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Seasonal distribution of harbour porpoises and possible interference of offshore wind farms in the German North Sea

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ABSTRACT: The seasonal distribution of harbour porpoises in the German North Sea was investigated, hot spot areas were identified and the proportion of porpoises potentially affected by the imminent construction of offshore wind farms was estimated. Data were collected during dedicated aerial surveys conducted year-round between 2002 and 2006 following line transect methodology. Survey effort amounted to 44 739 km during which a total of 5121 harbour porpoises was detected, including 258 calves. Our data suggest that porpoises move to distinct areas on a seasonal basis as their biological requirements change. They move into German waters in early spring, reach high numbers in early summer and move out of the area in autumn. The abundance estimates for the German exclusive economic zone and 12 n mile zone were highest in spring (55 048 animals; 95% CI: 32 395 to 101 671) and summer (49 687 animals; 95% CI: 29 009 to 96 385) and lowest in autumn with 15 394 animals (95% CI: 8906 to 29 470). Important aggregation zones were detected in offshore waters: in spring, 2 hot spots, Borkum Reef Ground and Sylt Outer Reef (SOR), were identified as key foraging areas. In summer, only the large hot spot SOR persisted, causing a strong north–south density gradient. In autumn, porpoises were more evenly distributed. Most mother-calf pairs were observed during spring and summer in the SOR, underlining its importance as a foraging area when reproductive costs are high. Spatial overlap exists between important areas for porpoises and areas where offshore wind farms are currently licensed or planned. The proportion of the national stock possibly exposed to the construction noise of 18 licensed wind farms was estimated applying different scenarios. Within a 20 km zone of responsiveness — as worst case scenario — 39% of the harbour porpoise stock in the German EEZ could be affected during construction.

KEY WORDS: *Phocoena phocoena* · Harbour porpoise · North Sea · Aerial survey · Distribution · Foraging · Reproduction area · Offshore wind farm · Generalised additive model

INTRODUCTION

The scheduled construction of offshore wind farms in the North Sea could affect marine mammals (Madsen et al. 2006). Major disturbances may arise from construction activities such as pile-driving and drilling, increased vessel traffic, pollutant emissions and stirred-up bottom sediments (Carstensen et al. 2006). Thorough knowledge of the distribution, density and seasonal movements of species present in the area is one key to assessing and mitigating potential effects of these human activities.

Beyond doubt, the global response to climate change must involve a move to carbon-free sources of electricity (Schiermeier et al. 2008). However, if current plans are realised, the construction of wind farms could be the greatest human impact in the North Sea next to fisheries (Hüppop et al. 2006). The offshore wind industry in Germany has the most ambitious plans in the world: by June 2008, 18 wind farms were approved and 47 more farms are in the approval process (Fig. 1; BSH 2008). The construction sites show spatial overlap with the designated 'sites of community importance', according to the Habitats Directive of the European

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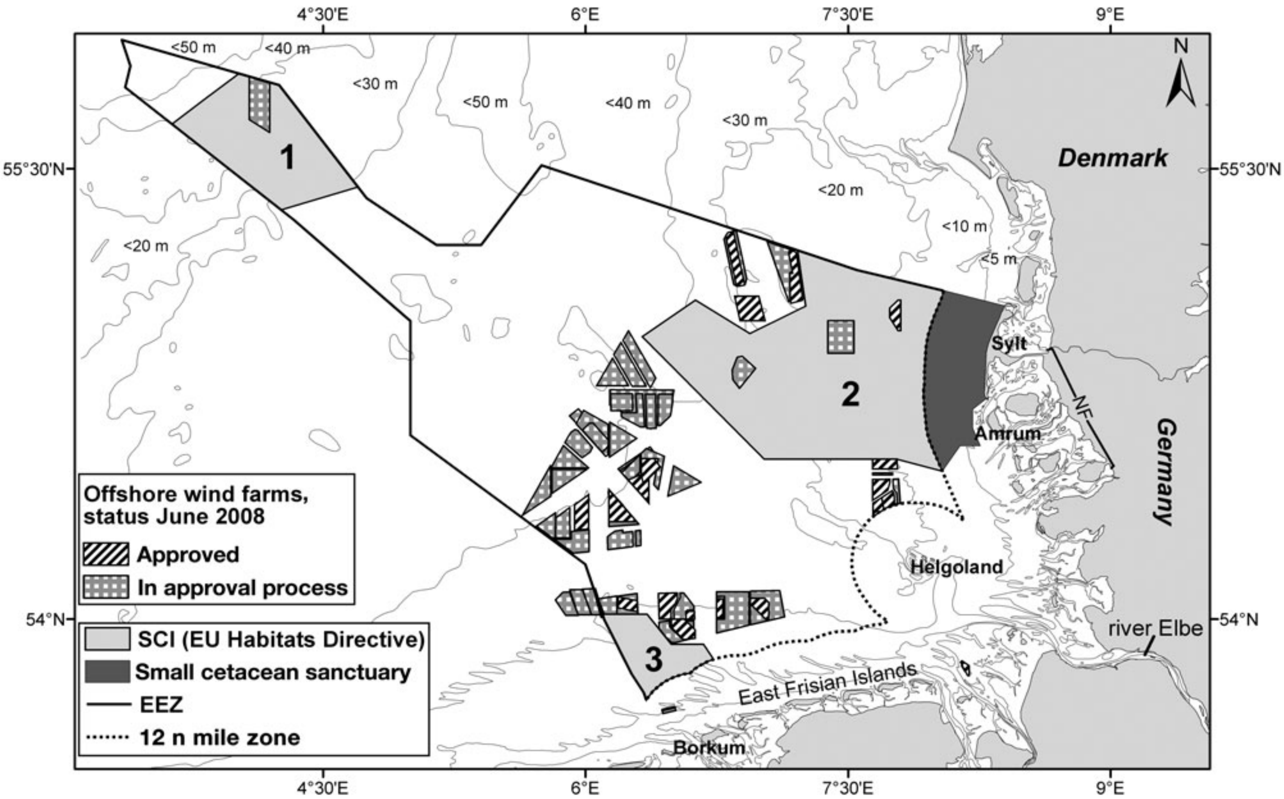

Fig. 1. Offshore wind farm sites (BSH 2008) and sites of marine protected areas in the German North Sea. Sites of community importance (SCI); 1: Doggerbank; 2: Sylt Outer Reef, and 3: Borkum Reef Ground. NF: North Frisian Islands, EEZ: exclusive economic zone

Union (Fig. 1), and it is therefore imperative to obtain baseline data on marine mammal distributions in order to assess the risk of, and mitigate for, the impact of construction.

The southeastern North Sea is an area with a wide range of human activities (Ducrotoy et al. 2000, OSPAR Commission 2000, Halpern et al. 2008). The harbour porpoise *Phocoena phocoena* (Linnaeus, 1758) is the most common cetacean in the North Sea (Hammond et al. 2002) and the only cetacean species found regularly in German waters (Scheidat et al. 2004, Siebert et al. 2006). There is evidence that harbour porpoise abundance in the southeastern North Sea has declined since the 1940s (Smeenk 1987, Reijnders 1992, Camphuysen & Leopold 1993). Various pressures have been identified, such as bycatch (Kock & Benke 1996, Vinther & Larsen 2004), prey depletion (Smeenk 1987) or habitat degradation due to chemical pollution (Siebert et al. 1999, Wünschmann et al. 2001, Beineke et al. 2005, Das et al. 2006). Recently, an increase in sightings as well as strandings has been observed in the southern North Sea (Camphuysen 2004, Kiszka et al. 2004, SCANS II 2008). In 2005, the SCANS II survey in the North Sea and European Atlantic resulted in an estimate of 385 617 individuals (95% CI: 261 266 to 569 153) within a survey area of 1.4 mio. km^2 (SCANS II 2008).

