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ORIGINAL ARTICLE

The harbour porpoise (*Phocoena phocoena*) in the central German Bight: phenology, abundance and distribution in 2002–2004

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Abstract The harbour porpoise (*Phocoena phocoena*) is widely distributed in the North Sea. During both the SCANS 1994 and 2005 surveys, porpoises were commonly encountered in offshore waters, for example in the central German Bight. However, information on year-round abundance and distribution of harbour porpoises in that area on a monthly basis was lacking. Between 2002 and 2004, we undertook 26 aerial line-transect surveys in a 2,600 km^2 area in the central German Bight, 100 km north of the Island of Borkum (Eastern Frisia). Data were analysed with DISTANCE software. A total of 406 porpoises were sighted. Sighting rates (=sightings/km transect) peaked in July 2002, February, May and September 2003, and in January and April 2004. Absolute densities ($g(0)$ corrected) ranged between 0.14 and 1.54 animals/km^2 (peak in April 2004). Proportion of calves varied between 3.4 and 27.3%. Our results show a highly irregular appearance of harbour porpoises in the study area with no apparent seasonal trends in occurrence but peaks in single months. We propose that the area is used as a transit route with harbour porpoise moving in from regions of high density in summer (Northern Frisia) and early spring (Eastern Frisia).

Keywords Harbour porpoise · Central German Bight

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Introduction

Effective conservation requires information on seasonal distribution and inter-annual trends of occurrence of the species in question. In the past, such information was missing for most cetacean species. In recent years, with the improvement of field techniques, and due to a higher effort of at-sea surveys, data have been collected that aid in the conservation of various cetacean populations in many regions (overview in Perrin et al. 2002). One region where cetacean conservation has recently received particular attention has been the German Bight. The German Bight is the southeastern part of the North Sea that abuts corners the Netherlands and Germany to the south as well as Denmark and Germany to the east. To the north it is limited by 56° N and to the west it is limited by 4° E in the vicinity of the Dogger Bank (Fig. 1). It is used very frequently by the most common cetacean species in northwestern European waters, the harbour porpoise (*Phocoena phocoena*). The German Bight is also a prospected area for large-scale offshore wind farm development with presumably negative effects on harbour porpoises (reviews by Madsen et al. 2006; Thomsen et al. 2006a). These and other anthropogenic influences have called for extensive studies on the occurrence and distribution of harbour porpoises in that region.

Results obtained so far indicate a relatively high variability in porpoise occurrence in the German Bight. In the summer of 1994, Hammond et al. (2002) found high densities in the eastern part, along the coast of Northern Frisia and Denmark, but decreasing densities in the centre of the Bight and in the southern areas off Eastern Frisia (coast of Netherlands and Lower-Saxony, Germany). Later investigations, using data from aerial surveys (1995/1996; 2002–2005), incidental sightings and strandings, confirmed the high summer-densities of porpoises off Northern Frisia

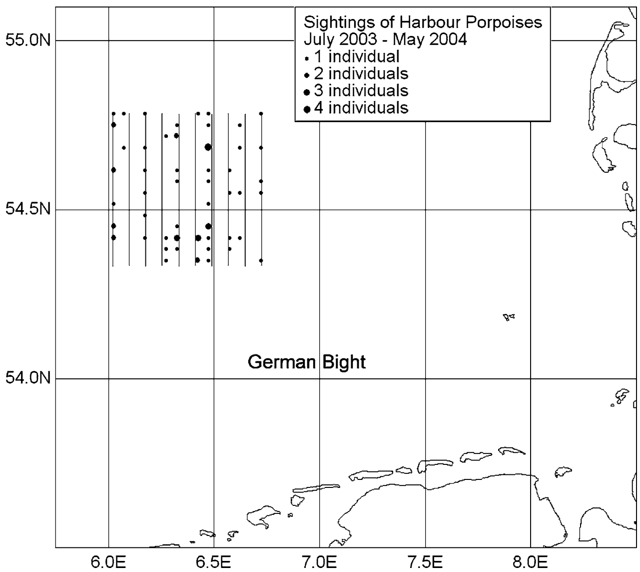

Fig. 1 The transect layout and the distribution of sightings of harbour porpoises during the porpoise-only surveys between July 2003 and May 2004 ($n = 69$)

