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Acoustic surveys confirm the high-density areas of harbour porpoises found by satellite tracking

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The population status of the harbour porpoise (*Phocoena phocoena*) has long been of concern in European waters. Consequently, the European Commission (EC) Habitats Directive obligates all EC member states to designate marine protected areas (MPAs) for harbour porpoises before 2012. These will be designated areas having the greatest density of porpoises. However, little is known about comparability between the monitoring methods used to examine porpoise distribution and density, and conflicting results may arise, especially when considering their varying sample size and temporal and spatial scales. Here, vessel-based acoustic surveys are seen as an independent method of testing the temporal and spatial permanence of previously identified areas of high density of harbour porpoises found by satellite-tracking them in inner Danish waters. Based on six acoustic surveys, a strong spatial accord was found between the number of acoustic detections of harbour porpoises and their density distribution obtained from 10 years of satellite tracking. The results confirm the presence and permanence of areas of high density of porpoises and validate the two methods for identifying and monitoring future MPAs for the species.

Keywords: cetacean, conservation, detection rate, Habitat Directive, kernel home range, monitoring, MPA, *Phocoena phocoena*, SAC.

Introduction

The harbour porpoise (*Phocoena phocoena*) has a northern hemisphere circumpolar distribution (Gaskin and Watson, 1985) divided into several spatially separated populations. Three populations have been recognized genetically from the North Sea to the Baltic Sea, with putative borders in the Kattegat and the western Baltic Sea (Andersen *et al.*, 2001; Teilmann *et al.*, 2004; Wiemann *et al.*, 2010). The population status of the harbour porpoise has long been of concern because of anthropogenic influences, the main threat being incidental bycatch in fisheries (Lowry and Teilmann, 1994; Tregenza *et al.*, 1997; Berggren *et al.*, 2002; Vinther and Larsen, 2004). Hence, the designation of marine protected areas (MPAs) is being implemented in the EU (92/43/EEC) as a means of protecting the species. According to the Habitat Directive (European Commission, 1992), MPAs (in the Habitat Directive referred to as "Special Areas of Conservation", or SACs) for each species should "be proposed only where there is a clearly identifiable area representing the physical and biological factors essential to their life and reproduction", and these areas should be "identifiable on the basis of the continuous or regular presence of the species (although subject to seasonal variations), good population density (in relation to neighbouring areas) and high ratio of young to adults during certain periods of the year" (European Commission, 2007). Therefore, before the designation of MPAs, the distribution of harbour porpoises must be thoroughly examined to establish the existence and stability of areas of high density of harbour porpoises.

In Danish waters, the identification of high-density areas of harbour porpoises has been conducted by analysing the tracks of 64 porpoises tagged with satellite transmitters between 1997 and 2007 (Sveegaard *et al.*, 2011). The results of that study show that harbour porpoises are not evenly distributed. In the Kattegat and the Belt Seas, nine high-density areas were identified: (i) the northern part of the Sound (north of 56°N), (ii) southern Samsø Belt and Kalundborg Fjord, (iii) northern Samsø Belt, (iv) Little Belt, (v) Great Belt, (vi) Flensburg Fjord, (vii) Fehmarn Belt, (viii) Smålandsfarvandet, and (ix) the waters around the northernmost tip of Jutland (Figure 1). The high-density areas of porpoises identified by satellite telemetry in Little Belt, Great Belt, Flensburg Fjord, and Fehmarn Belt were supported by previous aerial and boat-based visual and acoustic surveys (Heide-Jørgensen *et al.*, 1993; Teilmann, 2003; Gillespie *et al.*, 2005) and by static, passive acoustic monitoring using