The harbour porpoise depends on sound for orientation and foraging (Teilmann et al. 2002, Verfuss et al. 2005) and is very sensitive to different types of acoustic signals. Underwater noise is produced during construction, operation and dismantling of offshore wind farms. Especially during piling, hydraulic hammers create noise with considerable sound power levels (Nedwell & Howell 2004). The same holds for dismantling when foundations are blasted off the sea floor after 20 yr of operation (Nedwell & Howell 2004). The potential effects on harbour porpoises are hearing loss (either temporary or permanent), masking of natural noise, increased stress levels or abandonment of important habitat (Tougaard et al. 2003, Carstensen et al. 2006, Nowacek et al. 2007, Weilgart 2007, Lucke et al. 2009). Disturbance is the most commonly observed effect of noise on cetaceans (Richardson et al. 1995). It could be significant if animals were to be displaced from areas that are particularly important for feeding, reproduction or care of young (NRC 2005). However, the population-level impacts of such disturbance are largely unknown and would probably depend on the scale of the disturbance.

Before the present study, two kinds of dedicated surveys assessed the abundance and distribution of harbour porpoises: (1) two large-scale surveys conducted in summer, covering the complete North Sea and adjacent waters in a synoptic way (July 1994 and July 2005 during the SCANS surveys; Hammond et al. 2002, SCANS II 2008), and (2) surveys of selected smaller areas for case studies, conducted during recent years on a monthly basis (Thomsen et al. 2006, 2007) or in the 1990s only in summer (Heide-Jørgensen et al. 1993, Siebert et al. 2006). Thus, a lack of basic data on harbour porpoise distribution in our study area has been acknowledged, as surveys either provided a snapshot of a precise time interval or a detailed picture for a fraction of the area of interest.

The aim of the present study was to obtain a spatially and temporally explicit picture of harbour porpoise distribution in the German North Sea in order to assess the overlap with the planned construction of offshore wind farms and the potential effect on this species. Therefore, dedicated aerial line transect surveys were conducted throughout the year during 5 consecutive years. The seasonal distribution patterns of harbour porpoises were assessed and focal areas identified. Spatial overlap of preferred areas with offshore wind farms was investigated and the proportion of the national stock possibly affected by the imminent construction of offshore wind farms in the German North Sea was estimated. The present study provides the baseline for future comparisons.

MATERIALS AND METHODS

Study area. The study area (41 045 km^2) ranged from 3° to 9° E and from 53° 30′ to 56° N and included the exclusive economic zone (EEZ) and the 12 nautical mile zone of the German North Sea. The bottom topography of this shelf sea region is characterised by the shallow Wadden Sea (<10 m) and the post glacial valley of the river Elbe (>30 m), which extends from the Elbe estuary to the northwest and passes the Dogger Bank on the eastern side of Dogger Tail End (Becker et al. 1992). The hydrography is characterised by tidal currents and substantial gradients in salinity that are formed by the encounter of different water bodies. Two distinct water masses occur: the Continental Coast water mass is characterised by low salinity and low clarity and the Central North Sea water mass by high salinity, high clarity and a thermal stratification in summer (Becker et al. 1983).

Data collection. Aerial surveys were conducted year-round between 20 May 2002 and 10 October 2006. The area was divided into 4 geographic strata (Fig. 2, Table 1). One survey stratum could usually be surveyed within 1 d (5 to 9 h of flying).

The methodology followed standard line transect distance sampling techniques (Buckland et al. 2001). Surveys were flown along a systematic set of parallel transects (Fig. 2) placed either in east–west or north–south direction to run perpendicular to water

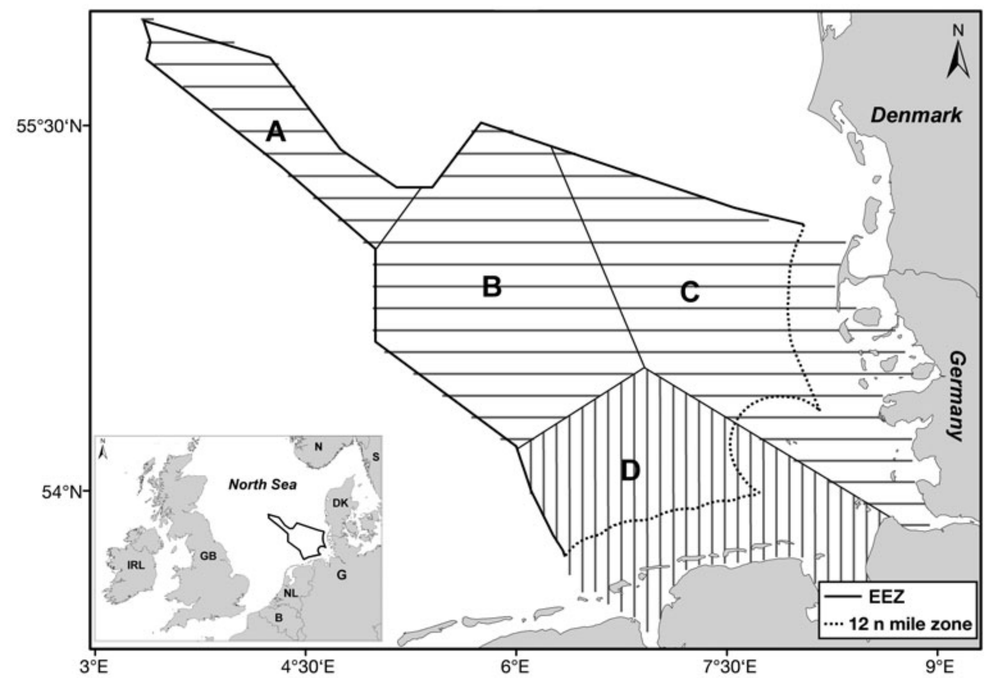

Fig. 2. Study area in the southeastern North Sea. Transects were equispaced: 10 km in Strata A to C and 6 km in Stratum D. EEZ: exclusive economic zone

Table 1. Survey design by geographic stratum

Stratum	Area (km^2)	n transects	Total transect length (km)	Mean duration of transect (min)
A	3903	11	396	12
B	11650	15	1165	26
C	13668	18	1369	25
D	11824	28	1912	22
Total	41045	72	4842	21

depth gradients as transect direction should not parallel physical or biological features (Buckland et al. 2001).

Surveys were flown at 100 knots (185 km h^{-1}) at an altitude of 600 ft (183 m) in a Partenavia P68, a twin-engine, high-wing aircraft equipped with 2 bubble windows to allow scanning directly underneath the plane. The survey team consisted of 2 observers, 1 data recorder (navigator) and the pilot. Communication between all team members was ensured via the intercom system. Sighting data were acquired simultaneously by the observers, each positioned on one side of the aircraft at a bubble window, scanning for animals with the naked eye. Observers rotated during breaks, i.e. every 2 to 3 h. The navigator entered all reported data directly into a laptop computer interfaced with a Global Positioning System (GPS). The aircraft's position was recorded every 2 s. Additionally, the start and end positions of the transect lines and the exact sighting positions were recorded.

A calm sea surface and good visibility are crucial during fieldwork as the harbour porpoise is one of the smallest cetacean species and shows an elusive behaviour at the water surface (Teilmann 2003). Surveys were only conducted during Beaufort sea states 0 to <3 and with visibilities >5 km. Environmental conditions were recorded at the beginning of each transect and updated with any change. Conditions included (1) Beaufort sea state, (2) water turbidity (judged visually; 0 — clear water with several meters of visibility to 2 — very turbid, no visibility under the surface), (3) percentage of cloud cover, and for each observer side, (4) glare (angle obscured by glare and intensity of glare) and (5) the observer's subjective view of the likelihood that, given all of the conditions, they would see a harbour porpoise should one be present. These subjective conditions could be either good, moderate or poor.