(Sonntag et al. 1999; Scheidat et al. 2004a, b, 2006; Siebert et al. 2006). However, densities in the southern part of the German Bight and surrounding waters were higher than expected based on previous findings, especially between February and May (Camphuysen 1994, 2004; Witte et al. 1998; Haelters et al. 2004; Scheidat et al. 2006; Thomsen et al. 2006b; for a preview of SCANS II results see Hammond 2006). These studies indicate two peaks in harbour porpoise occurrence in different parts of the German Bight at different times of the year: one in late winter and early spring off Eastern Frisia, the other during spring and summer off Northern Frisia. If porpoises travel from one region to the other, it should be expected that the central areas of the German Bight would be used as a transit route with high occurrence during probable times of migrations (spring, fall). Therefore, studies on the occurrence of harbour porpoises in the central German Bight are of special interest. Hammond et al. (2002) estimated porpoise densities in an area comprising the central German Bight (SCANS-survey-block G) to be 0.34 porpoises per km^2. In 2005, densities in the corresponding block (U) were estimated to be 0.23 porpoises per km^2. However, the survey blocks were quite large and effort restricted to four weeks in the summer of 1994 and 2005 (Hammond et al. 2002; Hammond 2006). For May–August 2002 and 2003, Scheidat et al. (2004b) estimated a density of 0.59 and 0.72/km^2 respectively for the offshore areas of the German Exclusive Economic Zone. Their results also indicate seasonality with higher numbers of porpoises and a more clustered occurrence in spring and summer compared to fall and winter. However, due to the large-scale of the survey, the effort was restricted in most cases to one survey per season and year in each survey block. No study has looked at harbour porpoises in the central German Bight on at least a monthly basis. Therefore, knowledge on the movements of porpoises in that area is lacking.

In this paper we present findings from a systematic study in a 2,600 km^2 offshore area in the central German Bight, 100 km north of the coast of Eastern Frisia. We collected data using line transect aerial surveys between 2002 and 2004. We will present data on relative and absolute densities of harbour porpoises. Based on our results, the significance of the central German Bight for harbour porpoises and the status of the species therein will be discussed.

Methods

Data collection

We collected data between July 2002 and July 2004 in a study area located in the central German Bight, about 100 km north of the island of Borkum, Eastern Frisia (54°20.000′–54°47.100′ N; 006°01.200′–006°43.500′ E; Fig. 1). The water depth varied from 30 m to >40 m. We used line transect methodology following the distance sampling approach after Buckland et al. (2001) (see also Thomsen et al. 2004 for a detailed methodology in German, and Thomsen et al. 2006b for further details). From July 2002 until June 2003, the survey area comprised 1,600 km^2 with 8 transect lines of 57.6 km length each, a spacing between the lines of 3.7 km, and a total transect length of 460 km. From the end of July 2003 until July 2004 app. 2,600 km^2 were surveyed with 10 transects of 50 km each, a line spacing of 5 km, and a total transect length of 500 km (Fig. 1). As survey airplane, we used a high-winged, twin-engine BN2-Islander, equipped with bubble windows on the rear seats. We only collected data in good or moderate survey conditions (seastate < 3 bft, visibility > 5 km). Data was collected during specialized porpoise trips at an altitude of 500 and 600 ft (152/183 m) as well as during combined porpoise/seabird surveys at an altitude of 250 ft (76 m). We started with three porpoise-only flights in July 2002, August 2002 and in February 2003; from May 2003 until July 2004, both methods were used for at least one survey per month (see Table 2).

