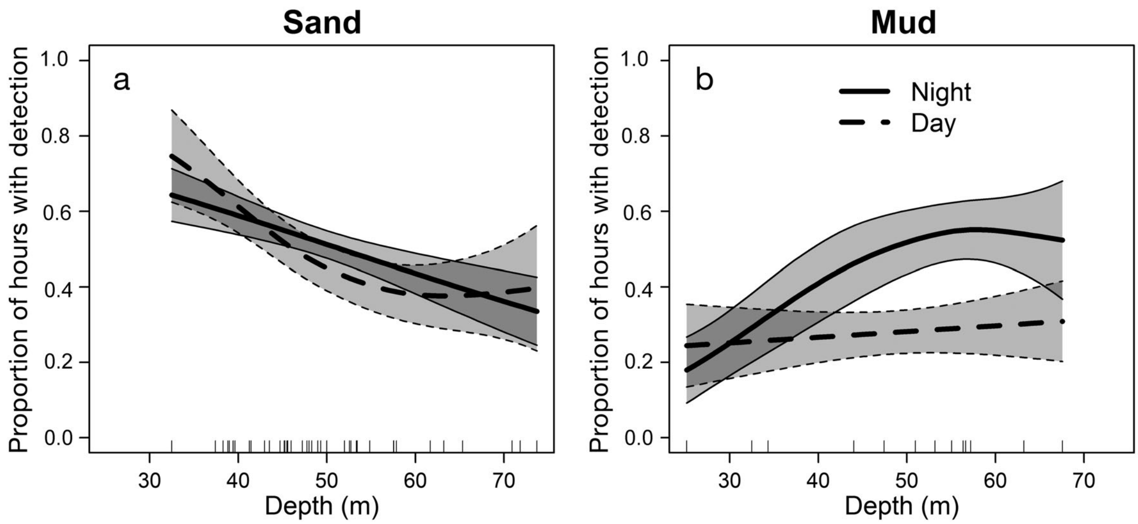

Fig. 4. Proportion of hours in which harbour porpoises *Phocoena phocoena* were detected in response to depth during the night and day in (a) sandy and (b) muddy habitats. The rug plot along the *x*-axis shows the depths at which C-PODs were moored in each habitat. The 95% confidence interval is also shown as the shaded region around each line

In those hours in which harbour porpoises were detected (DPH), the proportion of hours in which foraging buzzes were also detected increased during the night (mean day = 0.08 ± 0.20, mean night = 0.11 ± 0.20, $t(41791) = -16.42$, $p < 0.01$) and also in muddy habitats (mean sand = 0.08 ± 0.19, mean mud = 0.13 ± 0.23, $t(13752) = -21.45$, $p < 0.01$; Table 1).

Table 1. Mean ± SD proportion of detection-positive hours with foraging buzzes made by harbour porpoises *Phocoena phocoena*

Habitat	Daylight	2009	2010	2011	All years
Sand	Day	0.06 ± 0.17	0.07 ± 0.18	0.09 ± 0.20	0.07 ± 0.19
	Night	0.08 ± 0.19	0.11 ± 0.20	0.11 ± 0.20	0.10 ± 0.20
Mud	Day	0.11 ± 0.23	0.11 ± 0.23	0.14 ± 0.24	0.12 ± 0.23
	Night	0.13 ± 0.21	0.15 ± 0.22	0.17 ± 0.21	0.15 ± 0.22

DISCUSSION

Efforts to manage and conserve mobile species such as harbour porpoises have generally assumed that realistic distributions can be identified by modelling habitat associations from visual survey data. However, our study indicates that diurnal patterns in acoustic detections of harbour porpoises vary in habitats with different sediment and depth characteristics.

Previous visual surveys in this area have identified Smith Bank (Fig. 1), an offshore region with relatively shallow sandy habitats, as a locally preferred area for harbour porpoises (Brookes et al. 2013, Williamson et al. 2016). This was supported by the current results, where C-PODs deployed in sandy areas with a depth of 30–40 m (corresponding to the centre of Smith Bank) had the highest acoustic detections of the entire study area (detected in ~70% of hours). However, our results suggest that visual data could be underestimating the importance of adjacent muddy habitats, where detection increases during the night. This could have potentially significant impacts when determining appropriate conservation and management measures for harbour porpoises. For example, analysis of an extensive dataset of visual data led to the conclusion that harbour porpoises avoid areas with muddy sediments throughout the North Sea (Heinänen & Skov 2015). However, given the results presented here, it is possible that this finding could simply be an artefact of only using data collected during daylight hours. Studies which do not account for nighttime habitat use may be under-representing the importance of different habitat types for the species in question.

In practice, harbour porpoise habitat use is likely to be even more complicated than presented here. From our results, it is apparent that detections of harbour porpoises varied across different habitats and depths throughout daily cycles. Detections were not consistent across sediment types, with increased diurnal variation observed in deeper muddy areas. In addition, localised differences were observed between adjacent sites where some C-PODs recorded more detections at night, some more during the day, and some had very little change between night and day (Fig. 1). Further investigation is required to determine the reasons for such localised variations.