Data recorded for each harbour porpoise sighting included: (1) angle of declination to the group, (2) estimated group size and (3) number of calves (individuals were classified as calves if their size was less than half the size of the adult). The declination angle was measured by hand-held inclinometers when the group passed abeam of the plane.

Other marine mammal species recorded during the study included seals (370 sightings; see Herr et al. 2009 for details), white-beaked dolphin and minke whale (2 sightings each).

Data analysis. All data recorded in poor conditions were excluded from subsequent analysis. To estimate the proportion of animals missed on the transect line, the racetrack data collection method was used (Hiby & Lovell 1998, Hiby 1999). This method allows estimation of effective strip width (esw; Buckland et al. 2001), taking into account both the availability and the perception bias (Marsh & Sinclair 1989, Laake et al. 1997). Synchronous recording of GPS and sighting conditions allowed the assignment of sighting locations to sections of effort completed under consistent conditions. Hence, the estimates of esw appropriate to those conditions could be applied to those sections. The subjective assessment of good and moderate conditions, assessed separately to the left and right of the transect, was used to define sections completed under consistent conditions. Further details of the application of the racetrack method are described in Scheidat et al. (2008).

Encounter rates in each stratum were calculated by the ratio s_k/L_k, where s_k is the total number of sightings and L_k is the total number of km spent on effort in each survey month k, respectively. In order to test for significant differences in encounter rate between the 4 strata, generalised linear models GLM (McCullagh & Nelder 1989) were fitted. The Bonferroni correction was applied to lower the α value (to 0.0125) in order to account for multiple pair-wise comparisons (Zar 1998).

For the spatial analysis in ArcGIS 8.3, a grid with a resolution of 10 × 10 km was created, corresponding to the inter-transect spacing. Grid cells with a survey effort lower than 10 km were excluded from the analysis, resulting in a single set of representative cells per season. The overall number of harbour porpoises (n_i) and the effectively searched area (EA_i) per grid cell i were determined, and mean density estimates were calculated by the ratio n_i/EA_i.

EA_i was computed by:

$$EA_i = esw_L \times L_i + esw_R \times L_i$$

where esw_L is esw from the left side of the plane (km), esw_R is esw from the right side of the plane (km) and L_i is the effort in good or moderate conditions (km).

Latitude and longitude were assigned to the centre of each grid cell when testing for inter-annual and seasonal differences in spatial distribution. The seasonal density per stratum as well as 95% confidence intervals and coefficients of variation were estimated with a non-parametric bootstrap test, using transects as sampling units (see Scheidat et al. 2008 for details).

Statistical analysis. Data collected in the same season in all 5 study years (2002 to 2006) were pooled. Seasons were defined as spring (March to May), summer (June to August) and autumn (September to November). The winter months (December to February) were excluded due to low search effort. Prior to pooling, generalised additive models (GAM) were fitted (Hastie & Tibshirani 1990, Wood 2006) to detect any significant spatial variation between data collected in the same season but during different years. Harbour porpoise density values were normalised applying the *Z*-transformation (Zar 1998) before running the GAMs. A quasi error distribution was found to be appropriate. Two approaches were chosen (following Wood 2006): (1), assuming a symmetric distribution in different study years but during the same season, all data were pooled and harbour porpoise density was modelled using the locational covariates latitude and longitude, and (2) an asymmetric model was applied assuming differences in spatial distribution patterns between years. Both models were compared by an analysis of variance (ANOVA). If there was no significant difference between both models, no difference between the 2 tested years was assumed. In all seasons, all but 2 pairings showed no significant spatial variation. The number of pairs without significant variation totalled 4 in spring, 8 in summer and 4 in autumn. The lower number of pairs to be tested in spring and autumn was due to a lack of coverage in Strata A, B and D in spring 2004 and autumn 2006. Pooling was appropriate as the main aim of the present study was to identify focal areas used by harbour porpoises on a regular basis.

In addition, generalised additive mixed models (GAMM) (Lin & Zhang 1999, Wood 2006) were applied to examine latitudinal density gradients during the 3 seasons. Longitude was added as random effect factor.

To calculate GAM and GAMM, the package 'mgcv' (Wood 2006) in R v.2.6.2 (R Development Core Team 2008) was used.

Wind farm scenarios. In order to estimate the proportion of porpoises potentially affected during the construction of the 18 licensed wind farms, a few different scenarios were considered. Buffers were created around each of the 18 wind farm sites based on Richardson's zones of impact around an anthropogenic sound source (Richardson et al. 1995). If buffers overlapped, only combined buffers were used. If buffers extended to Danish or Dutch waters, this area was subtracted as no data on porpoise density were collected outside German borders. The radii of buffers were chosen based on existing knowledge. In Scenario 1, no buffer was applied. In Scenario 2, a small buffer of 2 km was applied in order to account for effects close to the constructions. In Scenarios 3 and 4 (10 and 15 km buffer, respectively), empirical values from Horns Rev (Denmark), the first offshore wind farm in the North Sea, were applied. At Horns Rev, behavioural reactions (e.g. displacement) of animals 10 to 15 km away from the construction site were recorded. As no visual surveys or acoustic data logging were conducted at distances greater than 15 km (Tougaard et al. 2003), it can be assumed that 15 km represents a minimum radius within which behavioural effects can be attributed to the construction. This, together with results of a recent temporary threshold shift (TTS) study conducted in Denmark (Lucke et al. 2009), is the reason we hypothesised in Scenario 5 that behavioural reactions of harbour porpoises could be triggered at even larger distances, up to 20 km away from the sound source (K. Lucke, pers. comm.).

The underlying temporal assumption is that all 18 wind farms will be constructed at the same time. These projects represent pilot phases during which about 80 turbines (5 to 6 MW each), erected on steel multipile foundations, will be built in each field. During the following planned expansions, which will lead to an enlargement of the affected area not taken into account here, the number of turbines will increase. In Horns Rev, it took between 0.5 to 2.5 h to drive 1 pile into the bottom and 6 mo total until all 80 monopiles were founded (Tougaard et al. 2003).

To obtain an estimate of the number of harbour porpoises potentially affected by the construction, a simplified approach was used: (1) the 18 pilot projects were assigned to the survey strata (B, C or D; see Fig. 2), for which seasonal densities were estimated; (2) densities were multiplied by the size of the area affected, including various buffer zones; (3) the number of potentially affected individuals was related to the estimated abundance for the total study area ('German stock') and the affected proportion calculated.

RESULTS

Survey effort and harbour porpoise sightings

During 91 survey days, 44 739 km of transect lines were surveyed within the 41 045 km^2 study area. A total of 4169 sightings of harbour porpoise groups were made on-effort. The number of sighted individuals totalled up to 5121, including 258 calves (Table 2). In most survey strata, encounter rates (ER) were highest during the period May to August (Fig. 3). In Stratum D, values were highest in April, May and September. ERs in Stratum C were significantly higher ($p < 0.0125$) than ERs in Stratum B in May, June and August. ERs in Stratum C were significantly higher ($p < 0.0125$) than ERs in Stratum D during all months except in April and November.

Table 2. *Phocoena phocoena*. Effort summary per season and main aerial survey results in good and moderate conditions. Data from the study years 2002 to 2006 were pooled. EA: effective search area. No. of ind. includes adults and calves

Season	Flight days	Track line length (km)	EA (km^2)	No. of groups	No. of ind.	No. of calves
Spring	28	14838	1637	1932	2225	28
Summer	38	17128	1711	1826	2355	199
Autumn	25	12773	1185	411	541	31
Total	91	44739	4533	4169	5121	258

Due to stable weather conditions, highest survey effort could be achieved during the summer months. However, it was also possible to obtain a good coverage in spring and autumn (Table 2). In spring and summer, more than 60 % of the transects were surveyed in Beaufort sea states 0 and 1. In autumn, surveys were conducted in sea states 0 and 1 for 43 % and in sea state 2 for 36 % of the survey time (Table 3).