Three observers were used during the surveys: two principal observers were placed at the rear bubble windows (search angle = 0°–<60°). One control observer was placed at a flat window behind the pilot (search angle = 20°–<60°). The principal observers switched places during a break at half time, the control observer switched places on each transect, depending on sighting conditions. Observers were acoustically isolated from each other through earplugs and headphones. From the onset of the survey, the observers searched continuously for porpoises. At each sighting, the exact time was noted (UTC, synchronised with an on-board GPS, model LX-20-2000 Flight Recorder, Filser Electronics) and recorded aurally on dictaphone. The sighting angle was measured with a clinometer (Suunto PM 5/360 PC) and also noted. Additionally, data on group size, travel direction and the behaviour of the animals were recorded. The flight-track was logged and stored continuously in 3 s intervals on a Notebook, which was connected to the on-board GPS and displayed using the Fugawi 3.0 software-program. Thus, it was possible to correct deviations from the track line immediately.

Data analysis

Calculation of sighting rates

Based on the field notes of the observers, the transects were assigned as *valid one sided*, *valid both sided* or *invalid*. Only valid transects were analysed. Since control and principal observers had different search angles (see above), only the sightings of the latter ones were used in the quantitative analysis. Porpoise-only flights (altitude: 152 m/183 m) and combined porpoise/seabird ones (76 m) were analysed separately. We first calculated the sighting rate, which was defined as the number of porpoises per km for each transect of each flight. We then calculated the mean sighting rate for each flight. Sighting rates across flights were compared with a Kruskal–Wallis *H*-test. If means differed, we performed a multiple all-pairwise comparison following Dunn's method (Zar 1984).

Calculation of absolute densities

Absolute densities were calculated with the DISTANCE 4.1, release 2, software-program (Thomas et al. 2003). Distances x to the observation were calculated as $x = v \times \tan(90° - \varphi)$ with v being the altitude in m and φ the angle of declination measured with the clinometer (Buckland et al. 2001). We then calculated the effective strip half-width (esw) cumulatively for all porpoise-only and combined seabird/porpoise flights separately. Here, we used a hazard-rate key function with a simple polynominal series expansion. The esw for the porpoise-only flights was 163 m (Fig. 2) and 112 m for the combined porpoise/seabird surveys. Densities were calculated for each flight as $D = n \times G/2\mu \times L$ (n = number of sightings, G = the average group size, L = total transect-length, μ = effective strip half-width; Buckland et al. 2001; details in Thomsen et al. 2006b).

Distribution of sightings

The observer noted the sighting time (UTC) using a digital stopwatch that was synchronized with the on-board GPS.

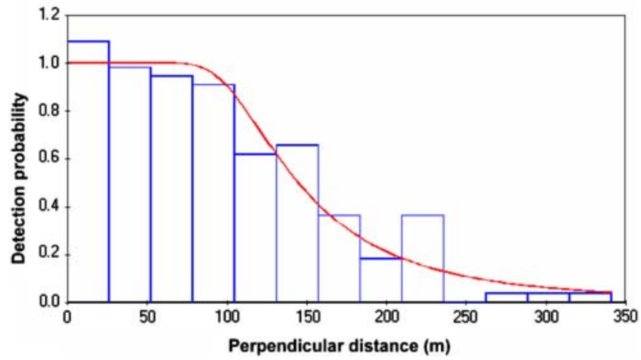

Fig. 2 Detection probability function for harbour porpoises during the porpoise-only aerial surveys (altitude = 183 m; model = hazard rate key function with simple polynominal series expansion; n = 171 sightings)

The sighting positions were determined from the GPS-track and were plotted into maps using the software-program ArcGIS (8.0). For the second year of observations (July 2003–July 2004), the study area was divided into 10 km circular zones around the centre of the study area, with almost even coverage across the 0–10 km, the >10 km–<20 km and the >20–30 km-zone. The number of sightings in each-zone was compared using a *H*-test (Kruskal–Wallis) or *F*-test in case of normal distribution.

g(0) correction

In cetacean surveys, the probability to detect an object on the track line is <1.0, because observers sometimes miss animals that are present (=perception bias) and diving individuals are unavailable for detection (=detection bias). The corrected density therefore is $D = Dx \times 1/g(0)$ (after Borchers 2003). We calculated $g(0)$ by using a mark-recapture method combined with published diving data for harbour porpoises after a method first used by Grünkorn et al. (2005). We estimated the perception bias as $p(m) = n12 \ / \ n1$, where $p(m)$ is the probability of detection by the principal observer, $n12$ the number of duplicates between main- and control observer (search angle = 20–45°), and $n1$ the number of individuals seen by the control observer. For the availability bias, we first multiplied the number of sightings on each flight with the individual surface time, i.e. the percentage of time porpoises are present in the 0–1 m water column (Teilmann 2000) to get an estimate on the average surface time. The average surface time for the porpoise only flights was 0.43 with the sighting probability being 0.49 (Table 1). This resulted in a $g(0)$ of $0.43 \times 0.49 = 0.21$. For the combined seabird/porpoise flights, surface time was 0.48 and the sighting probability was 0.43, resulting in a $g(0)$ of 0.21.