Variation in dynamic variables related to tidally driven currents is also likely to influence spatio-temporal patterns of distribution because prey are known to respond to these variables (e.g. Embling et al. 2010, Benjamins et al. 2016, Cox et al. 2016). Tidal currents and mixing can influence prey distribution and schooling throughout the water column, making them more accessible to predators at certain times of the tidal cycle (Embling et al. 2012, 2013). This will then influence predator distribution as they reduce energy expenditure by exploiting prey in predictable patches. Thus, management measures that only cover specific habitat types or times may be insufficient.

The findings in this study may be particularly relevant to the management of threats such as by-catch, where the risk to protected species may also increase nocturnally (Tregenza et al. 1997). In addition, our finding that foraging buzzes are detected more often at night, which supports previous studies (Todd et al. 2009, Brandt et al. 2014), indicates that harbour porpoises spend more time foraging at night, and also in muddy habitats. This highlights the need to understand the causes underlying nocturnal changes in behaviour and distribution when developing appropriate management measures.

Further insights could be obtained through longer-term PAM, thus overcoming some of the sampling issues associated with visual surveys. In particular, our results highlight the potential value of assessing the seasonal consistency in the nocturnal use of muddy habitats adjacent to offshore sandbanks that are recognised to hold high densities of harbour porpoises. Understanding the causes behind finer-scale variation in distribution ideally requires similarly fine-scale studies of variation in the prey fields that are likely to be driving these patterns; however, these data remain elusive.

As with any method, acoustic surveys have some limitations. Acoustic detections are more susceptible than visual surveys to behavioural changes of the animal, such as differences in body orientation, click intensity and also periods of silence that could influence the results. Harbour porpoises show variation between individuals in their echolocation patterns (Linnenschmidt et al. 2013). Unless porpoises echolocate, they will not be detected by an acoustic recorder, and given the narrow beam width of their echolocation clicks (Goodson & Sturtivant 1996, Koblitz et al. 2012), the direction that an animal is facing can substantially influence the probability that it will be detected even if it is echolocating. It is not currently possible to identify individual porpoises using PAM, and consequently, the number of individuals that are detected. This makes it difficult to estimate absolute abundance of porpoises when using PAM, which is often a goal for regulators. Williamson et al. (2016) found a strong correlation between acoustic detections during the day and modelled density from visual surveys, suggesting that more detections indicate more individuals. Although the manufacturers state that C-PODs are capable of detecting porpoises up to 400 m away (Chelonia Ltd. 2014a), the detection function of C-PODs is unknown and could be influenced by factors such as sea state, wind, current speed and sediment type, which may influence the background noise levels around the C-POD.

Fixed versus towed PAM also offers different benefits. Fixed PAM has the advantage of recording a long time-series of data in one location, with the potential disadvantage of poor spatial coverage, while towed PAM increases spatial coverage at the expense of temporal resolution. Towed PAM is a good complement to visual surveys as it can allow gaps due to poor weather to be filled in. However, towed PAM is usually used in conjunction with visual surveys, and therefore suffers the same bias toward daylight hours unless surveys are repeated during the night, which adds cost and is not usually performed.

Visual surveys also have limitations. The detection function can be difficult to estimate; although methods of doing this are better developed than for acoustic surveys (Buckland et al. 2004), estimating the proportion of animals that will be missed because they are under the surface requires more advanced survey design (Buckland et al. 2004, Hammond et al. 2013). Visual surveys require calm weather, low sea state, good visibility (no fog) and daylight (Hammond et al. 2013). Depending on the location of the surveys, these requirements can exclude a large proportion of potential surveying days, a limitation that is not faced by acoustic surveys.

From our results, we cannot determine whether the recorded differences in detection between different habitats are caused by a behavioural or a distributional shift. Either way, the results highlight that the bias in visual survey data towards daylight periods necessitates further investigation to explore the extent to which either distribution or behaviour may vary at different times of day. Currently, the combined use of visual surveys and static PAM is likely the most robust in determining complete habitat distributions.

Harbour porpoises are widespread and highly mobile, and it is recognised that the relative importance of their marine habitats may be transient (Evans 2008, Wilson 2016) and that their distribution may vary over time (Hammond et al. 2013). Our findings highlight some additional complexities of the patterns and drivers of fine-scale changes in harbour porpoise distribution over different habitats within UK waters. Such information will be critical for developing conservation and management measures across the entire range of the harbour porpoise population.

CONCLUSIONS

We have shown that acoustic detection rates of harbour porpoises are different between night and day in habitats with different sediment and depth characteristics. We suggest that this could arise from an underlying shift in distribution or behaviour between night and day. Habitat-specific variations in diurnal distribution patterns may potentially compromise the ability to make inferences on habitat use of harbour porpoises from visual surveys alone. This could lead to incorrect identification of distribution and consequent implications for management strategies or mitigation requirements. Therefore, we recommend the use of a combination of visual and fixed PAM carried out during the day and night when surveying the distribution of harbour porpoises and other species that might share similar behavioural patterns.

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