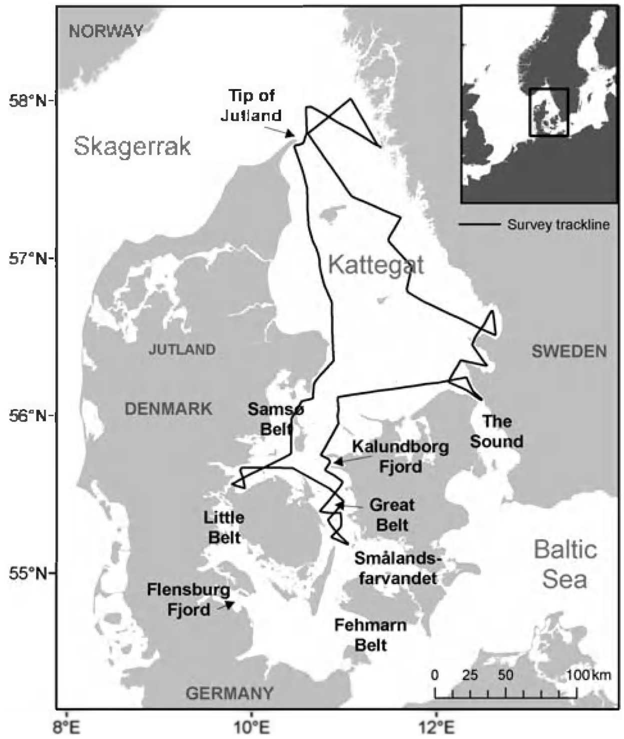

Figure 1. Map of the study area emphasizing the identified high-density regions for harbour porpoises. The trackline for the acoustic surveys in 2007 is shown as a black line. The map projection is universal transverse Mercator, Zone 32N, WGS84.

T-PODs (Verfuss *et al.*, 2007). The other high-density areas have not been identified, because no studies had been conducted in them.

Although the method of using satellite tracking of porpoises to identify high-density areas has the advantage of combining temporal and spatial information on a broad scale, it can be criticized for extrapolating data from relatively few animals to the distribution of the entire population, as well as being biased towards the locations at which the animals were captured and tagged. Hence, the aim of this study was to evaluate the validity of the satellite-based density models presented in Sveegaard *et al.* (2011) using an alternative method.

Harbour porpoises make distinctive narrowband echolocation click-sounds to navigate and search for prey. The dominant frequency of the "click" is around 130 kHz (Villadsgaard *et al.*, 2007). Such high-frequency clicks can readily be discriminated from other ocean sounds using a hydrophone and automatic detection software tuned to the frequency of porpoise clicks. Acoustic detection systems are less affected by sea state, weather, and light, which may hamper visual surveys. Moreover, they are believed to be more predictable and consistent in their performance than human visual observers and have proved to have a higher detection probability than visual observation in all but the calmest weather (Gillespie *et al.*, 2005; Kimura *et al.*, 2009). However, acoustic surveys are dependent on the level of background noise, including that of the survey vessel towing the array, and the vocal behaviour of the porpoises (Gillespie *et al.*, 2005). It is currently not possible to estimate the absolute abundance of porpoises from towed-array surveys because of uncertainties in estimating group size acoustically and the probability of detecting an animal close to the survey trackline. However, if conditions are kept constant, i.e. ship, tow speed, array sensitivity, and software settings, a relative index of abundance can be estimated for different areas and used to identify regions of high and low densities.

By applying acoustic surveys as an independent method covering a large area, we tested the temporal and spatial robustness of high and low areas of density identified previously by satellite tracking.

Methods

Survey design

Six acoustic surveys were conducted during 2007, one every second month from January to November. The survey transects were designed to pass through both low- and high-density areas identified by satellite tracking of porpoises in the Skagerrak, Kattegat, and the Danish straits (i.e. Little Belt, Great Belt, and the Sound; Figure 1). The total survey track length was 1220 km for each survey. However, because of poor weather, the fact that surveys were mainly carried out in windspeeds ≤ 10 m s^{-1}, and occasional high levels of background noise, the usable realized effort varied from 937 to 1208 km between surveys (Table 1).

Data collection

All surveys were conducted from the Swedish RV "Skagerak". The ship is 38 m long, 9 m wide, and has a draught of 3.8 m. It was operated under engine power and maintained a speed of ~10 knots throughout the surveys. It is essential that the vessel towing the acoustic hydrophones be relatively quiet so that the porpoise signals can be detected. This vessel was used during the second "Small Cetaceans in the European Atlantic and North Sea" (SCANS-II) survey and proved to be sufficiently quiet to detect porpoise echolocation (SCANS-II, 2008).

