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Echolocation detections and digital video surveys provide reliable estimates of the relative density of harbour porpoises

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Summary

1. Robust estimates of the density or abundance of cetaceans are required to support a wide range of ecological studies and inform management decisions. Considerable effort has been put into the development of line-transect sampling techniques to obtain estimates of absolute density from aerial- and boat-based visual surveys. Surveys of cetaceans using acoustic loggers or digital cameras provide alternative methods to estimate relative density that have the potential to reduce cost and provide a verifiable record of all detections. However, the ability of these methods to provide reliable estimates of relative density has yet to be established.

2. These methodologies were compared by conducting aerial visual line-transect surveys ($n = 10$ days) and digital video strip-transect surveys ($n = 4$ days) in the Moray Firth, Scotland. Simultaneous acoustic data were collected from moored echolocation detectors (C-PODs) at 58 locations across the study site. Density surface modelling (DSM) of visual survey data was used to estimate spatial variation in relative harbour porpoise density on a 4×4 km grid. DSM was also performed on the digital survey data, and the resulting model output compared to that from visual survey data. Estimates of relative density from visual surveys around acoustic monitoring sites were compared with several metrics previously used to characterise variation in acoustic detections of echolocation clicks.

3. There was a strong correlation between estimates of relative density from visual surveys and digital video surveys (Spearman's $\rho = 0{\cdot}85$). A correction to account for animals missed on the transect line [previously calculated for visual aerial surveys of harbour porpoise in the North Sea was used to convert relative density from the visual surveys to absolute density. This allowed calculation of the first estimate of a proxy for detection probability in digital video surveys, suggesting that 61% (CV $= 0{\cdot}53$) of harbour porpoises were detected. There was also a strong correlation between acoustic detections and density with Spearman's $\rho = 0{\cdot}73$ for detection positive hours.

4. These results provide confidence in the emerging use of digital video and acoustic surveys for studying the density of small cetaceans and their responses to environmental and anthropogenic change.

Key-words: abundance, acoustics, availability, C-POD, density surface modelling, digital survey, distance sampling, harbour porpoise

Introduction

Reliable information on the distribution and density of cetaceans is required to support a wide range of fundamental and applied ecological studies (e.g. Schipper *et al.* 2008). Considering that less than 25% of the world ocean surface has been surveyed for cetaceans (Kaschner *et al.* 2012), this is an area of research in need of development. The management of exploitation and bycatch has driven important developments in line-transect sampling methodology (Buckland *et al.* 2004) which can now provide broad-scale estimates of absolute density and abundance (e.g. Hammond *et al.* 2002, 2013). However, the need for skilled observers and specialist vessels can make it challenging to use these visual survey techniques when data are required at smaller spatial scales or higher temporal resolutions.

These requirements have spurred investigation into the use of alternative survey methods to provide more cost-effective estimates of density when addressing finer-scale questions. In particular, considerable effort has been put into developing passive acoustic techniques because cetacean vocalisations can

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be detected at night or in poor weather when visual observations are not possible (Thomas & Marques 2012).

The development of relatively low-cost echolocation detectors and data loggers (e.g. T-PODs and C-PODs; Chelonia Ltd., MouseholeCornwall, UK) has led to their extensive use in a wide range of studies of spatiotemporal changes in distribution (e.g. Gallus *et al.* 2012) and impact assessment (e.g. Brandt *et al.* 2011; Thompson *et al.* 2013). These studies are based on the assumption that variations in acoustic detection provide a reliable index of density; however, this remains untested. Furthermore, there is a lack of consensus on which acoustic metrics provide the best index of density. Some studies have used the number of detection positive hours (DPH) per day (e.g. Thompson *et al.* 2013), whilst others have used smaller detection bins of 10 min (e.g. Dähne *et al.* 2013) or ≤1 min (e.g. Brandt *et al.* 2011), or waiting times between detections (e.g. Dähne *et al.* 2013; Thompson *et al.* 2013). Methods for directly estimating absolute density from acoustic data are in development (e.g. Marques *et al.* 2013); however, these remain constrained by the difficulty of estimating detection probabilities and variations in the rate at which individuals echolocate (Thomas & Marques 2012).