Group sizes ranged from 1 to 6 ind. However, single individuals were sighted in 87 % of all recordings in spring and in 77 % in summer and autumn, respectively, resulting in an overall median group size of 1 ind. in all seasons.

Seasonal changes in distribution and density

In spring, harbour porpoise distribution was highly clumped. Two hot spot areas of particularly high densities could be detected (Fig. 4a). Porpoise densities reached highest values in the northeastern part of the German EEZ in an area from 40 to 130 km west of the North Frisian Islands of Amrum and Sylt, in the Sylt Outer Reef (SOR, see Fig. 1). This large aggregation zone was consistently observed during all study years. The second, smaller aggregation was located in the southwestern part of the German EEZ, approx. 60 km offshore the East Frisian Islands, in an area called Borkum Reef Ground (BRG, see Fig. 1). This hot spot could be observed from 2004 onwards and only during spring. In addition, high densities were observed in the vicinity of the island of Helgoland and on the submerged Dogger Bank (Stratum A) in the most westerly part of the EEZ. Most mother-calf pairs were found in the areas of higher densities, SOR having 46 % of the total observed, 25 % on the Dogger Bank and 11 % around both BRG and Helgoland.

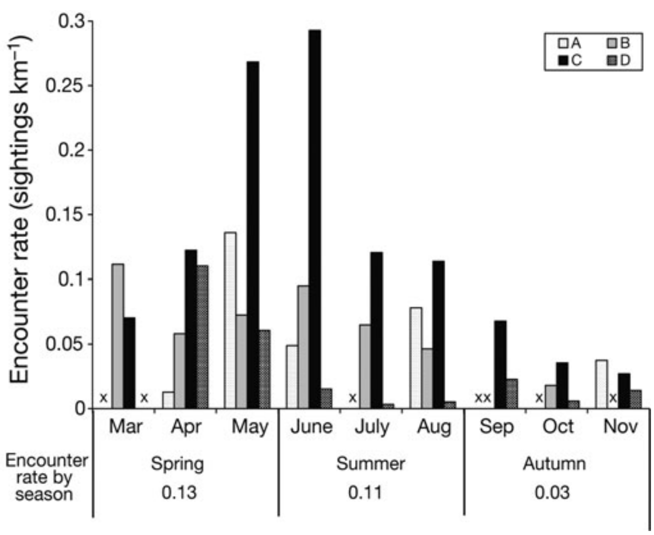

Fig. 3. *Phocoena phocoena.* Encounter rate from March to November, separated by survey stratum (A–D, see Fig. 2). Encounter rates by season are indicated. Data from 2002 to 2006 were pooled. x: no effort

In summer, a distinct north–south density gradient was observed (Figs. 4b & 5). This was mainly due to large aggregations of harbour porpoises that were detected in the northeastern part of the German EEZ, in contrast to much lower densities south of 54° 30′ N. This gradient was also detected in the distribution of mother-calf pairs: more than 84 % were sighted in the area of SOR.

In autumn, porpoises were more evenly dispersed throughout the study area (Fig. 4c). There was no specific aggregation area; instead, low-density 'cold spots' were detected. Overall, highest densities occurred in the area of SOR and near the island of Helgoland. The sighting rate was lowest in comparison to spring and summer (Fig. 3), indicating a migration of animals out of the German Bight during autumn. The harbour porpoises remaining in the area were sighted mainly (90 % of all sightings) in waters east of 6°30′E, but the coverage in the offshore strata (i.e. Stratum A) was poor. In comparison to the summer months, a higher number of porpoises was detected in the waters around the East Frisian Islands, although the densities were lower than during spring. The majority (76 %) of the 31 mother-calf pairs was found in the SOR area.

Abundance estimates were highest in spring (55 048 animals; 95 % CI: 32 395 to 101 671) as well as in summer (49 687 animals; 95 % CI: 29 009 to 96 385) and lowest in autumn with 15 394 animals (95 % CI: 8906 to 29 470) (Table 4).

The results of the GAMMs confirmed significant ($p < 0.001$) spatial differences in latitudinal distribution (Fig. 5). In all 3 seasons, a north–south density gradient was observed that was most pronounced in summer.

Table 3. Length (and percentage) of track lines surveyed in Beaufort sea state conditions 0 to 3. Data from 2002 to 2006 were pooled

Beaufort sea state	Spring		Summer		Autumn	
	Track length (km)	%	Track length (km)	%	Track length (km)	%
0	1616	10.9	1288	7.5	353	2.8
1	9694	65.3	9723	56.8	5219	40.5
2	2996	20.2	4662	27.2	4638	36.3
3	532	3.6	1455	8.5	2564	20.1

Effects of offshore wind farm construction

Table 5 summarises the different scenarios. The total area occupied by the 18 licensed wind farms in their pilot phases will encompass 730 km^2. In the first scenario, without any buffer, approx. 2% of the harbour porpoise stock in the German EEZ could be affected during construction. Within this close proximity to the sound source, individuals could suffer from hearing impairment (e.g. TTS; Lucke et al. 2009). The area affected by construction is largest in Stratum C and, as porpoise density is very high in this area, the estimated proportion of porpoises that could be exposed to the noise from the offshore constructions is highest in Stratum C for all scenarios in all seasons. The density in Stratum D is highest in spring and autumn (Table 4), therefore the proportion of porpoises affected in summer is likely to be low in Stratum D. When applying the buffer of 20 km, up to 39% of the national stock could be affected (Table 5).

DISCUSSION

General aspects

The data collected during this 5 yr study provide year-round information on seasonal changes in harbour porpoise density and distribution within the German EEZ in the North Sea. A consistency was shown for one of the identified hot spots: the Sylt Outer Reef (SOR) was a focal area in all study years and across all seasons. A lack of consistency was shown for the second (spring) hot spot at Borkum Reef Ground (BRG), which could not be detected before 2004. In order to evaluate the contribution of the German stock to the North Sea population, estimates of the present study were related to the recent abundance estimate for the total North Sea (SCANS II 2008). When grouping the SCANS II blocks H, L, U, V and Y (surface area: 361 073 km^2), to correspond as closely as possible to the borders of the putative sub-population 'Southern and Central North Sea' (IWC 2000), the contribution of the German stock (surface area: 41 045 km^2) to this sub-population is 36% in spring, 33% in summer and 10% in fall. The present study is important for all countries bordering the North Sea as information on seasonal movements and focal areas of harbour porpoises is provided and because possible effects on porpoises during the construction of offshore wind farms were quantified. In our worst case scenario, 39% of the harbour porpoise stock in German waters could be affected during construction.

Hot spot areas

The present study documents a patchy distribution, with harbour porpoises showing clear preferences for several discrete areas. Although aerial surveys cannot provide information on behavioural patterns, the observed hot spots suggest that these are areas where prey availability is high. Other top predators, like seals, were also recorded in the hot spots (Herr et al. 2009). Marine populations aggregate mainly during feeding, for reproduction, for protection from predators and during migration (Palacios et al. 2006). Porpoises in the North Atlantic feed on small shoaling fish species from both demersal and pelagic habitats (Santos & Pierce 2003). Recent analysis of stomach contents from our study area revealed that goby (Gobiidae), cod *Gadus morhua*, sole *Solea solea*, sandeel *Ammodytes* sp. and herring *Clupea harengus* are important constituents of their overall diet (Gilles et al. 2008). Standardised fisheries data show that, within the area of SOR, the pelagic clupeids herring and sprat *Sprattus sprattus* are most abundant, followed by the demersal fish species dab *Limanda limanda*, whiting *Merlangius merlangus* and plaice *Pleuronectes platessa* (Ehrich et al. 2006). The same species are abundant at BRG, with the exception of whiting, of which highest densities occur in the northern areas of the German EEZ (Ehrich et al. 2006). Additionally, SOR seems to be an important habitat for sandeels as the area is targeted by the industrial fishery that generally starts at the beginning of April, yielding highest catches from May to July (ICES 2007).