The towed array consisted of a 200-m tow cable with two high-frequency hydrophones 25 cm apart, with built-in preamplifiers and a depth gauge at the end. The hydrophones were towed 5–6 m deep. They were calibrated in a test tank during this study and found to have a mean sensitivity of -165 dB re 1 V/μPa at 130 kHz and were omnidirectional in the plane perpendicular to the tow cable within ± 6 dB. By playback of a series of artificial porpoise clicks (13 cycles of 130 kHz sine-wave, raised cosine envelope) in a calibration tank while reducing the amplitude, the detection threshold of the hydrophone array under low-noise conditions was determined to be 120 dB re 1 μPa peak to peak. Assuming a source level of porpoise clicks of 190 dB re 1 μPa peak to peak, this translates into a maximal detection distance of 500 m, assuming spherical spreading and an absorption coefficient of 35 dB km^{-1}.

The hydrophones were connected through a buffer box to a computer with a high-speed data-acquisition system (National Instruments PCI 6250) which sampled signals from each hydrophone at 500 kHz, at a 16-bit resolution. Time and GPS locations obtained from the ship were logged by the computer every 10 s.

Data were logged using an automated detection system developed for SCANS-II (SCANS-II, 2008). The system was based on the method described by Gillespie and Chappel (2002), but modified with digital real-time signal processing rather than analogue filters (SCANS-II, 2008). Harbour-porpoise clicks were

Table 1. Survey period, survey effort, and acoustic detections of harbour porpoises (*P. phocoena*) for each of the six acoustic surveys made in 2007.

Survey	Dates	Survey effort (km)	Number of acoustic detections	Detections per kilometre	Number of satellite locations
January/February	30 January–02 February 2007	1 037	75	0.072	332
March/April	27 March–30 March 2007	1 208	155	0.128	432
May/June	29 May–31 May 2007	937	138	0.147	1 210
July/August	13 August–15 August 2007	1 168	152	0.130	840
September/ October	01 September–04 September 2007	1 061	200	0.189	785
November/ December	19 November–22 November 2007	1 134	176	0.155	692

The number of satellite locations refers to the number of positions received from all tagged porpoises from 1997 to 2007 in the two months listed in the first column (one location porpoise^{-1} d^{-1}).

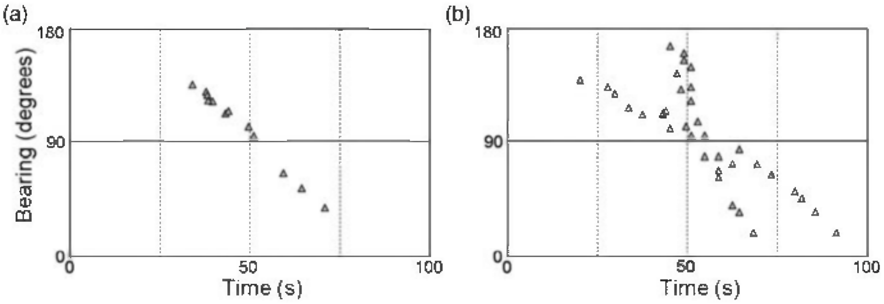

Figure 2. Examples of bearing–time plots showing click detections from harbour porpoises passing the towed hydrophones behind the survey vessel. (a) A single harbour porpoise, defined as a single track, and (b) two harbour porpoises, defined as multiple tracks. A click at a bearing of 180° is directly ahead of the array, a click at 0° astern, and one at 90° abeam to one side or the other.

automatically detected in real time by the software RainbowClick (www.ifaw.org), which identifies clicks based on four criteria: (i) peak frequency, i.e. 50% of the total energy should be between 110 and 150 kHz, (ii) bandwidth, i.e. measured peak width should be <55 kHz, (iii) energy ratio between the porpoise band (100–150 kHz) and a control band (40–90 kHz), i.e. minimum energy difference between the two bands should be 4 dB, and (iv) click length, the length or duration of the waveform containing 50% of the total energy should be <2 μs. The full waveform of each click was stored for subsequent offline analysis. From the time-of-arrival difference between the two hydrophones, a bearing to the vocalizing animal was estimated with a left–right ambiguity along the trackline. For further detail, see SCANS-II (2008).