Recent studies have also highlighted the potential for using digital imagery instead of human observations during aerial surveys of both seaducks (Buckland *et al.* 2012) and cetaceans (e.g. Heide-Jørgensen 2004; Koski *et al.* 2013). Digital surveys have several potential benefits. Cameras do not suffer from fatigue, it is easier to survey simultaneously for multiple taxa such as cetaceans, seabirds and turtles and a permanent record is created for subsequent quality assurance and analysis. Furthermore, surveys can be conducted from a higher altitude, which can allow offshore wind farms to be surveyed (Buckland *et al.* 2012). Koski *et al.* (2013) compared detections of cetaceans from digital surveys with those of visual surveys; however, it is not yet possible to use digital surveys to monitor the absolute density of cetaceans.

A critical assumption of conventional line transect sampling for unbiased estimation of density is that all animals are detected on the transect line (Buckland *et al.* 2004). In visual surveys of cetaceans, this assumption is violated both because some animals are beneath the surface and unavailable for detection (availability bias), and because some animals at the surface may be missed on the transect line (perception bias). Methods have been developed to account for these biases in aerial surveys that involve the use of tandem aircraft or, more efficiently, a single aircraft circling back over the transect line following a detection (Hiby & Lovell 1998). These methods have been successfully employed to estimate harbour porpoise abundance in European Atlantic shelf waters (Hammond *et al.* 2002, 2013; Scheidat *et al.* 2008).

Aerial digital surveys should have no perception bias because all animals within the surveyed strip that are at the surface should be detected. However, currently they cannot account for availability bias and the circle-back method cannot be implemented because detections of animals are not identified until after the survey is completed. Thus, whilst digital surveys can provide measures of relative density for cetaceans (e.g. Thompson *et al.* 2013), it is not yet possible to convert these into estimates of absolute density.

In this study, a series of surveys of harbour porpoises were conducted using aerial visual line-transect surveys, digital video strip-transect surveys and static passive acoustic monitoring (PAM). The primary aim was to assess whether measures of density obtained from PAM and digital surveys were reliable when compared with indices of density from conventional visual aerial surveys, for which robust correction to absolute density is possible. Secondary aims were to compare the performance of different acoustic metrics used to characterise variation in relative density and to provide a preliminary estimate of a scaling factor that can be considered as a proxy for the detection probability for aerial digital video surveys.

Materials and methods

All data were collected in the Moray Firth, Scotland, during August and September 2010 (Table S1, Supporting information, Fig. 1). Surveys were focussed in two 25 × 25 km offshore study blocks that were designed as part of related studies of harbour porpoise responses to industrial noise (Thompson *et al.* 2013), which took place in the following year.

VISUAL LINE-TRANSECT SURVEYS

Visual line-transect data were collected using standard protocols for broad-scale surveys of small cetaceans in the North Sea (Hammond *et al.* 2002, 2013), and density surface modelling was used to characterise variation in density across the study area (Hedley & Buckland 2004; Miller *et al.* 2013).

Surveys were conducted from a Partenavia P68 aircraft on 10 days in August and September 2010 (Table S1, Supporting information). Surveys were only flown on days in which sea conditions were ≤3 on the Beaufort scale, visibility was >5 km forward and the cloud base was above 200 m to allow surveys to be conducted at a height of 183 m. Within each study block, parallel north/south transect lines spaced at 4 km intervals were flown during each survey at a speed of 100 knots. The starting position was selected randomly from a 1 km offset so that, during the course of the whole survey period, the blocks were covered at 1 km spacing. Additional survey tracks were flown diagonally through the centre of the blocks, and at a distance of 1 and 5 km from the western and southern coasts (Fig. 1a).

Observations were made from both sides of the aircraft, with two experienced observers recording the time, species, number of animals and the declination angle of all sightings. GPS data were recorded every 5 seconds and interpolated to estimate the location of the aircraft during each sighting. The perpendicular distance from the trackline to the sighting was later calculated from the declination angle and flight altitude. The exact distance was used to calculate the positions of animals. Environmental variables were recorded by a third observer at the beginning of each transect and if the conditions changed during the transect; these included Beaufort scale, glare intensity, cloud cover and precipitation. A subjective measure of sighting conditions was recorded as four levels: poor, moderate, good and excellent. These levels related to the likelihood that a porpoise would be observed if it were present, and considered all variables that might influence observers' ability to detect animals. Data collected on all 10 days were used; however, only data collected during good or excellent sighting conditions were used for analysis.

