Influence of sea state on density estimates of harbour porpoises (*Phocoena phocoena*)

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ABSTRACT

A ship-based line transect survey was conducted in the Great Belt, Denmark, from 7-20 April 1994, covering an area of 705 linear kilometres. A total of 497 sightings were collected in sea state 0-3. A comparison of relative abundance stratified by sea state revealed that sea state had a significant effect on the estimated sighting rate, effective search width, density and abundance within sea state 0-3. However, no significant difference was found between sea state 2 and 3. Comparison of abundance estimates of the same area on two different days surveyed in sea state 0, revealed no significant difference. The relative abundance estimate was 1,526 harbour porpoises in sea state 0 within the surveyed area (326.2km^2) based on the line transect method. This is the highest density of harbour porpoises (4.9 harbour porpoise/km^2) reported in Europe. There is a strong indication that sea state has a significant effect on abundance estimation of harbour porpoises in ship-based conventional line transect surveys. This is important for future surveys in two ways: (1) the reliability of a comparison of abundance for different surveys strictly depends on the sea state in which the surveys were conducted; and (2) when estimating absolute abundance, effects of sea state should be explicitly addressed. One way is to separately analyse data from each sea state and apply a *g*(0) estimate for each sea state.

KEYWORDS: HARBOUR PORPOISE; SEA STATE; LINE TRANSECT; SURVEY-VESSEL; DENSITY; ABUNDANCE; NORTH ATLANTIC

INTRODUCTION

Several methods have been used for abundance estimation of cetaceans (e.g. strip transect, line transect, point transect, cue-counting and acoustic surveys, see Hiby and Hammond, 1989; Buckland *et al.*, 1993). Distance based methodology is the most commonly applied and is certainly preferable when counting small species such as harbour porpoises (Hammond *et al.*, 2002). In particular, this is because the probability of detecting an animal decreases rapidly with distance; a strip transect survey for example, will give a downward biased density estimate (Heide-Jørgensen *et al.*, 1992).

Many authors have noted the obvious problem of decreasing sightability of cetaceans with increasing Beaufort sea state. Clarke (1982) stated that sea state has a severe effect on the sightability of harbour porpoises when above 3. Scott and Gilbert (1982) found a lower sighting rate of dolphins with increasing sea state under aerial surveys. Gunnlaugsson *et al.* (1988) found for aerial surveys off Iceland that 66.7% of harbour porpoises were seen in sea state 0-1, 31.9% in sea state 2 and only 1.4% in 3 or more ($n = 72$). However, they noted that the influence of sea state is difficult to quantify; the effects of environmental factors will be confounded by the variation in the actual densities and distribution of the animals. Hiby and Hammond (1989) suggested that even though a significant difference may be found, it is still problematic to use calibration factors to allow for comparison of different surveys. Instead they suggest only to survey under conditions favourable for obtaining reliable estimates.

This study uses data collected from a ship-based line transect survey for harbour porpoises and investigates the influence of sea state on abundance estimates.

MATERIALS AND METHODS

Survey area and design

The survey was conducted between 7 and 20 April in Jammerland Bay in the Great Belt in Denmark and the boundaries used for extrapolation of density and abundance were 55°30’-55°40’N, 10°50’-11°10’E excluding land and water north of the northern peninsula (Fig. 1). The area was chosen based on the high density of harbour porpoises found in the northern part of the Great Belt, during aerial surveys carried out in June 1991 and 1992 (Heide-Jørgensen *et al.*, 1992; 1993).

It is an advantage to have some prior knowledge of the distribution of the animals to stratify a survey efficiently and ideally the transect lines should cross any density gradients if present (e.g. IWC, 1997). The aerial survey data previously collected were not sufficiently detailed (and conducted later in the season) for this purpose but suggested that density was high throughout the area. Therefore, prior to the survey, a random systematic line placement grid was designed in a relatively small area bordered by the peninsulas in the bay. The lines were placed both perpendicular and parallel to the coast and depth contours. An attempt was made to repeat the same transect grid throughout the survey period. The same transects were therefore surveyed several times within the same day, and on different days. The expected high coverage of a relatively small area should provide an excellent opportunity for comparison of results across sea state. The extrapolation area was selected subsequently to include all surveyed transects.

Surveys of migrating animals must be designed carefully (against the migration path) in order not to arrive at a biased estimate of abundance. It is generally believed that migration of harbour porpoises through Danish waters occurs during spring (Teilmann and Lowry, 1996). For this study, it was important that no significant shift in density occurred, because results from different days were to be pooled and compared. To examine this further, density estimates (at a constant sea state, 0) on the 16 and 20 of April are compared below.