Acoustic survey data analysis

The porpoise signals automatically detected in real time were evaluated visually to ensure that the frequency spectrum and click intervals matched the criteria for porpoises used during SCANS-II, as mentioned above. Visual inspection of the data involved detailed examination of each click for length, amplitude, waveform, and spectra. If the survey ship passed either a single porpoise or a school of echolocating porpoises, it appeared in the software as a track of porpoise clicks showing a consistent bearing. When a number of porpoise-like clicks was identified, they were categorized as either an "event", a "single track", or "multiple tracks", as defined during SCANS-II (Figure 2). An event was a group of porpoise clicks without any clear bearing, a single track a line of clicks clearly passing the hydrophone, and multiple tracks were similar to single tracks but with several lines of clicks. The tracks were assigned a group size of either 1 (event or single track) or 2 (multiple tracks) porpoise encounters in the following analysis. This is a conservative approach because even large groups of porpoises will count for only two animals if they pass the hydrophones simultaneously. However, harbour porpoises rarely move in large groups and, in 2005, the mean group size in the study area was estimated to be 1.57 (area S; SCANS-II, 2008). Moreover, an underestimation of group size will affect the correlation between the two methods, acoustic surveys vs. satellite telemetry, negatively, so underestimating their agreement. This is because multiple tracks are more likely in areas with many porpoises, leading to an underestimation of density in those areas. Occasional single-porpoise clicks not related to or near any track or event were excluded.

All data were entered into ArcGIS v9.3. The trackline was divided into transects of 1 km, and the average detection rate per kilometre transect (porpoises km^{-1}) was calculated. A transect leg of 1 km was selected to avoid a situation where transect legs crossed several kernel categories, as would often be the case with longer leg lengths. These transect legs may be considered temporally independent, because it is unlikely that the same porpoise will follow the survey ship and hence be detected more than once when the maximum range of detection is 500 m. The number of detections within and between the 1-km transect legs may be spatially autocorrelated, because areas of high harbour-porpoise density are >1 km^2. However, because we compared two monitoring methods, including their ability to detect the spatial structure of the population, the presence of spatial autocorrelation was not problematic for the comparison. The comparison was therefore not performed on a continuous spatial scale, one segment with the next adjacent segment, but rather one segment of the survey data with one grid cell of the kernels derived from satellite telemetry.

Diel variation in the acoustic detections across all six surveys, i.e. variation between periods of night and day, was compared by means of a Kruskal–Wallis test.

Satellite-tracking data analysis

Kernel-density analyses based on the locations from the satellite-tracked porpoises were conducted in ArcMap v9.3 using the fixed kernel-density estimator (Worton, 1989) in Hawth's Analysis Tools v.3.27 (Beyer, 2004). To compare satellite tracking with the individual acoustic surveys, satellite kernel densities were calculated based on the locations from the two months adjoining each survey. For example, kernel-density estimations for the survey that took place at the end of January were based on locations from January/February of the years 1997–2007.

The numbers of satellite-tracked porpoises were not evenly distributed across the year (Table 1), so the kernel density-estimation grids for the six surveys, which each comprised the locations from all tracked porpoises for two adjacent months, are based on different numbers of locations, with January/February being the lowest (332 locations) and May/June the highest (1210 locations; Table 1).

The analyses of kernel density were performed according to the method and settings described by Sveegaard *et al.* (2011), except that the kernel analysis in the present study used one location per transmission day instead of one location every fourth day. Sveegaard *et al.* (2011) chose to use every fourth day to preclude autocorrelation and concluded that the reduction in data did not alter the identified high-density areas significantly. For this study, however, we included one location per transmission day to optimize the number of locations in the two-month kernel analysis. Further, whereas Sveegaard *et al.* (2011) divided kernel-density grids into 10% polygon volume contours (PVCs), it was decided that this spatial scale was too fine for the relatively few acoustic detections in this study. Therefore, the kernel-volume contours were calculated for three PVCs, namely 30%, highest density containing 30% of all locations within the smallest possible area, 60%, and 90%. To avoid spatial autocorrelation, the polygons were subtracted from each other resulting in PVC 30% still containing 30% of all locations on the smallest possible area, PVC 60% now containing 31–60% of the porpoise locations and with the shape of a ring around the 30% contour, and 90% containing 61–90% of the porpoise locations. This procedure did not completely exclude spatial autocorrelation, but it reduced it substantially.