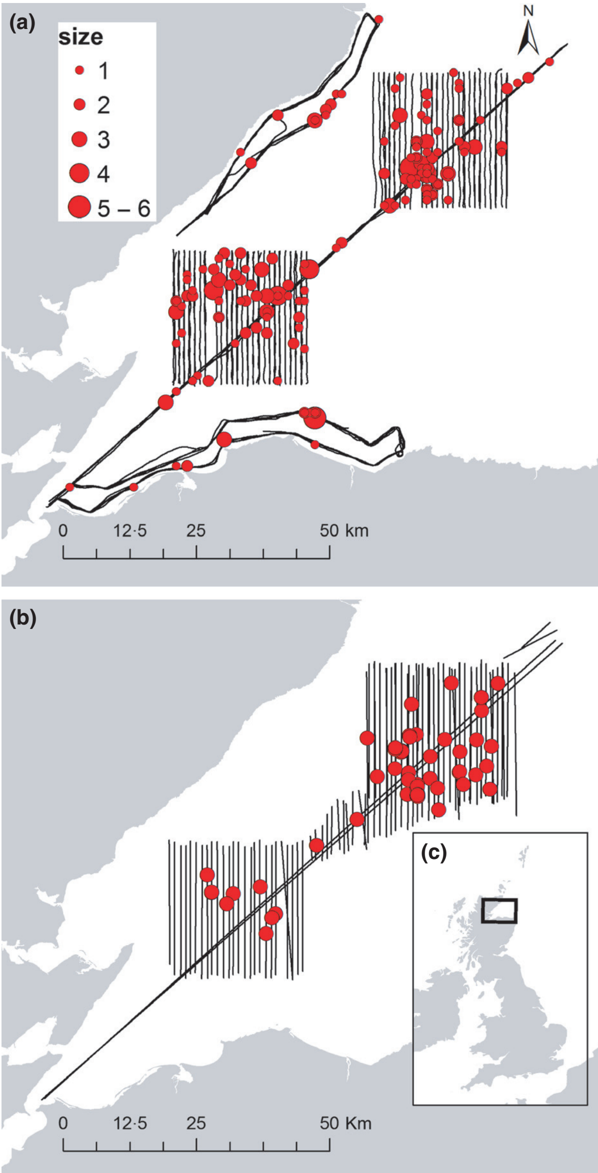

Fig. 1. Survey tracks and sighting locations for a) visual surveys and b) digital video surveys conducted in the Moray Firth during August and September 2010. The number of individuals in each sighting (cluster size) was recorded for visual surveys; however, in digital surveys, the location of each individual was recorded. Inset c) shows the location of the Moray Firth in relation to the British Isles.

Although the aircraft had bubble windows, the observers were unable to see the closest 20° below the aircraft on either side, equivalent to a perpendicular distance of 66 m at 183 m altitude. Sixty-six metres were therefore subtracted from the perpendicular distance of sighting data. Distance sampling software (Thomas *et al.* 2010) was used to investigate the influence of several covariates on detection probability for these visual surveys, including observer, sea state, sighting conditions, glare, precipitation and cloud cover. Sighting covariates were checked for collinearity (Fig. S1, Supporting information). Detection functions using both the half-normal and hazard-rate key functions were investigated. The most appropriate model was selected based on AIC and the goodness-of-fit using a Kolmogorov–Smirnov test (Buckland *et al.* 2004). The best detection function was then used to correct the number of animals detected in segments of effort (4 km for north/south transects) and used in the density surface modelling for the visual surveys.

DIGITAL STRIP-TRANSECT SURVEYS

Digital video surveys were conducted by HiDef Aerial Surveying Ltd. on 4 days in August and September 2010 (Table S1, Supporting information) using an Aztec aircraft. Each survey was started on a randomly selected route across pre-determined transects. The surveys were flown between 244 and 457 m altitude depending on cloud height. Four cameras with either 135 mm or 85 mm lenses were used and, depending on altitude, the strip width was between 80 m and 150 m. Survey tracks and sighting locations of harbour porpoises are shown in Fig. 1b.

The video data were analysed by trained observers at HiDef Aerial Surveying Ltd., who extracted all non-avian objects for identification by specialists at WWT Consulting Ltd. Given that these were strip surveys using digital video, a uniform detection function was assumed (see Buckland *et al.* 2012) to calculate the density surface for the digital surveys, using an effective (half) strip width of 40–75 m depending on height. Modelled results from these digital surveys represent estimates of spatial variation in relative density that can be compared with estimates of density from visual surveys.