Table 1 Estimation of $g(0)$ for the porpoise-only flights (altitude = 152/183 m)

Date	Number of sightings[a]	Individual surface time	Total surface time	N1	N1&2
07/28/02	24	0.41	9.84	8	2
02/14/03	32	0.44[b]	14.08	7	5
05/26/03	23	0.45	10.35	17	9
06/22/03	13	0.39	5.07	2	1
07/28/03	10	0.41	4.10	7	2
09/13/03	18	0.39	7.02	9	5
03/06/04	15	0.55	8.25	3	2
Sum	135		58.71	53	26

N1&2 = duplicate sightings of control and principal observer between 20° and 45°, N1 = sightings of control observer only

Availability bias/average surface time = 0.43

Perception bias/sighting probability = 0.49

[a] Sightings of principal observer in valid transect sections

[b] Average after Teilmann (2000)

Results

A total of 346 sightings with 406 individuals (mean group size = 1.17) were obtained (Table 2). Porpoises were most often encountered alone (86.4%). Pairs and groups of three or four animals were rare (10.7, 2.3 and 0.6%, respectively). A total of 17 calves were observed, with average proportion of calves between 3.4% in May 2003 and 27.3% in July 2004 (July 2002: 8.6%, June 2003: 16.6%, September 2003: 10.71%, June 2004: 7.1%).

Porpoises occurred highly irregular in the study area with no apparent seasonal trends, but peaks in single months (e.g. February, April, July, January) (Table 2, Fig. 3). During the porpoise-only flights, most sightings per km were obtained in February 2003, followed by July 2002, May 2003, January 2004 and September 2003. The remaining 6 months showed rather low sighting rates (Fig. 3). However, the differences in sighting rates across months were not significant (H-test, $df = 10$, $H = 17.70$, $P = 0.06$). During the combined porpoise/seabird flights, most porpoises were seen in April 2004, followed by May 2003, June 2004 and February 2004. There were significant differences in sighting-rates across months with those in April 2004 being significantly higher than those in December 2003 (H-test, $df = 11$, $H = 28.83$, $P = 0.002$; Dunn's method $P < 0.05$).

Absolute estimates of abundance ranged between 0.14 and 1.54 porpoises per km^2 with the temporal occurrence as described above and the maximum being in April 2004 (Table 3). Only four surveys resulted in densities >1.0/km^2 (February and May 2003, April 2004). 11 out of 26 surveys resulted in densities >0.5 and <1.0/km^2. The estimates for the remaining 11 surveys were < 0.5 / km^2. The mean absolute density during the whole study period was 0.63 porpoises/km^2 (0.06 ± SE; $n = 26$) with the absolute densities being normally distributed (K–S-test, $P = 0.35$).

Table 2 Harbour porpoise sightings in 2002–2004

Date	Altitude (m)	Km on effort	S	I	Calves
07/28/02	152	467	24	35	3
08/16/02	152	288	4	5	1
02/14/03	183	443	32	36	
05/16/03	76	396	18	18	
05/26/03	183	402	23	29	1
06/14/03	183	393	6	6	
06/16/03	76	427	6	9	4
06/22/03	183	337	13	15	1
07/28/03	183	400	10	16	
07/31/03	76	425	9	10	
09/04/03	76	377	6	6	1
09/13/03	183	427	18	22	2
09/28/03	76	502	12	13	
10/16/03	76	400	4	5	
12/04/03	76	472	3	3	
01/21/04	76	503	11	12	
01/21/04	183	321	14	19	
02/28/04	76	494	18	18	
03/06/04	183	478	15	15	
03/25/04	76	428	14	14	
04/13/04	183	247	5	5	
04/20/04	76	430	21	23	
04/26/04	76	504	33	39	
05/29/04	183	276	7	8	
06/22/04	76	360	12	14	1
07/16/04	76	504	8	11	3
Sum		10,701	346	406	17