Comparison of methods

Acoustic porpoise detections per kilometre of trackline were calculated within each kernel PVC category, i.e. within 30, 60, and 90% and for the trackline outside the kernel 90% PVC as well, hereafter denoted "PVC_{out}" (~outside PVC range). A non-parametric Kruskal–Wallis test was then used to test whether or not acoustic detections were evenly distributed across kernel categories for each of the six surveys separately. If this was not the case, the Kruskal–Wallis test was followed by pairwise contrasts of kernel categories using a Bonferroni *post hoc* test, which corrects for multiple comparisons, to establish which categories differed significantly from each other in respect of acoustic detections. Although the statistical analyses were carried out on ranked data, mean values and associated standard errors are provided in all graphic presentations to facilitate visual comparisons.

The distribution of acoustic detections across kernel categories was also tested for all six surveys combined. In contrast to the analyses of individual surveys, requirements for the application of parametric statistics were met, and one-way ANOVA was used, followed by Bonferroni *post hoc* tests.

Results

Acoustic surveys

The lengths of the six surveys carried out were in the range 937–1208 km per survey, with the average number of acoustic detections per kilometre ranging from 0.072 in January/February to 0.189 in September/October (Table 1). The detections of harbour porpoises were not evenly distributed along the trackline, but showed higher densities in certain areas on all surveys, especially in southern areas such as Great Belt (Figure 3).

A seasonal change in distribution was found in the northern part of the Sound with a high density of porpoises from May to October and low densities during winter and early spring (i.e. November–March). Great Belt was the only area in which the densities of porpoises were high throughout the year. Elsewhere, e.g. in the central Kattegat, few porpoises were detected at any time (Figure 3).

Estimation of kernel density

Estimation grids for kernel density were produced for each of the six surveys (Figure 3). Only two high-density areas (30%) were consistently identified in all six surveys, the northern tip of Jutland and Great Belt. The northern part of the Sound, northern Samsø Belt, and northern Little Belt had high densities of porpoises from May to August, while the southern Samsø Belt and Kalundborg Fjord supported high densities in November and December. In general, the central Kattegat had a very low density of harbour porpoises throughout the year, except during March/April, when three high-density areas were identified along the Swedish coast.

There was no significant difference between the number of porpoise detections per km transect by night (mean 0.13 detections km^{-1}) and by day (mean 0.11 detections km^{-1}) across the six surveys (Kruskal–Wallis test, $\chi^2_{23} = 17.63$, $p = 0.777$).

Comparison of methods

In all six surveys, the acoustic detections of porpoises were not evenly distributed across kernel categories (Kruskal–Wallis test, January/February $\chi^2 = 11.930$, $p = 0.008$; March/April $\chi^2 = 28.658$, $p < 0.005$; May/June $\chi^2 = 18.945$, $p < 0.005$; July/August $\chi^2 = 9.206$, $p = 0.027$; September/October $\chi^2 = 12.287$, $p = 0.007$; November/December $\chi^2 = 29.558$, $p = 0.005$; Figure 4). *Post hoc* testing showed that in three surveys (March/April, May/June, and November/December), the numbers of porpoise detections per kilometre were significantly higher in the 30% kernel than in PVC_{out} (outside the kernel range) and in four surveys (March/April, May/June, July/August, and September/October), the numbers of detections were significantly higher in the 60% than in PVC_{out} (Figure 4). The seemingly lower level of acoustic detections in the 30% than in the 60% kernel category during the July/August and September/October surveys was not