PASSIVE ACOUSTIC SURVEYS

Acoustic data were collected using 58 C-PODs (Chelonia Ltd. UK) which were deployed from April to October 2010 in regions covered by visual surveys (Thompson *et al.* 2013). Only acoustic data from between 6 a.m. and 6 p.m. on the 10 days in which visual surveys occurred were used for analysis.

C-PODs were moored 5 m above the seabed and continually monitored the frequency range between 20 and 160 kHz for cetacean vocalisations (Chelonia Ltd. 2014a). C-PODs are capable of detecting porpoise clicks up to a maximum range of 400 m (Chelonia Ltd. 2014a). When clicks were detected, the C-POD recorded the centre frequency, frequency trend, duration, intensity and bandwidth of each click (Chelonia Ltd. 2014a). These data were downloaded upon recovery and processed using version 2·025 of the cpod.exe software to distinguish harbour porpoise click trains from those of other odontocetes (Chelonia Ltd. 2014b).

Data from the hours of daylight (6 a.m.–6 p.m.) on each of these 10 days were then analysed to determine whether harbour porpoise click trains were present in a range of different time intervals that varied in duration from ten to ninety minutes. Daily estimates of the relative density of harbour porpoises at each sampling site were then expressed as the proportion of these different intervals that contained positive detections or 'Detection Positive Intervals' (DPI_{10} to DPI_{90}). Thus, DPI_{60} was equivalent to the DPH used in many other studies, but the performance of shorter and longer time intervals was also explored. Detection positive minutes, another common metric, is generally calculated on a daily (Brookes, Bailey & Thompson 2013) or hourly scale (Brandt *et al.* 2011). This metric was therefore calculated in both ways, with detection positive minutes per day represented as DPM/D and per hour as DPM/H. In addition, the median waiting time (WT) between detections made at each site was also calculated. A minimum WT of ten minutes was used to ensure that vocalisations were separate events and not continuations of the previous detection (Dähne *et al.* 2013).

DENSITY SURFACE MODELLING

Density surface modelling was performed on a scale of 4 × 4 km over the entire study region for both the visual and digital aerial data sets based on previous research in this area (Brookes, Bailey & Thompson 2013). Generalised additive models (GAMs; Wood 2006) were used to predict porpoise density across the 4 × 4 km surface from the counts of porpoises. The response variable for the visual surveys was the number of animals detected along each effort segment (4 km for north/south transects), and for the digital surveys, the number of animals detected within the strip in each segment. Models were compared which used quasi-Poisson, negative binomial and Tweedie error distributions.

Candidate environmental variables were depth, slope, sediment type and distance from the coast. Environmental variables were checked for collinearity between each other (Fig. S3, Supporting information). Depth on a raster grid of approximately 180 m and polygons of sediment type at a 1:250 000 scale were provided by SeaZone Solutions Ltd. (2005b,a). These were then processed and converted to a 4 × 4 km grid as in Brookes, Bailey & Thompson 2013. Sediment type was expressed as the proportion of sediment that was sand or gravelly sand within each 4 × 4 km block based on previous studies of harbour porpoise habitat association in this area (Brookes, Bailey & Thompson 2013). Sand and gravelly sand are known to provide suitable habitat for sand eels (Holland *et al.* 2005) and whiting (Atkinson, Bergmann & Kaiser 2004), two of the main prey species for harbour porpoise (Santos *et al.* 2004), and may therefore be considered a proxy for prey distribution.

When comparing estimates of relative density from visual and digital surveys, g(0) was assumed to be 1 for both survey types. The quantity g (0) is the probability of detection on the track line accounting for both perception and availability bias. Direct estimates of g(0) could not be made during the relatively short series of visual surveys.

Summary plots from the models were used to select between quasi-Poisson, negative binomial and Tweedie distributions, and the best DSM was selected based on its GCV/REML score and the percentage of deviance explained. The best model was then used to predict porpoise density throughout the survey region on the 4 × 4 km grid. Surveys were only conducted in water depths of up to 75 m; therefore, densities were only predicted in areas with depths <80 m. In addition, after inspection of histograms of the data, densities were not predicted for areas with a slope >1° for visual surveys, and for digital surveys, a slope >0·5° and depth <20 m. Model variance was calculated according to Wood (2006).

Data from all surveys were analysed in R (version 3.1.0, R Core Team 2014). The R package `mrds` (Laake *et al.* 2014) was used to calculate the detection function for the visual data (using the 'single observer' option), and package `dsm` (Miller *et al.* 2013, 2014) was used for density surface modelling. R code for the DSM is provided in Appendix S1 (Supporting information). Maps were constructed using ESRI ArcGIS 10.2.1 (ESRIRedlands, Redlands, California, USA).