In spring, the 2 hot spots BRG and SOR seem to play an important role as key foraging areas from where porpoises spread out. In summer, the pronounced north–south density gradient could have been caused

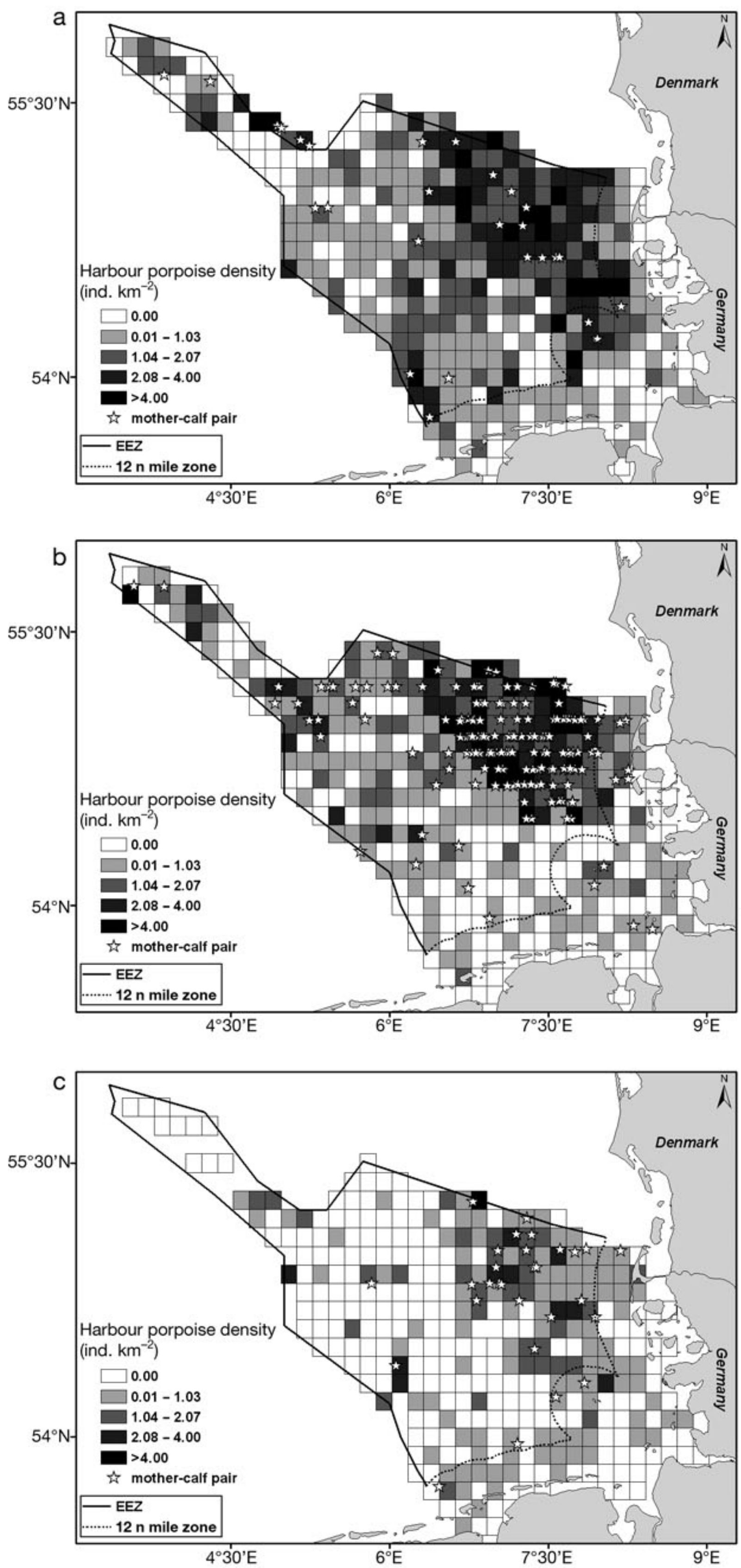

Fig. 4. *Phocoena phocoena.* Spatial distribution of harbour porpoise density (ind. km^{-2}) during (a) spring (March–May), (b) summer (June–August), (c) autumn (September–November). Data from 2002 to 2006 were pooled. Grid cell size: 10 × 10 km. EEZ: exclusive economic zone

by animals moving from the south to the north. It might also be that harbour porpoises entered the area of SOR from the north. Indeed, Danish aerial surveys along the border to Germany in the North Sea revealed a high density area about 50 to 100 km off the coast which complements the high density area found during our surveys in SOR (Teilmann et al. 2008). A similar area was detected during the SCANS II survey in July 2005, where the hot spot extended northwest across the Danish North Sea sector (SCANSII 2008). In autumn, porpoises seemed to start moving out of the study area. The described seasonal pattern is also reflected in data on strandings and incidental sightings (Siebert et al. 2006). Although a coverage of the total study area could not be achieved during winter, the few surveys in winter resulted in consistent lowest sighting rates, completing the annual cycle of distribution patterns.

The density of porpoises in the southwest increased during the course of the study from 2004 onwards, mainly in spring. A second hot spot was observed at BRG. This could also explain the absence of spatial symmetry for 2 of the study years (2002 and 2003) that were checked prior to pooling. At the same time, the southern neighbouring countries Netherlands, Belgium and France were reporting an increase in harbour porpoise strandings and incidental sightings (Camphuysen 2004, Kiszka et al. 2004). In fact, a return of harbour porpoises to Dutch coastal waters was reported after their virtual disappearance from the area in the early 1960s (Camphuysen 2004). A study in the area off Eastern Frisia and in parts of Dutch waters supports the results, reporting an increase in sightings from February 2004 until the beginning of May 2004 (Thomsen et al. 2006). Besides that, the

Table 4. *Phocoena phocoena.* Seasonal density and abundance estimates for each stratum and for total study area. CI: 95% confidence interval; CV: coefficient of variance

Area	Mean density	95% CI		Abundance	95% CI		CV
		Low	High		Low	High	
Spring							
A	0.62	0.20	1.52	2420	764	5929	0.52
B	0.78	0.43	1.48	9038	5025	17271	0.32
C	2.45	1.42	4.50	33493	19434	61441	0.31
D	0.85	0.45	1.72	10097	5352	20319	0.34
Total	1.34	0.79	2.48	55048	32395	101671	0.30
Summer							
A	0.95	0.42	2.13	3705	1646	8321	0.41
B	0.95	0.51	1.92	11124	5902	22340	0.35
C	2.41	1.37	4.75	32880	18719	64990	0.33
D	0.17	0.08	0.36	1978	994	4221	0.39
Total	1.21	0.71	2.35	49687	29009	96385	0.33
Autumn							
A	0.60	0.00	1.96	2353	0	7656	0.77
B	0.20	0.07	0.45	2296	823	5204	0.48
C	0.62	0.36	1.22	8535	4900	16732	0.32
D	0.19	0.09	0.40	2210	1091	4761	0.39
Total	0.38	0.22	0.72	15394	8906	29470	0.33

SCANS II survey showed that, in comparison to the SCANS survey from 1994, porpoise density estimated in the survey blocks north of 56° N was approximately half the density estimated in 1994, and density in survey blocks south of 56° N in 2005 was approximately twice the density estimated in 1994 (SCANS II 2008). As there was no difference in the overall abundance of porpoises in the North Sea in 1994 and 2005, it is thought that the geographical shift could be due to changes in harbour porpoise distribution in response to a changing distribution of their prey (SCANS II 2008).