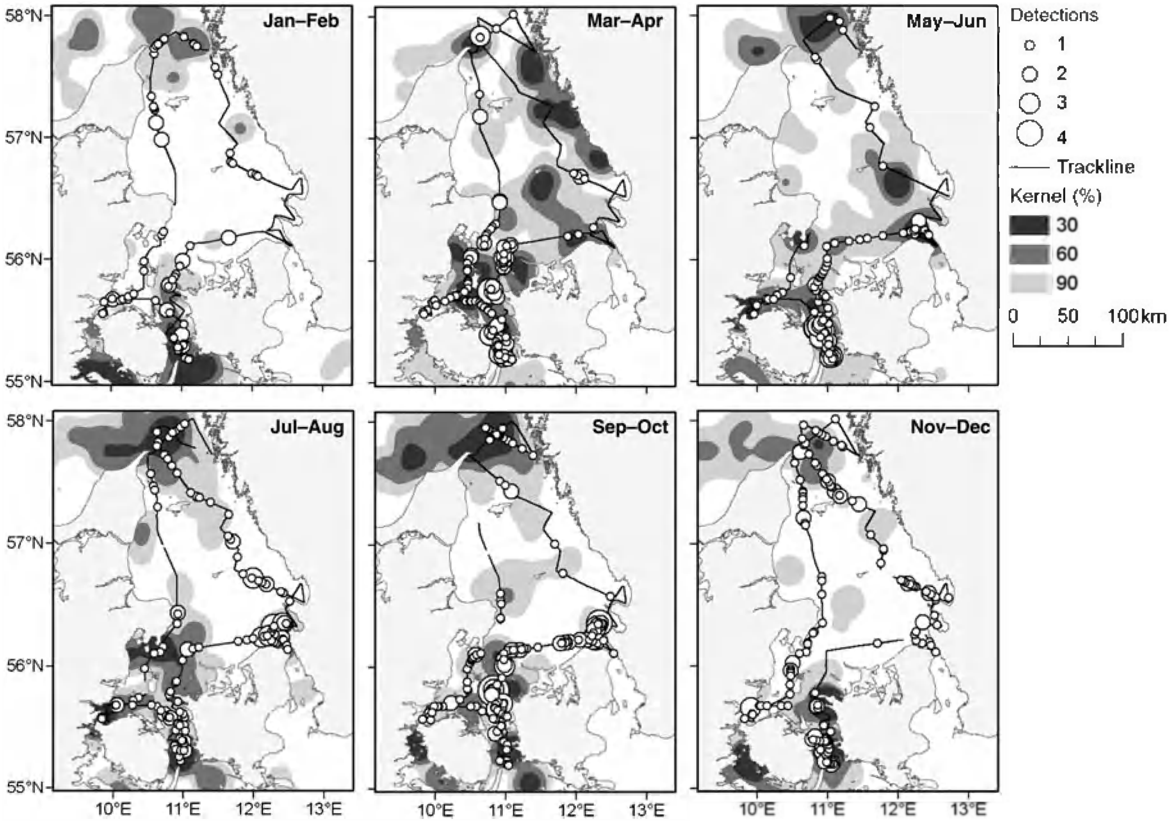

Figure 3. The distribution of detections of harbour porpoises (white dots) during the six acoustic ship surveys in 2007. The size of the dots corresponds to the number of detections per kilometre. The survey trackline is shown in black. The underlying kernel-density, percentage-volume contours are generated from satellite-tracked porpoises during the years 1997–2007: high-density areas (30%) are shown in dark grey and the lower densities (60 and 90%) in increasingly lighter grey. The map projection is universal transverse Mercator, Zone 32N, WGS84.

statistically significant (Figure 4). The pattern was clearer when the averages of all six surveys were compared (Figure 5); there was a significant correlation ($r^2 = 0.466$) between the density of acoustic detections of porpoises and kernel density from satellite-tracking locations ($F_{3,20} = 5.826$, $p = 0.0050$).

Discussion

Together, the six acoustic surveys demonstrated a difference between the number of acoustic detections and the kernel-density estimates from the satellite-telemetry data arranged as four PVC categories. Although not all pairwise comparisons of kernel categories produced significant differences in *post hoc* tests, all individual surveys indicated general correspondence between the two methods, i.e. areas identified as high-density areas from the satellite-telemetry data also yielded significantly more acoustic detections in the towed-array survey. Considering the different nature of the data obtained from short-term acoustic detection and long-term satellite tracking in addition to potential year-on-year variation in porpoise distribution, the level of accord between the two methods strongly supports the identified high-density areas as being stable over at least 10 years, the period from the beginning of the telemetry studies to the completion of the acoustic surveys.