COMPARISON OF DATA FROM DIFFERENT SURVEY METHODS

The most intensive visual and digital aerial surveys were conducted within the two offshore 25 × 25 km survey blocks. Comparisons of visual and digital survey data therefore focussed on these areas.

The scaling factor for digital surveys, which can be considered as a proxy for the detection probability of visual surveys, was estimated by dividing the relative density from the digital surveys by the absolute density from the visual surveys. To scale the visual survey estimates up to absolute density, the relative density from the DSM was divided by a value for g(0) = 0·45 (CV = 0·30) estimated from extensive aerial surveys of harbour porpoise in similar habitats and sighting conditions across the North Sea (Hammond *et al.* 2013). In order to incorporate the standard deviation of the density prediction at each cell and the CV of the availability for the visual surveys, the density estimate of each cell was bootstrapped 1000 times using the SD from the predicted density of each cell to generate random variables of each cell within the offshore study region using a log-normal distribution. The code used to perform this is provided in Appendix S2 (Supporting information).

To compare visual and acoustic results, the output from the density surface model of visual survey data was used to calculate the mean relative density of harbour porpoises across survey squares within 1 km of each C-POD sampling site (Table S5, Supporting information). Resulting estimates of relative density around each C-POD site were then compared with mean values of the different acoustic metrics for the ten survey days (Table S5, Supporting information).

Spearman's rank-order correlation was used to compare the different types of survey data.

Results

Visual surveys covered 3148 km over 10 survey days, and recorded 187 sightings of harbour porpoises. Some sightings were of groups, resulting in a total of 285 porpoises observed (Fig. 1a). Over this same period, digital surveys covered 2155 km over 4 survey days, resulting in 97 detections of harbour porpoises (Fig. 1b). Strip widths of digital surveys varied slightly between surveys because flight heights were sometimes reduced to avoid low cloud. Of 83 digital transects, 70 had a strip width of 150 m, 12 had a strip width of 100 m and one had a strip width of 80 m.

Sighting conditions were tested for collinearity and glare was found to be collinear with both sighting conditions and cloud cover with correlation coefficients of 0·51 and 0·57, respectively (Fig. S1, Supporting information). Therefore, no detection functions were used which included both sighting conditions and glare, or cloud cover and glare. The best-fitting detection function for visual data was a half-normal model which included observer, cloud cover and sea conditions as covariates (Table S2, Fig. S2, Supporting information).

The environmental covariates depth and distance to coast were collinear with a correlation coefficient of 0·7 (Fig. S3, Supporting information); depth was preferred over distance to coast because for the digital survey, most of the data were collected at similar distances to the coast. The environmental covariates selected in the density surface models for both visual and digital survey data included depth, slope and the proportion of sediment that was sand or gravelly sand. A Tweedie error distribution was found to be preferable based on inspection of summary plots of the model (shown for Tweedie and negative binomial in Figs S4 and S5, Supporting information). This was also supported by examining a histogram of the predicted densities from the model, which appear to follow a Tweedie distribution (Fig. S6, Supporting information). For a comparison of the DSMs tested, see Table S3 (Supporting information) for the visual surveys and Table S4 (Supporting information) for the digital surveys. The selected density surface model explained 31·6% of the deviance for the visual surveys and 39·3% of the deviance for the digital surveys. See Fig. S7 (Supporting information) for maps showing the spatial pattern of the standard error of density predictions from the selected models for visual and digital data.

Density surface model outputs for visual surveys (Fig. 2a) and digital surveys (Fig. 2b) demonstrated that these independent data sets produced similar patterns of spatial variation in density across the overall study area. In general, both data sets indicated that harbour porpoise densities were lower in inshore and coastal areas and highest over offshore sandbanks. Spearman's $\rho = 0{\cdot}85$ was estimated between relative density from visual and digital surveys. The scaling factor for digital surveys was estimated to be 0·61 with CV = 0·53 (See R code in Appendix S2, Supporting information).

Comparison of the visual survey and PAM data indicated that C-POD detections provided a reliable index of the relative density of harbour porpoises (Fig. 3). Whilst all the acoustic metrics were correlated with local density around each C-POD, the strongest relationship (Spearman's $\rho = 0{\cdot}75$) was for a detection positive interval of 90 min (DPI_{90}) (Table 1). The correlation coefficient for the more commonly used metric of detection positive hours (DPH = DPI_{60}) was also strong ($\rho = 0{\cdot}73$). There was very little difference between the correlation of density and detection positive intervals of 30–90 min.