Vessel and shipboard methodology

The oil spill fighter *Gunnar Seidenfaden* from the Danish Ministry of Environment (now Ministry of Defence) was chosen for the survey because of its vessel characteristics

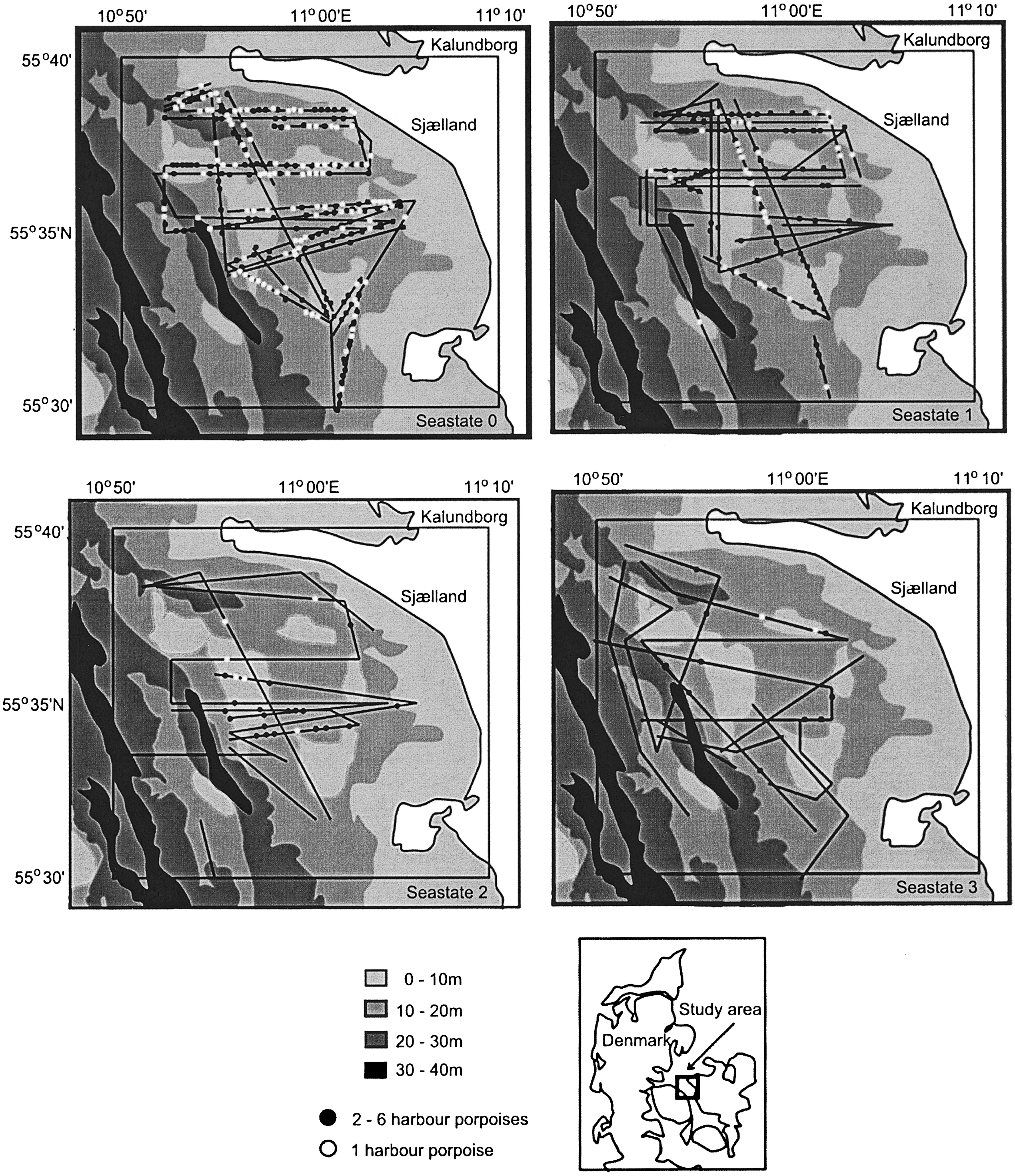

Fig. 1. Survey area, depth curves, transects, and harbour porpoise observations during sea states 0-3. The tracklines show the effort made in each sea state.

(56m long, 12m wide, 1,660 tonnes (868 BRT), maximum cruise speed 12 knots). Three separate sighting platforms were available: one in front of the bridge at 10m (primary platform); one on top of the wheel house at 12m (recorder and tracker platforms); and one on scaffolding at 16m above sea level (secondary platform). Twenty experienced observers participated in the survey. At any one time, three observers were placed on the primary platform and two observers on the recorder platform, while a team of two observers were both either on the tracker platform or during other periods on the secondary platform. Observers worked in half-hour shifts for up to 13 hours a day.