Seasonal movement of harbour porpoises has been recognized before this study in other geographic areas and has been described as a gradual net movement rather than coordinated migration (Read and Westgate, 1997; Verfuss *et al.*, 2007). Such a pattern was confirmed by Sveegaard *et al.* (2011), who found seasonal changes in the distribution of satellite-tracked porpoises: porpoises tagged in inner Danish waters moved south in winter, whereas porpoises tagged in the Skagerrak moved west towards the North Sea. It was proposed that the major movements took place during August/September and March/April, although summer and winter habitats overlapped to some extent. The present study found seasonal changes in the distribution of high-density areas of porpoises in the northern Sound corresponding to the change in distribution found by Sveegaard *et al.* (2011).

The use of acoustic surveys as a means of examining the distribution of porpoises and other cetaceans has been applied increasingly in recent years (Gillespie *et al.*, 2005; Boisseau *et al.*, 2007; SCANS-II, 2008; Li *et al.*, 2009). As this survey method is unaffected relative to visual surveys by weather, observer variability, and available manpower, it can constitute a reliable, cost-effective alternative to methods such as visual surveys from boats or aircraft. Nevertheless, several critical issues have yet to be clarified. Most importantly, it remains to be shown that reliable absolute-density estimates can be derived from acoustic surveys. If porpoises, for example, are either attracted or deterred, such behaviour will affect density estimates. Palka and Hammond (2001) showed that harbour porpoises avoided survey vessels at a range of up to 1 km from the ship. This may be a significant bias during visual surveys if not corrected for. However, provided vessel-avoidance