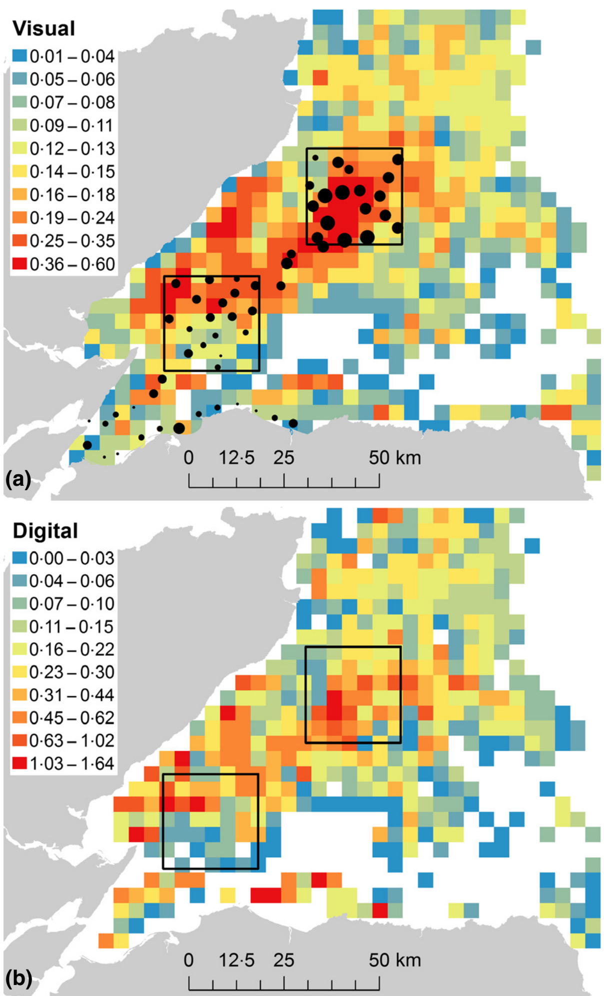

Fig. 2. Map showing the results of the density surface models for a) visual survey data and b) digital video survey data. Units are porpoise/km^2. The locations of the C-PODs are shown by black dots with their size proportional to the number of detection positive sixty-minute intervals per day recorded at each location. The black squares show the perimeter of the two offshore survey regions for reference.

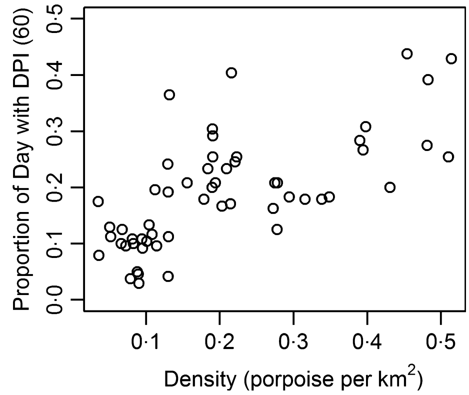

Fig. 3. The proportion of the day with detection positive sixty-minute intervals (DPI_{60}) from acoustic records are shown against relative porpoise density estimated from visual aerial surveys.

Table 1. Spearman's rank correlation coefficients for harbour porpoise density estimated from visual surveys compared to mean detection positive minutes per day (DPM/D) and hour (DPM/H), detection positive intervals of 10–90 min ($DPI_{10–90}$) and waiting time between detections (WT)

	Spearman's Rho
WT	−0·4027341
DPM/H	0·5638265
DPM/D	0·5638265
DPI_{10}	0·6591468
DPI_{20}	0·6802365
DPI_{30}	0·7006154
DPI_{40}	0·7126618
DPI_{50}	0·728339
DPI_{60}	0·7293056
DPI_{70}	0·7203502
DPI_{80}	0·7334497
DPI_{90}	0·7480634