Data collected from the recorder, tracker and primary platforms were used in this analysis. On the recorder platform, two people recorded effort data on a computer (*Victor* 400n equipped with the software program *Cruise4*) linked to a GPS (Global Positioning System, *Garmin* 55 AVD). On the tracker platform, two people searched well ahead and on each side of the vessel, in order to track porpoises from before they were expected to react to the vessel and until they had passed abeam. On the primary platform, three people observed independently from the tracker platform in a 180° arc in front of the vessel. All sightings were reported as they were made to the recorder platform on VHF radios.

In high density areas, separation of animals can be difficult. This will have important implications for abundance estimation, if double counting is high. Although for some sightings it is impossible to be certain if it is the same or a new animal, by having an experienced person keeping track of all sightings and helping the observers to determine if the pod had been sighted before, and by making all the observers aware of the problem, double counting is believed to be of minor importance in this study.

For each sighting the following information was recorded: platform; observer code; time; radial distance; angle from heading; school size; cue; behaviour; and aspect of the porpoise. Line transect sampling requires that the perpendicular distance from the trackline to all sightings can be estimated (Buckland *et al.*, 1993).

Effort and environmental data

Every 15 minutes (or whenever conditions changed), the following effort and environmental data were recorded: transect number; observer positions; sea state[1]; swell height; swell angle; glare width; glare strength; rain; fog; sun angle (horizontal and vertical); wind direction. The position, speed and compass heading were automatically recorded by the GPS/computer system.

A number of environmental factors such as rain, fog, glare, wind direction, swell and sea state may increase or reduce the probability of detecting cetaceans. The primary focus of this study is to examine the influence of sea state, which experience suggests is the most important for a small species that spends most of its time submerged and during surfacing exposes only a small part of its body.

Rain and fog are not considered a problem for this survey as effort was suspended when visibility decreased to less than 1,000m. Surveying also ceased if the sea state exceeded 3.

Sea-state	Wind speed	Description
0	0.0-0.5 m/s	Sea like a mirror
1	0.5-1.8 m/s	Patchy areas with ripples
2	1.8-3.4 m/s	Small wavelets all over. No whitecaps.
3	3.4-5.4 m/s	Large wavelets all over. Few whitecaps here and there.

Data analysis

Data collection and analysis followed the line transect method described by Buckland *et al.* (1993) with modifications by Hammond *et al.* (1995; 2002). The computer software ‘Distance’ (Laake *et al.*, 1994) was used for the analysis. Given the difficulties in determining $g(0)$ (e.g. Palka, 1996) and the primary purpose of this study, only relative abundance was estimated from the sightings collected by the primary team. Based on likelihood ratio tests of four different models (hazard-rate+cosine, half-normal+hermite, uniform+polynomial and uniform+cosine) the uniform probability function with cosine adjustments (Fourier series) was chosen (see Buckland *et al.*, 1993 for formula). The model was chosen on the basis of the lowest AIC value (Akaike’s Information Criterion) and the χ^2-goodness of fit was tested and the model accepted if $p > 0.05$ (Buckland *et al.*, 1993).

Sightings made from the primary platform were stratified by sea state (0-3). Data from sea state 0 was truncated at 900m, sea state 1 at 800m and sea states 2 and 3 at 400m. Following Buckland *et al.* (1993, p.15), these truncation points excluded extreme values which would give little information and make it difficult to fit the function and estimate $f(0)$. The perpendicular distances from the trackline were pooled in 100m intervals for sea state 0 and 1, and in 50m intervals for sea states 2 and 3 in order to achieve similar numbers of intervals for fitting the probability function.

The program Distance was used to estimate the following parameters and their associated variances from the dataset:

(1) the number of sightings per kilometre on effort (sighting rate, n/L, n = number of sightings, L = length of transects);
(2) the probability density function of perpendicular distances, evaluated at zero distance ($f(0) = 1/\text{ESW}$, ESW = Effective half-Search Width; the distance within which the number of objects missed is the same as the number detected beyond it);
(3) the mean pod size for the primary platform (S).

These parameters were calculated for the different sea states and for sea state 0 for the surveys on 16 and 20 April. These dates were the only days where adequate numbers of sightings were collected within the same sea state to allow for reliable comparisons of density.