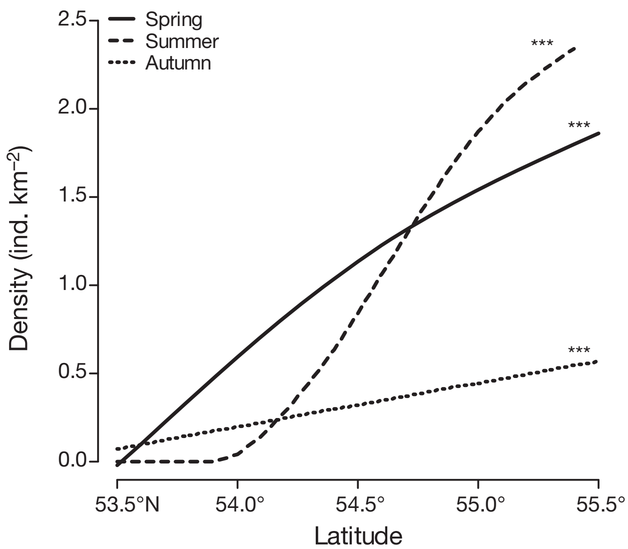

Fig. 5. *Phocoena phocoena.* Fitted models (generalised additive mixed models, GAMM) showing north–south density gradient. Data from 2002 to 2006 were pooled. ***$p < 0.001$

Occurrence of mother–calf pairs

The identification of areas where mating and calving occur may be important, as this period is of special significance in the annual life cycle of harbour porpoises. However, in the case of smaller odontocetes, there is often no clear separation between feeding and breeding areas, as opposed to most of the mysticetes (Hindell 2002). The harbour porpoise is known to 'live life in the fast lane', i.e. all reproductive and life history traits are accelerated during their short average life span of about 10 yr (Read & Hohn 1995). As female harbour porpoises are thought to be 'income breeders' (Sibly & Calow 1986, Read 2001) and reproductive costs are significant (Lockyer 2007), it is concluded that they must be able to continually locate areas where prey species with high energy content are abundant. The harbour porpoise exhibits strong seasonality in its reproductive cycle (Börjesson & Read 2003), and the majority of births in our study area occur from June 6 to July 16 (Hasselmeier et al. 2004), shortly before mating. Occurring in high densities could have advantages for locating mates. The return to certain grounds, maybe to those where foraging was successful in the

Table 5. *Phocoena phocoena.* Estimated number of individuals (and proportion, %) of harbour porpoises that could be exposed to noise from the construction of offshore wind farms (OWF) in the German North Sea under different scenarios (see 'Materials and methods'). Zone of impact: area around an anthropogenic sound source (after Richardson et al. 1995): (1) zone of audibility, (2) zone of responsiveness, (3) zone of masking, (4) zone of hearing loss, discomfort or injury

Scenario (no.)	Stratum	No. of affected ind. (%) Spring	Summer	Atumn	Area affected by OWF (km^2)	Zone of impact	Source
No buffer							
(1)	B	147 (0.27)	181 (0.37)	37 (0.24)	190	1, 2, 3, 4	Lucke et al. (2009)
	C	843 (1.53)	828 (1.67)	215 (1.40)	344		
	D	167 (0.30)	33 (0.07)	37 (0.24)	196		
	Total	1158 (2.10)	1042 (2.10)	289 (1.88)	730		
2 km buffer							
(2)	B	391 (0.71)	482 (0.97)	99 (0.65)	505	1, 2, 3	K. Lucke (pers. comm.)
	C	2350 (4.27)	2307 (4.64)	599 (3.89)	959		
	D	469 (0.85)	92 (0.19)	103 (0.67)	550		
	Total	3210 (5.83)	2880 (5.80)	801 (5.20)	2013		
10 km buffer							
(3)	B	1276 (2.32)	1570 (3.16)	324 (2.11)	1645	1, 2	Tougaard et al. (2003),
	C	8244 (14.98)	8094 (16.29)	2101 (13.65)	3364		Carstensen et al. (2006)
	D	1735 (3.15)	340 (0.68)	380 (2.47)	2032		
	Total	11256 (20.45)	10004 (20.13)	2805 (18.22)	7041		
15 km buffer							
(4)	B	1689 (3.07)	2078 (4.18)	429 (2.79)	2176	1, 2	Tougaard et al. (2003)
	C	13742 (24.96)	13491 (27.15)	3502 (22.75)	5608		
	D	2979 (5.41)	584 (1.17)	652 (4.24)	3489		
	Total	18410 (33.44)	16153 (32.51)	4583 (29.77)	11273		
20 km buffer							
(5)	B	2137 (3.88)	2630 (5.29)	543 (3.53)	2754	1, 2	K. Lucke (pers. comm.)
	C	15588 (28.32)	15302 (30.80)	3972 (25.80)	6361		
	D	3809 (6.92)	746 (1.50)	834 (5.41)	4460		
	Total	21533 (39.12)	18678 (37.59)	5349 (34.74)	13575		

previous year, may therefore be essential in order to meet mating partners and to find enough food for the high energy demand of birth, mating and the first months of lactation (Lockyer et al. 2003).

Potential impact of offshore wind farms

The distribution patterns of harbour porpoises presented here show considerable spatial overlap between preferred areas of porpoises and areas where offshore wind farms are licensed, most notably in the northeast and southwest of the study area. This is the first study that addresses the potential effects on harbour porpoises during windfarm construction and shows that — in the worst case — 39% of the porpoise stock in the German EEZ could be affected within a 20 km zone of responsiveness. However, for this scenario, we assumed that all pile-driving for the 18 approved wind farms would occur within 1 yr. This is not totally unrealistic: according to statements of the various operators, first projects are scheduled to start construction in 2009, with others following in 2010/2011. If pile-driving was spread out over several years, a smaller percentage of porpoises may be affected each year. Although our approach of estimating the proportion of porpoises exposed to the activity is simplified, it should be seen as a pilot study that incorporates available knowledge from the few erected offshore wind farms. Ecologically, it would have been more meaningful to assess the significance of the number of porpoises exposed to disturbance in relation to an abundance estimate for the North Sea population as a whole, e.g. by incorporating estimates of the recent SCANS II survey. However, for this approach, all types of offshore activities and the construction plans of all countries bordering the North Sea would have had to be incorporated, which would have been beyond the scope of this study.

Behavioural and physiological effects on porpoises can be expected during construction (Tougaard et al. 2003, Carstensen et al. 2006, Weilgart 2007). Although porpoises displaced by construction activities would not be lost to the population, they might be displaced to less suitable areas. The absence of an obvious behavioural reaction alone would not prove the absence of a response, but rather reflect the inability of measuring it. It was formerly assumed that animals that move away from disturbance do so because they are more affected than those that remain. However, recent studies suggest that the departing animals may be those with sufficient condition to do so (Bejder et al. 2006, Beale 2007). Moreover, where disturbance is concentrated in or nearby critical habitat, animals may have no other option but to stay. An example of bottlenose dolphins (*Tursiops* sp.) in Australian waters showed that long-term population impacts of disturbance may occur without dramatic or even observable short-term reactions (Bejder et al. 2006).

It was not possible to include temporal scenarios at this stage, as it is not known for how long harbour porpoises may be affected. Construction of the existing large wind farms Horns Rev (North Sea) and Nysted (Baltic Sea) lasted 6 to 12 mo. In Nysted, porpoises avoided the area to a large extent, and this avoidance still persisted after 2 yr of operation, although with indications of a slow, gradual recovery (Carstensen et al. 2006). Thus, construction impacts may not only be short-term. Especially when considering the cumulative effects of a large number of wind power projects over time, there will be installations under construction at any given time (Madsen et al. 2006), as the current plans in Germany clearly show.