Discussion

Passive acoustic monitoring devices and digital aerial surveys are increasingly being used to explore how small cetaceans respond to natural and anthropogenic environmental change in coastal ecosystems (Brandt *et al.* 2011; Thompson *et al.* 2013). This provides great potential for more cost-effective and safer monitoring programmes and greater transparency in data collection than visual surveys. Some regulators within Europe have already decided that future monitoring of seabirds and marine mammals at offshore wind farms should be based upon digital aerial surveys (e.g. BSH 2013). However, whilst the potential practical benefits of these techniques are widely recognised, their acceptance has been constrained by uncertainty over their ability to provide reliable estimates of spatial and temporal variation in relative density. This study has shown that both acoustic and digital detections of harbour porpoises were correlated strongly with estimates of relative density obtained using established visual line-transect methodology that can, in turn, be corrected to provide estimates of absolute density. This comparison of different metrics also supports previous suggestions that the use of longer Detection Positive Intervals of 30–90 min should provide a stronger and more linear relationship with density (Brookes, Bailey & Thompson 2013) than the shorter intervals used in some previous studies. These results provide confidence in the continued use and development of acoustic and digital surveys and can now underpin finer-scale studies of spatial and temporal variation in harbour porpoise density and distribution.

Our focus was on harbour porpoises, primarily because these are the most abundant small cetacean in many temperate waters (Hammond *et al.* 2002) and commonly interact with fisheries and other coastal and offshore developments (e.g. Brandt *et al.* 2011). Indeed, concerns over impacts on this species have been a key driver in the development of these new survey techniques. This study highlights the potential for these techniques to support future work on this species within the North Sea, but further work will be required to explore the extent to which these results can be applied to other cetacean species and other ecosystems.

Harbour porpoises produce highly regular and distinct echolocation clicks, making them particularly suitable for PAM using click detectors (Akamatsu *et al.* 2007). Other species of cetacean may echolocate less predictably or not at all (Van Parijs *et al.* 2009), and it is not currently possible to discriminate between different dolphin species based upon their click characteristics (Thompson, Brookes & Cordes 2015). Species misidentification from acoustic detections is not a problem in this study because only one species of porpoise is found in the study area; however, further research would be necessary to discriminate between species in other areas (Caillat, Thomas & Gillespie 2013). The coloration and small size of harbour porpoises also makes them relatively straightforward to identify from digital images. Species identification will be more challenging for many other cetaceans, especially within more diverse communities. Identification of closely related species may also be problematic during visual surveys. For digital surveys, the production of permanent digital records provides potential for detailed post-survey data evaluation when species identification is uncertain. Similar comparisons of survey techniques for other species will be more challenging because they typically occur at much lower densities and/or are more patchily distributed (Hammond *et al.* 2013). In this study, other species were detected during both the visual and digital surveys, but sample sizes were insufficient for more detailed analysis.

This comparison of techniques was underpinned by density surface modelling (DSM) of the visual line-transect data, which allowed characterisation of fine-scale variation in the density of harbour porpoises across the study area. The choice of potential covariates was shaped by results from previous regional habitat modelling that had used a wider range of data sources that included the visual aerial survey data used here (Brookes, Bailey & Thompson 2013). The selected DSM for both visual and digital surveys predicted that the highest densities of harbour porpoises occurred around the Smith Bank, an offshore sandbank that is recognised to be important for other marine mammals and seabirds (Mudge & Crooke 1986; Sharples *et al.* 2012). Harbour porpoises were observed less frequently in the inshore waters of the Moray Firth.

More detailed comparison of the model predictions was made using data from the two offshore blocks in which there was intensive survey effort using both techniques. Here, there was a good correlation (Spearman's $\rho = 0{\cdot}85$) between the digital and visual estimates of density. These analyses suggest that digital survey techniques can provide similarly robust measures of relative abundance to those obtained by traditional visual line-transect surveys. However, both visual and digital aerial surveys require additional information on the availability of animals to estimate absolute abundance, and visual surveys must also be corrected for perception bias (Laake *et al.* 1997; Thomas *et al.* 2010). In this study, neither the design nor the intensity of the visual surveys permitted obtaining an independent estimate of availability or estimating perception bias. Instead, a value of g(0) from similar aerial surveys of North Sea habitats in good sighting conditions with experienced observers (Hammond *et al.* 2013) was used as an approximate correction. During digital surveys, however, there should be little or no perception bias.

In future, it would be valuable to obtain finer-scale estimates of g(0) (see Barlow 2015) or develop techniques to directly estimate availability from digital surveys. In the meantime, comparison of the DSMs based upon these two aerial survey data sets provides a first indication of availability using video-based digital aerial surveys. Calculations suggest that under the conditions experienced within this survey, approximately 61% of harbour porpoises were detected in the digital strip transect. However, it should be noted that as well as uncertainty introduced by using a g (0) correction from a different survey, the percentage of detections may be expected to differ for different digital methodologies, and potentially under different environmental conditions. Here, digital video surveys were used, where each point on the sea surface could be observed for up to one-second as the plane passed over. In contrast, availability might be expected to be lower where single digital still images are taken (Koski *et al.* 2013).