Pod size estimation can be problematic. It can easily be underestimated if only a single sighting is made because of the undemonstrative behaviour of the animals. One might expect the tracker platform to give a more reliable estimate of the mean pod size than the primary platform, because the trackers follow the pods for a period of time (although it might be argued that larger pods are easier to follow for several surfacings and thereby the pod size could be overestimated). It was therefore decided to estimate the pod size from pods sighted three times or more by the tracker platform. This was used for calculation of density and abundance in all sea states, except for the comparison between 16 and 20 April where the pod size from the primary platform was used for both days.

Density (D) was estimated by the formula (Burnham *et al.*, 1980):

$$D = f(0) * S * n / (2 * L)$$

The relative abundance (N) was found by multiplication of the density by the area used for extrapolation (A). No correlation was found between n/L, ESW and S ($p > 0.05$), and they were therefore assumed to be independent. The coefficient of variation (CV) for the density was therefore estimated as:

$$\text{CV}(D) = \sqrt{\text{CV}(n/L)^2 + \text{CV}(f(0))^2 + \text{CV}(S)^2}$$

while the log-based confidence limits (assuming that D is log-normally distributed) were found by the formula (Buckland *et al.*, 1993):

$$D_{\text{lower}} = D/C \text{ and } D_{\text{upper}} = D * C$$

where:

$$C = \exp\left[t_{df} * \sqrt{\ln\left(1+\text{CV}(D)^2\right)}\right]$$

where t_{df} is the two-sided t-distribution percentile with degrees of freedom (df) computed as

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[1] The definition of sea state 0-3 is given below (see pictures and definition on *http://www.besco.de/min_seastate.htm*)

$$df = (CV(D))^4/([CV(n/L)]^4/(k\text{-}1)+[CV(f(0))]^4/(n\text{-}m)+[CV(S)]^4/(n\text{-}1))$$

where k is the number of transects and m is the number of parameters estimated in the probability density function $f(x)$.

Since the variances of the density estimates were unequal (F-test), a d-test was used at $p < 0.05$ level to test the difference between density estimates:

$$d = (x - y) / \surd\,(se(x)^2 + se(y)^2)$$

where x and y are the average abundance for two samples. The variable d follows the Fisher-Behrens distribution.

A correction factor for the relative abundance estimates in different sea states (ss) was calculated as the deviation from N in sea state 0 assuming that the abundance in sea state 0 is the least biased:

$$\text{Correction factor } (m) = N(ss0) / N(ssX)$$

where X is the sea state. The CV for this ratio is approximately (Colquhoun, 1971; Buckland *et al.*, 1993):

$$CV\ (N(ss0)/N(ssX)) \cong \surd\,[CV\ (N(ss0))^2 + CV\ (N(ssX))^2]$$

The 95% confidence interval estimate of the ratio is too extensive to show here; see Colquhoun (1971).

RESULTS

There were 705km of transects surveyed and 497 harbour porpoise groups seen from the primary platform during 14 days of surveying. Data were collected during sea states 0, 1, 2 and 3 for transect lengths of 227.4km, 200.6km, 144.8km and 131.9km, and total observations of 318, 147, 21 and 11 harbour porpoise pods, respectively (Fig. 1, Table 1). Nearly all days included more than one sea state, so the combined effort for each sea state was spread over the whole survey period.

Comparison of the results from sea state 0 collected on 16 April ($n = 115$ sightings) and 20 April ($n = 179$ sightings) showed no significant difference with respect to the relative abundance estimate, density of pods or mean pod size. However, the sighting rate and the ESW were significantly higher on 20 April as compared with 16 April (Table 2).

Harbour porpoises were assumed to be evenly distributed within the surveyed area of 326.2km^2 that was used for the extrapolations. This appears to be true by visual inspection of Fig. 1. The pod size estimated by the tracker platform only increased in 21% of the observations from the first sighting to the third sighting of the same pod, decreased in 4% and remained the same in 75% of the cases. The independent pod size obtained from the tracker platform was 2.286 ($n = 70$, CV = 0.07, Table 1), which was significantly higher than the average pod size obtained from the primary platform (1.467; $p < 0.01$). Calculations of relative abundance when the tracker platform pod size was used, gave point estimates of 1,526 harbour porpoises (CV = 0.13) in sea state 0; 941 harbour porpoises (CV = 0.20) in sea state 1; 231 harbour porpoises (CV = 0.31) in sea state 2; and 120 porpoises (CV = 0.40) in sea state 3 (Table 1, Fig. 2). Since no significant difference for any parameter was found between sea states 2 and 3 the results were pooled to obtain a larger sample size and a better fit of the model (Fig. 3). Sea states 2 and 3 pooled gave a point estimate of 218 (CV = 0.29) harbour porpoises (Table 1, Fig. 3).