Wind farms in the German EEZ require the approval of the Federal Maritime and Hydrographic Agency (BSH 2008). Authorisation has to be declined if the safety and easy flow of shipping is hindered or if the marine environment is endangered (Wustlich & Heugel 2006). Following legislation, a step-by-step expansion (pilot phase: maximum 80 turbines) is intended, where the next step (enlargement of area) presupposes a positive result with regard to environmental impacts. During and after construction of the pilot phase, the owner is obliged to carry out effect monitoring according to BSH guidelines.

Mitigation measures are widely used in order to minimise the environmental impact of big construction projects. In Germany, state of the art measures are mandatory. With respect to pile-driving for offshore windfarms, these measures could include a soft-start/ramp-up procedure to allow animals to move away before the sound gets too loud (Richardson et al. 1995), air-bubble curtains to reduce the source level of the pile-driving noise (Würsig et al. 2000) or acoustic harassment devices (AHD) (e.g. pingers, seal scarer) to 'scare' marine mammals from the vicinity of construction activity (Tougaard et al. 2003, Carstensen et al. 2006). However, some of these are controversial as they may lead to habituation (e.g. soft-start, AHD) or attract animals by initially weak sounds (Compton et al. 2008).

Following the precautionary principle, we recommend temporal and spatial restrictions on the construction of new wind farms in the identified focal areas SOR and BRG: we recommend not to licence the wind farm sites currently in the approval process on the SOR and advise that construction in the BRG should not be carried out during spring, unless future surveys indicate that the spring hot spot has disappeared.

The potential cumulative effects of the construction of several wind farms in the range of the harbour porpoise has to be assessed strategically, and in certain areas through the collaboration of neighbouring countries. Other pressures on this species should also be taken into account, such as bycatch (main threat in the area), pollutants and food depletion. Future work should assess the significance of the disturbance for the population. The present study is a first step towards estimating the number of harbour porpoises that may be affected by the construction of wind farms. Although the data represent a good time series for any cetacean species in European waters covering a large area, a mobile species like the harbour porpoise might change its distribution quite dramatically within a decade (see SCANS II 2008) and, consequently, hot spots can move. Nevertheless, detailed baseline data on porpoise distribution were collected over a 5 yr study period and provide a reasonable temporal window that may be used for any before/after comparison.

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LITERATURE CITED

Beale C (2007) The behavioral ecology of disturbance responses. Int J Comp Psychol 20:111–120

Becker GA, Fiuza A, James I (1983) Water mass analysis in the German Bight during MARSEN, phase I. J Geophys Res 88:9865–9870

Becker GA, Dick S, Dippner J (1992) Hydrography of the German Bight. Mar Ecol Prog Ser 91:9–18

Beineke A, Siebert U, McLachlan M, Bruhn R and others (2005) Investigations of the potential influence of environmental contaminants on the thymus and spleen of harbor porpoises (*Phocoena phocoena*). Environ Sci Technol 39: 3933–3938

Bejder L, Samuels A, Whitehead H, Gales N (2006) Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. Anim Behav 72: 1149–1158

Börjesson P, Read AJ (2003) Variation in timing of conception between populations of the harbour porpoise. J Mammal 84:948–955

BSH (Bundesamt für Seeschifffahrt und Hydrographie) (2008) Wind farms. www.bsh.de/en/Marine_uses/Industry/ Wind_ farms/index.jsp

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling. Estimating abundance of biological populations. Oxford University Press, New York

Camphuysen CJ (2004) The return of the harbour porpoise (*Phocoena phocoena*) in Dutch coastal waters. Lutra 47:113–122

Camphuysen CJ, Leopold MF (1993) The harbour porpoise *Phocoena phocoena* in the southern North Sea, particularly the Dutch sector. Lutra 36:1–24

Carstensen J, Henriksen OD, Teilmann J (2006) Impacts of offshore wind farm construction on harbour porpoises: acoustic monitoring of echolocation activity using porpoise detectors (T-PODs). Mar Ecol Prog Ser 321:295–308

Compton R, Goodwin L, Handy R, Abbott V (2008) A critical examination of worldwide guidelines for minimising the disturbance to marine mammals during seismic surveys. Mar Policy 32:255–262

Das K, De Groof A, Jauniaux T, Bouquegneau JM (2006) Zn, Cu, Cd and Hg binding to metallothioneins in harbour porpoises *Phocoena phocoena* from the southern North Sea. BMC Ecol 6:1–22

Ducrotoy JP, Elliott M, de Jonge VN (2000) The North Sea. Mar Pollut Bull 41:5–23

Ehrich S, Kloppmann M, Sell A, Böttcher U (2006) Distribution and assemblage of fish species in the German waters of North and Baltic Seas and potential impact of wind parks. In: Köller J, Köppel J, Peters W (eds) Offshore wind energy. Research on environmental impacts. Springer, Berlin, p 149–180

Gilles A, Andreasen H, Müller S, Siebert U (2008) Nahrungsökologie von marinen Säugetieren und Seevögeln für das Management von NATURA 2000 Gebieten. Teil: Marine Säugetiere. Final report, submitted to the German Federal Agency for Nature Conservation (BfN). F+E FKZ 805 85 018 (in German)

Halpern BS, Walbridge S, Selkoe KA, Kappel CV and others (2008) A global map of human impact on marine ecosystems. Science 319:948–952

Hammond PS, Berggren P, Benke H, Borchers DL and others (2002) Abundance of harbour porpoises and other cetaceans in the North Sea and adjacent waters. J Appl Ecol 39:361–376

Hasselmeier I, Abt K, Adelung D, Siebert U (2004) Stranding patterns of harbour porpoises (*Phocoena phocoena*) in the German North and Baltic Seas; when does the birth period occur? J Cetacean Res Manag 6:259–263

Hastie T, Tibshirani R (1990) Generalized additive models. Chapman & Hall, London

Heide-Jørgensen MP, Teilmann J, Benke H, Wulf J (1993) Abundance and distribution of harbour porpoises *Phocoena phocoena* in selected areas of the western Baltic and the North Sea. Helgol Meersunters 47:335–346

Herr H, Scheidat M, Lehnert K, Siebert U (2009) Seals at sea: modelling seal distribution in the German bight based on aerial survey data. Mar Biol 156:811–820

Hiby AR (1999) The objective identification of duplicate sightings in aerial survey for porpoise. In: Garner GW, Amstrup SC, Laake JL, Manly BFJ, McDonald LL, Robertson DG (eds) Marine mammal survey and assessment methods. Balkema, Rotterdam, p 179–189

Hiby AR, Lovell P (1998) Using aircraft in tandem formation to estimate abundance of harbour porpoises. Biometrics 54:1280–1289

Hindell MA (2002) Breeding sites. In: Perrin WF, Würsig B, Thewissen HGM (eds) Encyclopedia of marine mammals. Academic Press, San Diego, CA, p 169–171

Hüppop O, Dierschke V, Exo KM, Fredrich E, Hill R (2006) Bird migration and offshore wind turbines. In: Köller J, Köppel J, Peters W (eds) Offshore wind energy. Research on environmental impacts. Springer, Berlin, p 91–116

ICES (International Council for the Exploration of the Sea) (2007) Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak — combined spring and autumn. ICES CM 2007/ACFM:18 & 30. ICES Copenhagen

IWC (2000) Report of the IWC-ASCOBANS working group on harbour porpoises. J Cetacean Res Manag 2(Suppl.): 297–305

Kiszka J, Haelters J, Jauniaux T (2004) The harbour porpoise (*Phocoena phocoena*) in the southern North Sea: a comeback in northern French and Belgian waters? Report for ASCOBANS. AC11/Doc. 24. www.service-board.de/ ascobans_neu/files/ac11-24.pdf