In visual surveys, detection probability decreases as worsening sea conditions increase perception bias; aerial surveys for harbour porpoises are thus typically conducted in conditions of Beaufort scale no >3 (e.g. Hammond *et al.* 2013). Surveys here were conducted in relatively good sea conditions (Beaufort scale 1–3) and assumed that sea conditions did not affect availability. Further analyses of existing data collected under a wider range of sea conditions and altitudes are now required to explore the effect on cetacean detections. This will be particularly important for optimising the design of future joint digital aerial surveys for birds and cetaceans (see Buckland *et al.* 2012). Similarly, it would be valuable to compare data across a wider range of water depths, oceanographic conditions and seasons to assess how factors such as water turbidity (Preisendorfer 1986) influence availability.

Extension of these comparisons between echolocation detections and visual estimates of density would also be valuable in a wider range of habitats. Here, water depths up to 75 m were sampled, and PAM was conducted in areas in which the estimated absolute densities of harbour porpoises varied from 0·07 to 1·14 individuals per km^2. As such, this is likely to be broadly representative of habitats and densities experienced at other North Sea sites (Hammond *et al.* 2002, 2013). However, it should be noted that this work was conducted at sites with relatively low tidal energy. Previous studies have shown that higher energy tidal sites produce markedly different levels of high-frequency background noise (Bassett, Thomson & Polagye 2010), and the resulting acoustic interference may require alternatives to static moorings in certain habitats (Wilson, Benjamins & Elliott 2013).

Conclusions

This study demonstrated that estimates of relative density from digital and acoustic surveys of harbour porpoises were strongly correlated (ρ = 0·85 and ρ = 0·73, respectively) to estimates from visual surveys that can be corrected for availability and perception bias to generate absolute density. An initial estimate of the scaling factor for detection probability of digital surveys was calculated to be 0·61. These results provide confidence in the emerging use of digital and acoustic surveys for monitoring the density of cetacean populations. An application of this technique could be studying the responses of small cetacean populations to environmental and anthropogenic change, creating the potential for survey programmes that permit detailed geo-referencing and long-term archiving of individual animal recordings for additional verification and future analysis. In future, these techniques are likely to be especially important where surveys are required to demonstrate compliance with national or international regulations because they provide a permanent and verifiable record of cetacean detections.

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Data accessibility

Data are available from the Dryad Digital Repository: http://dx.doi.org/10,5061/dryad.cf04g

Author contributions

Laura Williamson created the DSM, compared data sets and co-wrote the manuscript with PT. Kate Brookes managed the visual aerial surveys and PAM deployments, led the visual survey team, processed visual and acoustic data, advised on the DSM and provided input to the manuscript. Beth Scott provided advice on statistical analysis and provided input to the manuscript. Isla Graham processed visual, digital and acoustic data sets, advised on analysis and provided input to the manuscript. Gareth Bradbury managed the digital aerial surveys, acted as an observer on the visual aerial surveys and led the identification and processing of digital data. Philp Hammond provided advice on survey design and analysis and provided input to the manuscript. Paul Thompson managed the overall project, advised on all aspects of data collection processing and analysis and co-wrote the manuscript with LW.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Dates and times of visual and digital surveys.

Table S2. Detection function selection.

Table S3. Density surface model selection for visual surveys.

Table S4. Density surface model selection for digital surveys.

Table S5. Mean and standard deviations of estimates from visual and acoustic surveys.

Fig. S1. Correlation between the sighting condition covariates.

Fig. S2. Detection function of visual survey data.

Fig. S3. Correlation between the environmental covariates.

Fig. S4. Summary plot for the selected DSM of visual survey data using Tweedie distribution.

Fig. S5. Summary plot for the selected DSM of visual survey data using negative binomial distribution.

Fig. S6. Histogram of predicted densities from density surface model using a Tweedie distribution.

Fig. S7. Estimates of the standard error of the predicted densities.

Fig. S8. Comparison of absolute and relative densities (porpoise/km^2) for visual and digital surveys.

Fig. S9. Acoustic indices plotted against density.

Appendix S1. R code used for DSM.

Appendix S2. R code used for estimating detection probability of digital surveys.