The regression between windspeed (m/s) and sea state (Beaufort) gave a good fit ($r^2 = 0.995$), the sea state scale is therefore used as equidistant, in Figs 2 and 4.

A comparison of the four sea states revealed a tendency towards higher abundance estimates in lower sea states. Significant decreases in the sighting rate (n/L), density of pods (DS) and relative abundance (N) were found with increasing sea state ($p < 0.05$, Table 3). However, no

Table 1

Survey results for seastate 0, 1, 2, 3 and 2 + 3.

Seastate	0	1	2	3	2+3
Area (km^2)	326.2	326.2	326.2	326.2	326.2
Effort (L, km)	227.4	200.6	144.8	131.9	276.7
Number of transects	31	31	19	16	35
Truncation (W, m)	900	800	400	400	400
Number of sightings (n)	318	147	21	11	32
Model	Uniform/cosine	Uniform/cosine	Uniform/cosine	Uniform/cosine	Uniform/cosine
Number of adjustment parameters (m)	3	3	1	1	2
Sighting rate (n/L)	1.3984	0.733	0.145	0.0834	0.1156
Standard error (SE)	0.1349	0.1265	0.0392	0.0254	0.0243
Coefficient of variation (CV)	0.0965	0.1726	0.2704	0.3044	0.21
ESW (1/f(0), m)	323.57	290.43	234.39	258.08	198.05
Standard error (SE)	18.116	24.313	33.306	62.683	36.377
Coefficient of variation (CV)	0.056	0.0837	0.1421	0.2429	0.1837
Density of pods (DS, pods/km^2)	2.1609	1.2619	0.3094	0.1615	0.2919
Standard error (SE)	0.241	0.242	0.0945	0.0629	0.0814
Coefficient of variation (CV)	0.1115	0.1918	0.3055	0.3894	0.279
Average pod size (S)	2.286	2.286	2.286	2.286	2.286
Coefficient of variation (CV)	0.0709	0.0709	0.0709	0.0709	0.0709
Density (D, porpoises/km^2)	4.9399	2.8846	0.7073	0.3693	0.6673
Confidence interval (CL)	3,8035-6,4158	1,9243-4,3241	0,3784-1,3220	0,1688-0,8079	0,3799-1,1720
Abundance estimate (N)	1526	941	231	120	218
Confidence interval (CL)	1241-2093	628-1410	123-431	55-263	124-382
Standard error (SE)	213.0173	192.4345	72.442	47.496	62.762
Coefficient of variation (CV)	0.1322	0.2045	0.3136	0.3958	0.2879

Table 2

Comparison of data collected in seastate 0 from two different days, 16 and 20 April (d-test $p<0.05$).

Seastate 0	16 April	20 April
Area (km^2)	326.2	326.2
Effort (L, km)	101.8	104.9
Number of transects (k)	12	15
Truncation (m)	900	900
Number of sightings (n)	115	179
Model	Uniform/cosine	Uniform/cosine
Sighting rate (n/L)	1.1297	1.7064
Standard error (SE)	0.16064	0.2277
Coefficient of variation (CV)	0.1422	0.1334
Significant difference	**Yes**	**Yes**
ESW (1/f(0), m)	270.61	360.14
Standard error (SE)	18.341	30.922
Coefficient of variation (CV)	0.0678	0.0859
Significant difference	**Yes**	**Yes**
Average pod size (S)	1.552	1.5642
Standard error (SE)	0.0628	0.0639
Coefficient of variation (CV)	0.0405	0.0408
Significant difference	**No**	**No**
Density of pods (DS, pods/km^2)	2.0872	2.369
Standard error (SE)	0.3288	0.3759
Coefficient of variation (CV)	0.1575	0.1586
Significant difference	**No**	**No**
Density (D, porpoises/km^2)	3.2394	3.7057
Confidence interval (CL)	2.3098-4.543	2.6589-5.1648
Abundance (N)	1057	1209
Confidence interval (CL)	753-1482	867-1685
Standard error (SE)	171.92	198.06
Coefficient of variation (CV)	0.1626	0.1638
Significant difference	**No**	**No**

significant difference was found between sea states 2 and 3 (perhaps due to sample size considerations). The ESW for sea states 0, 1 and 3 were not significantly different (Table 3), although there is a decreasing trend in the point estimates.