Km on effort = valid effort on both sides, S number of sightings, I number of individuals

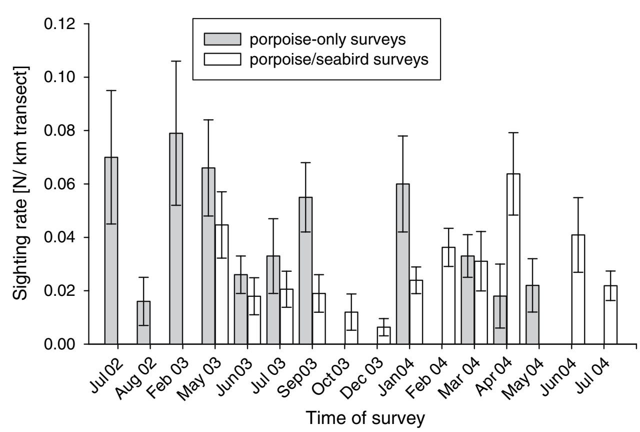

Fig. 3 Relative frequency of occurrence (n/transect/km) of harbour porpoises during the study period (mean ± SE)

Table 3 Densities of harbour porpoises in the study area in 2002–2004

Date	Altitude (m)	$g(0)$	esw (m)	Density (Ind./km^2)	Density CV	Area size (km^2)	N	±SE
07/28/02	152	0.21	163	0.88	0.32	1,630	1,439	459
08/16/02	152	0.21	163	0.23	0.47	1,630	388	183
02/14/03	183	0.21	163	1.23	0.34	1,630	2,020	688
05/16/03	76	0.21	112	1.06	0.29	2,670	2,858	822
05/26/03	183	0.21	163	0.98	0.24	1,630	1,600	391
06/14/03	183	0.21	163	0.26	0.49	1,630	427	209
06/16/03	76	0.21	112	0.33	0.32	2,670	885	280
06/22/03	183	0.21	163	0.66	0.30	1,630	1,079	323
07/28/03	183	0.21	163	0.42	0.29	2,670	1,148	329
07/31/03	76	0.21	112	0.49	0.32	2,670	1,332	421
09/04/03	76	0.21	112	0.37	0.46	2,670	1,003	465
09/13/03	183	0.21	163	0.72	0.21	2,670	1,936	412
09/28/03	76	0.21	112	0.56	0.46	2,670	1,504	697
10/16/03	76	0.21	112	0.23	0.53	2,670	629	335
12/04/03	76	0.21	112	0.14	0.51	2,670	400	204
01/21/04	76	0.21	112	0.51	0.22	2,670	1,376	298
01/21/04	183	0.21	163	0.74	0.28	2,670	2,002	571
02/28/04	76	0.21	112	0.85	0.20	2,670	2,292	460
03/06/04	183	0.21	163	0.53	0.27	2,670	1,444	381
03/25/04	76	0.21	112	0.76	0.34	2,670	2,060	700
04/13/04	183	0.21	163	0.34	0.63	2,670	929	585
04/20/04	76	0.21	112	1.14	0.21	2,670	3,075	644
04/26/04	76	0.21	112	1.54	0.31	2,670	4,126	1,267
05/29/04	183	0.21	163	0.43	0.34	2,670	1,164	402
06/22/04	76	0.21	112	0.78	0.34	2,670	2,095	715
07/16/04	76	0.21	112	0.37	0.25	2,670	999	254

$g(0)$ Probability of detection at distance = 0 from the transect-line, *esw* effective strip half-width, *CV* coefficient of variation, *N* estimated number of animals present in the study area, ±*SE* standard error

In the second year of observations (July 2003–July 2004), porpoises were evenly distributed within the study area (Fig. 1). The distribution of sightings in the 10-km zones around the centre was not significantly different across zones (porpoise-only: *H*-test, $H = 1.587$, $df = 2$, $P = 0.45$, porpoise/seabird surveys: *F*-test, $F = 0.711$, $df = 3$, $P = 0.557$).