Kock KH, Benke H (1996) On the by-catch of harbour porpoise (*Phocoena phocoena*) in German fisheries in the Baltic and the North Sea. Arch Fish Mar Res 44:95–114

Laake JL, Calambokidis J, Osmek SD, Rugh D (1997) Probability of detecting harbor porpoises from aerial surveys: estimating g(0). J Wildl Manag 61:63–75

Lin X, Zhang D (1999) Inference in generalized additive mixed models by using smoothing splines. J R Statist Soc B 61:381–400

Lockyer C (2007) All creatures great and smaller: a study in cetacean life history energetics. J Mar Biol Assoc UK 87: 1035–1045

Lockyer C, Desportes G, Hansen K, Labberte S, Siebert U (2003) Monitoring growth and energy utilisation of the harbour porpoise (*Phocoena phocoena*) in human care. NAMMCO Scientific Publications 5:107–120

Lucke K, Siebert U, Lepper PA, Blanchet MA (2009) Temporary shift in masked hearing thresholds in a harbor porpoise (*Phocoena phocoena*) after exposure to seismic airgun stimuli. J Acoust Soc Am 125(6) in press

Madsen PT, Wahlberg M, Tougaard J, Lucke K, Tyack P (2006) Wind turbine underwater noise and marine mammals: implications of current knowledge and data needs. Mar Ecol Prog Ser 309:279–295

Marsh H, Sinclair DF (1989) Correcting for visibility bias in strip transect surveys of aquatic fauna. J Wildl Manage 53: 1017–1024

McCullagh P, Nelder J (1989) Generalized linear models. Chapman and Hall, London

Nedwell J, Howell D (2004) A review of offshore windfarm related underwater noise sources. Subacoustech Rep 544R0308 to COWRIE (Collaborative Offshore Wind Research Into the Environment), London

Nowacek DP, Thorne L, Johnston DW, Tyack PL (2007) Responses of cetaceans to anthropogenic noise. Mammal Rev 37:81–115

NRC (National Research Council) (2005) Marine mammal populations and ocean noise: determining when noise causes biologically significant effects. National Academies Press, Washington, DC

OSPAR Commission (Convention for the Protection of the Marine Environment of the North-East Atlantic) (2000) Quality status report 2000, Region II — Greater North Sea. OSPAR, London

Palacios DM, Bograd SJ, Foley DG, Schwing F (2006) Oceanographic characteristics of biological hot spots in the North Pacific: A remote sensing perspective. Deep-Sea Res II 53: 250–269

R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org

Read AJ (2001) Trends in the maternal investment of harbour porpoises are uncoupled from the dynamics of their primary prey. Proc R Soc Lond B Biol Sci 268:573–577

Read AJ, Hohn AA (1995) Life in the fast lane: The life history of harbor porpoises from the Gulf of Maine. Mar Mamm Sci 11:423–440

Reijnders PJH (1992) Harbour porpoises *Phocoena phocoena* in the North Sea: Numerical responses to changes in environmental conditions. Neth J Aquat Ecol 26:75–85

Richardson WJ, Greene CR, Malme C, Thomson D (1995) Marine mammals and noise. Academic Press, New York

Santos MB, Pierce GJ (2003) The diet of harbour porpoise (*Phocoena phocoena*) in the Northeast Atlantic. Oceanogr Mar Biol Annu Rev 41:355–390

SCANS II (Small Cetaceans in the European Atlantic and North Sea) (2008). Final report to the European Commission under project LIFE04NAT/GB/000245. Gatty Marine Laboratory, University of St Andrews, St Andrews. http://biology.st-andrews.ac.uk/scans2/index.html

Scheidat M, Kock KH, Siebert U (2004) Summer distribution of harbour porpoise (*Phocoena phocoena*) in the German North Sea and Baltic Sea. J Cetacean Res Manag 6: 251–257

Scheidat M, Gilles A, Kock KH, Siebert U (2008) Harbour porpoise *Phocoena phocoena* abundance in the southwestern Baltic Sea. Endang Species Res 5:215–223

Schiermeier Q, Tollefson J, Scully T, Witze A, Morton O (2008) Energy alternatives: electricity without carbon. Nature 454:816–823

Sibly R, Calow P (1986) Physiological ecology of animals. Blackwell Scientific Publications, Oxford

Siebert U, Joiris C, Holsbeek L, Benke H, Failing K, Frese K, Petzinger E (1999) Potential relation between mercury concentrations and necropsy findings in cetaceans from German waters of the North and Baltic Seas. Mar Pollut Bull 38:285–295

Siebert U, Gilles A, Lucke K, Ludwig M, Benke H, Kock KH, Scheidat M (2006) A decade of harbour porpoise occurrence in German waters — analyses of aerial surveys, incidental sightings and strandings. J Sea Res 56:65–80

Smeenk C (1987) The harbour porpoise *Phocoena phocoena* (L. 1758) in the Netherlands: stranding records and decline. Lutra 30:77–90

Teilmann J (2003) Influence of sea state on density estimates of harbour porpoises (*Phocoena phocoena*). J Cetacean Res Manag 5:85–92

Teilmann J, Miller LA, Kirketerp T, Kastelein RA, Madsen PT, Nielsen B, Au WWL (2002) Characteristics of echolocation signals used by a harbour porpoise (*Phocoena phocoena*) in a target detection experiment. Aquat Mamm 28: 275–284

Teilmann J, Sveegard S, Dietz R, Petersen IK, Berggren P, Desportes G (2008) High density areas for harbour porpoises in Danish waters. NERI Technical Report 657. National Environmental Research Institute, University of Aarhus. www.dmu.dk/Pub/FR657.pdf

Thomsen F, Laczny M, Piper W (2006) A recovery of harbour porpoises (*Phocoena phocoena*) in the southern North Sea? A case study off Eastern Frisia, Germany. Helgol Mar Res 60:189–195

Thomsen F, Laczny M, Piper W (2007) The harbour porpoise (*Phocoena phocoena*) in the central German Bight: phenology, abundance and distribution in 2002–2004. Helgol Mar Res 61:283–289

Tougaard J, Carstensen J, Henriksen OD, Skov H, Teilmann J (2003) Short-term effects of the construction of wind turbines on harbour porpoises at Horns Reef. Technical report HME/362-02662 to TechWise A/S, Roskilde. www.hornsrev.dk/Miljoeforhold/miljoerapporter/Hornsreefporpoises2002. pdf

Verfuss UK, Miller LA, Schnitzler HU (2005) Spatial orientation in echolocating harbour porpoises (*Phocoena phocoena*). J Exp Biol 208:3385–3394

Vinther M, Larsen F (2004) Updated estimates of harbour porpoise (*Phocoena phocoena*) bycatch in the Danish North Sea bottom-set gillnet fishery. J Cetacean Res Manag 6:19–24

Weilgart L (2007) The impacts of anthropogenic ocean noise on cetaceans and implications for management. Can J Zool 85:1091–1116

Wood S (2006) Generalized additive models: an introduction with R. Chapman and Hall/CRC, Boca Raton, FL

Wünschmann A, Siebert U, Frese K, Weiss R and others (2001) Evidence of infectious diseases in harbour porpoises (*Phocoena phocoena*) hunted in the waters of Greenland and by-caught in the German North Sea and Baltic Sea. Vet Rec 148:715–720

Würsig B, Greene CR, Jefferson TA (2000) Development of an air bubble curtain to reduce underwater noise of percussive piling. Mar Environ Res 49:79–93

Wustlich G, Heugel M (2006) Legal framework conditions for the licensing of offshore wind farms. In: Köller J, Köppel J, Peters W (eds) Offshore wind energy. Research on environmental impacts. Springer, Berlin, p 15–20

Zar J (1998) Biostatistical analysis. Prentice Hall, NJ

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