Based on these results, the following correction factors (scaled to estimates made from data collected at sea state 0) are:

Sea state 1: × 1.6 (CV = 0.23, CI = 1.52-1.74)
Sea state 2: × 6.6 (CV = 0.34, CI = 6.02-7.30)
Sea state 2+3: × 7.0 (CV = 0.32, CI = 6.50-7.56)
Sea state 3: × 12.7 (CV = 0.42, CI = 10.97-14.72)

The points are fitted to an exponential function which gave the best fit (Fig. 4, $r^2 = 0.985$).

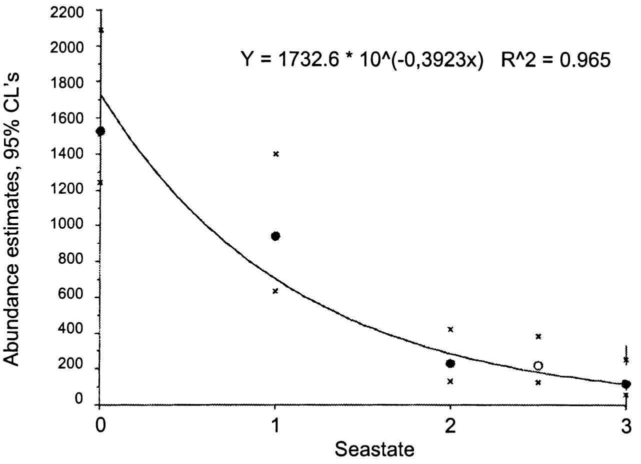

Fig. 2. Abundance point estimates (black dots) for each sea state with 95% confidence intervals (x symbols). An exponential regression is fitted to the point estimates. The pooled estimate for sea state 2+3 is shown, but not included in the fit.

DISCUSSION

Pod size

Estimates of pod size from sightings in 'passing mode' (no direction or speed changes on transect), will always be vulnerable to underestimation, since not all members of a pod will be visible at all surfacings. Furthermore larger groups are more detectable than smaller groups, which will cause overestimation of the average pod size. However, this problem is smaller than for many other cetaceans since harbour porpoises occur in relatively small groups (< 6 in this study). Estimation of pod size will be more reliable if each pod is tracked for a number of surfacings. Although the risk of detecting larger pods than the true average is still a problem, it is probably of the same magnitude for all platforms. The pod size estimated from the tracker platform was significantly higher than that derived from the primary platform. Therefore, the tracker platform is considered the most reliable estimate of the true pod size.

Density and relative abundance

In order to avoid the need to try and estimate *g(0)* and the effects of possible vessel attraction/avoidance, in this study only relative abundance is calculated, and it is assumed that the proportion of animals detected on the trackline and responsive movements are constant throughout the survey.

The higher sighting rate and ESW from 20 April compared to 16 April resulted in the same density estimate. The reason why harbour porpoises could be detected further

Table 3

Results of d-tests ($p<0.05$) comparing the values calculated for each seastate of sighting rate (*n*/L), effective search width (ESW), density of pods (DS) and abundance (N). Numbers indicate the seastates which were found to be significantly different from the seastate in the specified column. A dash indicates that no difference was found.

Seastate	0	1	2	3	2 + 3
n/L	1, 2, 3, 2+3	0, 2, 3, 2+3	0, 1	0, 1	0, 1
ESW	2, 2+3	2+3	0	-	0, 1
DS	1, 2, 3, 2+3	0, 2, 3, 2+3	0, 1	0, 1	0, 1
N	1, 2, 3, 2+3	0, 2, 3, 2+3	0, 1	0, 1	0, 1