Discussion

Our study demonstrates a year-round but highly irregular appearance of harbour porpoises in the central German Bight during the period of 2002–2004. In contrast to other areas, the occurrence of porpoises was not correlated with seasons (e.g. Thomsen et al. 2006b; Scheidat et al. 2006; Siebert et al. 2006), but characterized by rather erratic peaks in density in certain months and in all seasons.

We should remember at this point that our calculation of $g(0)$ might be viewed as only a rough estimate and that other methods, for example the circle-back procedure (Hiby and Lovell 1998), might be more accurate, given that sample sizes are big enough. However, the value of 0.21 is in line with values from other investigations and we therefore assume it to be quite realistic (Hiby and Lowell 1998; Hammond et al. 2002; for a detailed discussion on this topic see Thomsen et al. 2005, 2006b). Another point that might be raised is that density estimates in comparably small survey areas, like the one used here, are particularly prone to small-scale and rather random shifts in distribution, especially for species moving around as much as harbour porpoises (Teilmann 2000). It is important in such cases to avoid misinterpretation of presumably distributional shifts as temporal changes (Buckland et al. 2001). We are aware of this uncertainty in interpreting our results; however, this critique might also apply for large-scale surveys with comparably low coverage within survey blocks, as in this case, clusters of animals within strata might be missed. We are therefore confident that we picked a rather efficient trade-off between area size and coverage. Our results on the seasonality of harbour porpoises off Eastern Frisia, obtained in an area of comparable size as the one used here (see

Thomsen et al. 2006b), agree well with the ones from other studies in that region (Camphuysen 2004; Haelters et al. 2004).

We found the overall absolute density to be 0.63 porpoises per km^2, a value that is very similar to the ones obtained by larger-scale surveys covering our study area and adjacent waters (Scheidat et al. 2004b). Harbour porpoise densities in our study area might have remained at a relatively constant level since 1994, as the results of the SCANS I and II surveys in blocks comprising the central German Bight are similar (Hammond et al. 2002; Hammond 2006). The findings that the differences across sighting rate values for the porpoise-only flights were non-significant should not be too easily interpreted as being due to random-sampling variability. The number of transects is crucial in line-transect sampling and the value we had to choose to guarantee a safe return after survey with still ample coverage of the region (8/10) is at the lower limit of what is needed to produce quantitative results (Buckland et al. 2001). We therefore assume that the peaks we obtained in single months are based on true biological phenomena that would prove to be statistically significant with the addition of more transects (see Thomsen et al. 2006b). The results of the porpoise/seabird surveys, with the sighting rate in April 2004 being significantly higher than during other months, support this conclusion.

The differences between surveys might be explained by two not mutually exclusive mechanisms. From previous studies, it is apparent that the central German Bight is located between two regions with high densities of harbour porpoises during different times of the year. One is located off Northern Frisia with high densities between May and August (Hammond et al. 2002; Scheidat et al. 2004a, b; Siebert et al. 2006). The other is located off Eastern Frisia, with high occurrence of porpoises from February to the beginning of May (Camphuysen 2004; Haelters et al. 2004; Piper et al. 2004; Thomsen et al. 2006b). It is possible that porpoises from these high-density areas move into and out of the central German Bight on a rather sporadic basis. That would explain the relatively high densities we found in February, April, May and July. It would also explain the comparably high number of calves we found in certain surveys, as Northern Frisia and adjacent waters might function as a calving ground for porpoises in the North Sea (Sonntag et al. 1999; Hammond et al. 2002; Siebert et al. 2006). Another or an additional way to interpret the results would be that porpoises transit the central German Bight during migratory movements from Northern Frisia into offshore areas in fall and winter. That would explain the higher densities we found in September and January. The high densities we found in April and May would be explained by another migratory movement that might take place during late spring, when porpoises move out of Eastern Frisia. These hypotheses could only be tested using marked animals or with satellite telemetry.

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