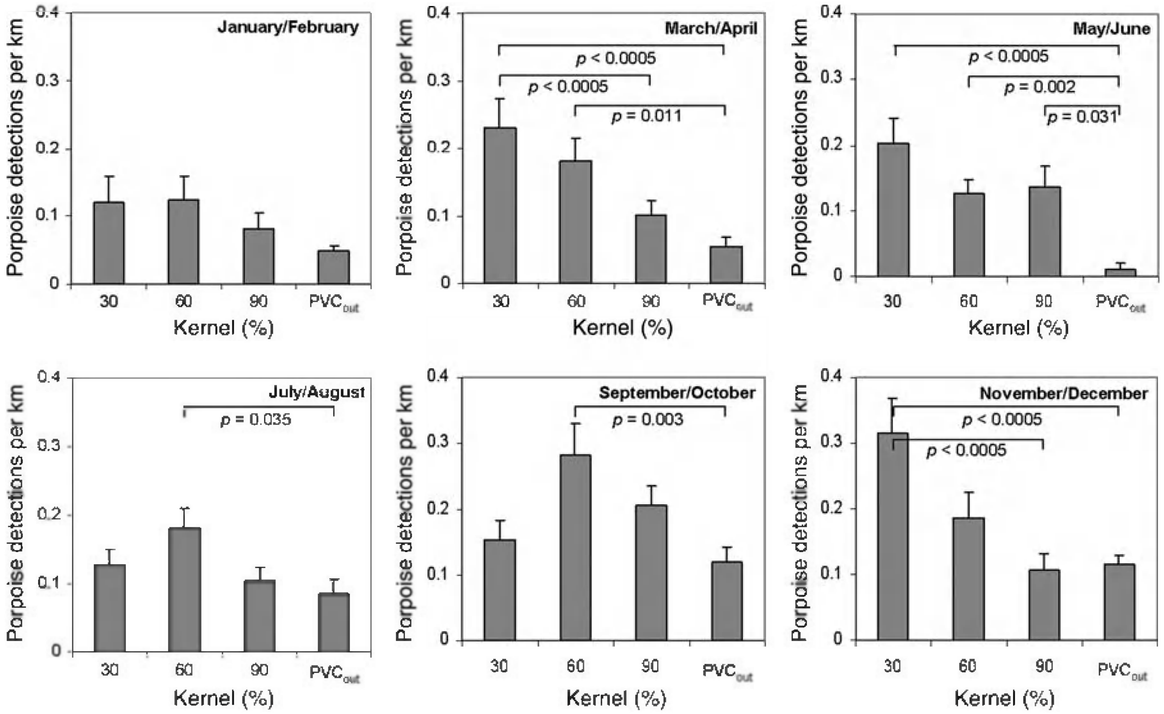

Figure 4. The relationship between densities of harbour porpoises (*P. phocoena*) found by acoustic detections during six ship surveys in 2007 (mean porpoise detections km^{-1} and s.e.) and by satellite telemetry during the years 1997–2007 (kernel %). PVC_{out} denotes the number of acoustic detections outside the range of the kernel PVCs. Each graph represents one survey (Table 1) as well as all positions from the satellite-tagged porpoises over each 2-month period. In terms of *post hoc* tests, the horizontal lines above the bars show significant differences between kernel categories.

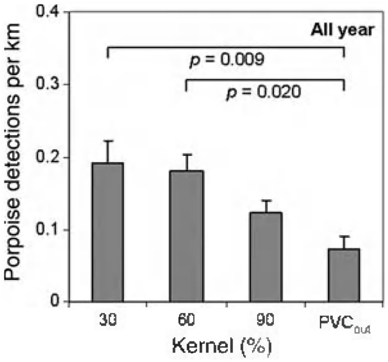

Figure 5. The relationship between densities of harbour porpoises (*P. phocoena*) found from the mean of all acoustic ship surveys during 2007 (porpoise detections km^{-1}, mean of six surveys and s.e.) and satellite telemetry during the years 1997–2007 (kernel %). PVC_{out} denotes the number of acoustic detections outside the range of the kernel PVCs. Acoustic detections were not evenly distributed across kernel categories (one-way ANOVA, $F_3 = 5.826$, $p = 0.005$). In terms of *post hoc* tests, the horizontal lines above the bars show significant differences between kernel categories.

behaviour is similar between individual porpoises or constant within a geographic area being surveyed, and when the same ship is used throughout, the relative density index will not be influenced.

Another potential bias relates to whether porpoise echolocation activity has a constant diel and seasonal pattern. Teilmann *et al.* (2007) found that harbour porpoises tagged with time-depth recorders displayed higher dive rates during October and November than during summer and suggested that this may be caused by increased foraging during autumn, compensating for greater energy requirements as the water temperature decreases. A generally greater foraging activity is probably linked to more echolocation activity, and because the hydrophones of a towed array are positioned only a few metres below the water surface, a higher frequency of deep dives by feeding porpoises is likely to reduce the rates of acoustic detection. How these issues influence the detection rates during acoustic surveys is unknown, but the present study found a marked seasonal difference in detection rate, with lower rates in January/February and higher ones in September/October.

Diel variation in echolocation activity may also influence detectability. Porpoises may be relatively silent during periods of rest and increase their echolocation activity during foraging. Dive rates of harbour porpoises vary diurnally, with dive rates highest during daylight (Teilmann *et al.*, 2007) and night dives being fewer but deeper (Westgate *et al.*, 1995). The differences are believed to be caused by diel changes in prey distribution. However, in the present study, we did not find a significant difference in detections between day and night. This may be the result of porpoises responding to the ship by echolocating towards it or investigating the hydrophone array regardless of the time of day.

Acoustic surveys present many possibilities for future monitoring. The aim of this study was to evaluate the distribution and densities of porpoises found by satellite tracking. Consequently, the survey trackline was constructed to cover areas of both high and low densities of the porpoises. However, acoustic surveys may, with appropriate application of distance-sampling methods, be used to estimate porpoise abundance. In contrast to the present study, the layout of tracklines needs then to follow a random rather than a fixed design (Thomas *et al.*, 2010).

The results presented here have provided insight relating to the conservation of harbour porpoises and most importantly show that high-density areas can be identified that appear to be stable over time. This provides support to the approach of protecting porpoise key habitats by the designation of MPAs, such as is required by, for example, the EU Habitat Directive (European Commission, 1992), because it is based on the idea of spatial and temporal stability. If the high-density areas of porpoises change from year to year, the designated MPAs will not benefit them. The high-density areas identified in this study are, however, relatively stable between years, with some seasonal variation. When implementing a management plan for such areas, knowledge of the seasonal changes in porpoise density may help target conservation effort towards the appropriate seasons when, for example, the porpoises are present in relation to fisheries.

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