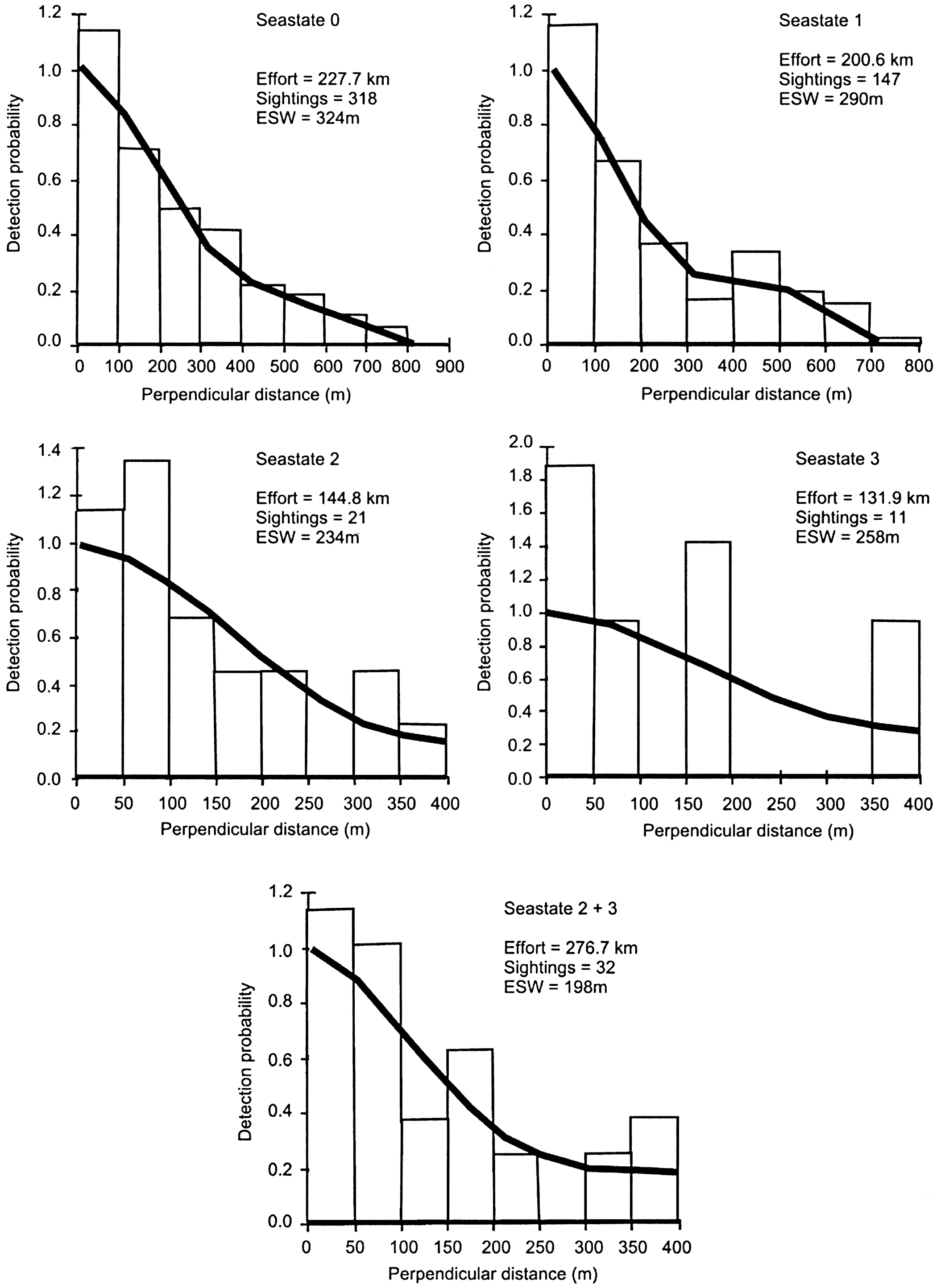

Fig. 3. Distribution of sightings of harbour porpoises at various perpendicular distances from the trackline for sea state 0-3 and 2+3. Data have been fitted to the Uniform function with cosine adjustments (Fourier series). The fitted curves show the expected number of sightings, $f(x)$. The effort and number of sightings for each sea state inside the truncation point is shown.

away on 20 April are unclear. For example, Gunnlaugsson *et al.* (1988) found an apparent relationship between sightings rate and cloud cover. The influence of glare on sightability varies with cloud cover, direction of the vessel and sea state. As glare is not believed to be a major problem on ship-based surveys in low sea state, its influence was not addressed in this study. While it is conceivable that wind direction may influence the probability of detecting an animal, here it is assumed to have the same effect under all sea state conditions.

Although it was only possible to compare the same sea state for two different days, the lack of difference in abundance between them does not contradict the assumption of no migration.

A minimum[2] estimate of 1,526 harbour porpoises (density = 4.9 per km^2) was obtained, in sea state 0, for the surveyed part of the Great Belt during April 1994. This is the highest density of harbour porpoises reported in Europe. Aerial line

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[2] Without correcting for $g(0)$, in particular.

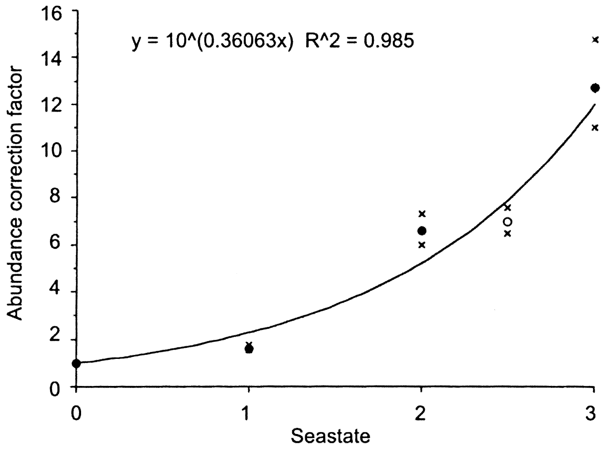

Fig. 4. Abundance correction factors for each sea state (black dots) with 95% confidence intervals (x symbols, calculated as the deviation from the abundance in sea state 0). An exponential regression is fitted to the point estimates. The pooled estimate for sea state 2+3 is shown (open circle), but not included in the line fit.

transect surveys in June 1992 revealed a relative density of 0.48 harbour porpoises/km^2 in the whole Great Belt (Heide-Jørgensen *et al.*, 1993). Absolute density of harbour porpoises in the Great Belt and surrounding waters was 0.644 animals/km^2 during a ship-based survey and 0.725 animals/km^2 during an aerial survey, both in July 1994 (Hammond *et al.*, 1995; 2002). The much higher density found in April 1994 might be due to the southerly spring migration through Danish waters, where harbour porpoises are believed to move into the Danish belts and the Baltic Sea (Teilmann and Lowry, 1996). One harbour porpoise initially satellite-tagged in the Great Belt during autumn showed this pattern. After wintering in the North Sea it returned to the Great Belt in mid-April (Teilmann *et al.*, 2001). It is not known whether this high density is a predictable local phenomenon during the survey period or the result of spawning of herring in the study area or the presence of other important food items. Only regular surveys with high coverage throughout the year, combined with telemetry studies can answer more general questions of habitat selection and movements of harbour porpoises in Danish waters.

Effect of sea state

The results from this study show that sighting rates decrease with increasing sea state in an area where the relative abundance is constant. In theory ESW should also decrease and thereby compensate for the lower sighting rate and give similar density estimates in all sea states. Although ESW decreased to some extent, the density estimate decreased significantly with higher sea state. On the two days surveyed in sea state 0, the ESW compensated for the change in sighting rate and no difference in density was detected. Apparently the change in ESW does not compensate sufficiently for the sighting rate decrease between sea states. The conclusion is that estimates of abundance from ship-based surveys of harbour porpoises will be biased downwards if any effort in sea state greater than 0 is included.

The above conclusion is supported to some extent by the results from two comparable ship-based surveys of harbour porpoises in US waters (Barlow, 1988; Palka, 1996). Barlow (1988) pooled sea states 0 and 1 and found a lower (although not significant) sighting rate for sea state 2. Palka (1996) found decreasing sighting rates with increasing sea state and similar ESW values to those found in the present study. She also estimated *g*(0) and found that it was almost constant from sea state 0-3. The changes in ESW and *g*(0) could therefore not fully compensate for the decreasing sighting rate, with a net result of a decrease in the estimated density with increasing sea state, although this was not significant. The main reason Palka (1996) did not find as clear results as in the present study could be the greater variation in the parameters and the density confidence intervals (up to about ±100%) probably due to greater variability in harbour porpoise density in her surveyed area.

Aerial surveys in 1992 in the inner Danish waters found that the ESW was similar in sea state 0 and 1 (133 and 138m) but substantially lower in sea state 2 (91m, Heide-Jørgensen *et al.*, 1993). Heide-Jørgensen *et al.* (1993) did not calculate if sea state was an influential factor on the abundance estimates but limited the effort used in the density estimate in sea state 2 or higher.

The correction factors calculated in this study should be used with caution, and only when using the same methods and vessel specifications. However, they do provide some idea of the magnitude of the effect of sea state on estimates of abundance of harbour porpoises. Hiby and Hammond (1989) generally believed that the best way to account for sea state was only to use date from appropriate conditions. However, to follow this approach for harbour porpoises with such low recommended sea states would be practically difficult; it would be unrealistic to expect to cover large areas in northern Europe, with its ever-changing weather, adequately. Although one might expect that estimating *g*(0) would compensate for some of the difference between sea states (a higher proportion of animals may be missed on the trackline with increasing sea state), Palka (1996) did not find that *g*(0), based on duplicate sightings, changed significantly with sea state. No studies thus far have shown that the effect of sea state can be fully compensated by the survey method.

In conclusion, there is strong indication that sea state has a significant effect on abundance estimation of harbour porpoises in ship-based conventional line transect surveys. This is important for future surveys in two ways. First, the reliability of a comparison of abundance for different surveys strictly depends on the sea state in which the surveys were conducted. Second, when estimating absolute abundance, effects of sea state should be explicitly addressed.

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