

Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters

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Summary

1. The status of small cetaceans in the North Sea and adjacent waters has been of concern for many years. Shipboard and aerial line transect surveys were conducted to provide accurate and precise estimates of abundance as a basis for conservation strategy in European waters.
2. The survey, known as SCANS (Small Cetacean Abundance in the North Sea), was conducted in summer 1994 and designed to generate precise and unbiased abundance estimates. Thus the intensity of survey was high, and data collection and analysis methods allowed for the probability of detection of animals on the transect line being less than unity and, for shipboard surveys, also allowed for animal movement in response to the survey platform.
3. Shipboard transects covered 20 000 km in an area of 890 000 km². Aerial transects covered 7000 km in an area of 150 000 km².
4. Three species dominated the data. Harbour porpoise *Phocoena phocoena* were encountered throughout the survey area except in the Channel and the southern North Sea. Whitebeaked dolphin *Lagenorhynchus albirostris* and minke whale *Balaenoptera acutorostrata* were found mainly in the north-western North Sea.
5. *Phocoena phocoena* abundance for the entire survey area was estimated as 341 366 [coefficient of variation (CV) = 0.14; 95% confidence interval (CI) = 260 000–449 000]. The estimated number of *B. acutorostrata* was 8445 (CV = 0.24; 95% CI 5000–13 500). The estimate for *L. albirostris* based on confirmed sightings of this species was 7856 (CV = 0.30; 95% CI = 4000–13 000). When Atlantic whitesided dolphin *Lagenorhynchus acutus* and *Lagenorhynchus* spp. sightings were included, this estimate increased to 11 760 (CV = 0.26; 95% CI 5900–18 500).
6. Shortbeaked common dolphin *Delphinus delphis* were found almost exclusively in the Celtic Sea. Abundance was estimated as 75 450 (CV = 0.67; 95% CI = 23 000–149 000).
7. Current assessments and recommendations by international fora concerning the impact on *P. phocoena* of bycatch in gillnet fisheries in the North Sea and adjacent waters are based on these estimates.

Key-words: conservation, line transect sampling, management, minke whale, *Phocoena phocoena*, shortbeaked common dolphin, sightings survey, whitebeaked dolphin.

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Introduction

The status of small cetaceans, particularly the harbour porpoise *Phocoena phocoena* L., in the North Sea and adjacent waters has been of concern for many years. This concern has stemmed from substantial incidental catches in fishing operations (Clausen & Andersen 1988; Berggren 1994; Lowry & Teilmann 1995; Tregenza *et al.* 1997; Vinther 1999), from declines in the number of stranding records (Smeenk 1987; Collet *et al.* 1994) and incidental sightings in coastal waters (Verwey & Wolff 1983; Evans *et al.* 1986; Evans 1990; Berggren & Arrhenius 1995a,b), and from the possible risks from contaminants (Morris *et al.* 1989; Law & Whinnett 1992; Law *et al.* 1992; Simmonds 1992; Kuiken *et al.* 1993; Berggren *et al.* 1999; Jepson *et al.* 1999) and disturbance (Evans, Canwell & Lewis 1992).

There is a need for basic information on the biology of *P. phocoena* and other small cetaceans, including their current abundance. Some quantitative data have been used to estimate relative or absolute abundance (Heide-Jørgensen *et al.* 1992, 1993; Leopold, Wolf & van der Meer 1992; Camphuysen & Leopold 1993; Berggren & Arrhenius 1995b; Bjørge & Øien 1995; Northridge *et al.* 1995). Except for Northridge *et al.* (1995), these studies have covered only parts of the North Sea and adjacent waters and in all cases the methodologies limit the inferences possible from the data. In particular, where line transect sampling was conducted, the standard assumption was that all animals on the transect line were detected. This is unlikely for cetaceans in general and certainly not for *P. phocoena*.

The need for accurate and precise estimates of abundance of *P. phocoena* and other small cetaceans throughout the North Sea and adjacent waters has been recognized by the UN Convention on the Conservation of Migratory Species (Bonn Convention), through its Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS); the European Union, through its Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora; the UN Environment Programme, through its Global Plan of Action for Cetaceans; the International Council for the Exploration of the Sea (ICES); the North Sea Ministerial Conference; and the International Whaling Commission (IWC). The latter specifically recommended that *P. phocoena* abundance should be estimated using dedicated sightings surveys in the North and Baltic Seas (IWC 1992).

Project SCANS (small cetacean abundance in the North Sea and adjacent waters) was initiated in 1993 to fulfil this need. The objectives were to identify concentrations of *P. phocoena* and other small cetaceans in this area and to estimate their abundance in order to provide essential information for conservation, management and future monitoring.

The project involved an intensive shipboard and aerial survey using line transect sampling (Hiby & Hammond 1989; Buckland *et al.* 1993). *Phocoena phocoena*

is a difficult species for such surveys because its small size and undemonstrative behaviour at the surface make it hard to detect except in good conditions. Because of this and the aim of obtaining precise abundance estimates, the survey intensity was greater than is typical.

In addition, the aim of obtaining accurate estimates of abundance dictated that important potential sources of bias in methodology needed to be addressed. This particularly applied to estimation of the probability of detecting animals on the transect line and the possibility that animals might respond to the survey ships. Previous shipboard surveys for *P. phocoena* have used methods that allowed estimation of the probability of detecting animals on the transect line (Barlow 1988; Palka 1995a) but have not addressed the potential problem of responsive movement. In aerial surveys, Barlow *et al.* (1988) did not directly estimate the probability of detecting animals on the transect line. The development of methods for shipboard and aerial line transect surveys specifically tailored to the estimation of absolute abundance of *P. phocoena* thus formed an integral part of the project. This methodology should also be appropriate for other species.

Survey area and design

The survey area (Fig. 1) covered that area specified in ASCOBANS (<http://www.ascobans.org>) excluding most of the Baltic Sea proper, where densities were expected to be too low to conduct an effective survey. The Celtic Sea was included because of a particular concern about the impact of *P. phocoena* bycatches in bottom set gillnet fisheries (Tregenza *et al.* 1997).

The survey area was stratified into blocks on the basis of logistical constraints and taking account of existing information on cetacean distribution and relative abundance, particularly for *P. phocoena* (Heide-Jørgensen *et al.* 1992, 1993; Camphuysen & Leopold 1993; Northridge *et al.* 1995; P.G.H. Evans, unpublished data).

Most blocks were surveyed by ship. Aerial surveys were flown in blocks covering coastal waters that were either difficult to survey by ship and/or that were expected to have high densities of *P. phocoena*. Block K was also surveyed by air as an efficient way to obtain some information on distribution but was not expected to yield an estimate of abundance. Blocks A–I were surveyed by nine ships for a total of 7 ship months between 27 June and 26 July 1994. With the exception of block G, a single vessel surveyed each block. Two aircraft surveyed in tandem formation blocks I' (a subset of block I), L, X and Y and a single aircraft surveyed blocks J, K and M between 26 June and 3 August 1994 (Table 1).

Shipboard survey methods

Methods to estimate abundance from shipboard surveys were based on standard line transect sampling

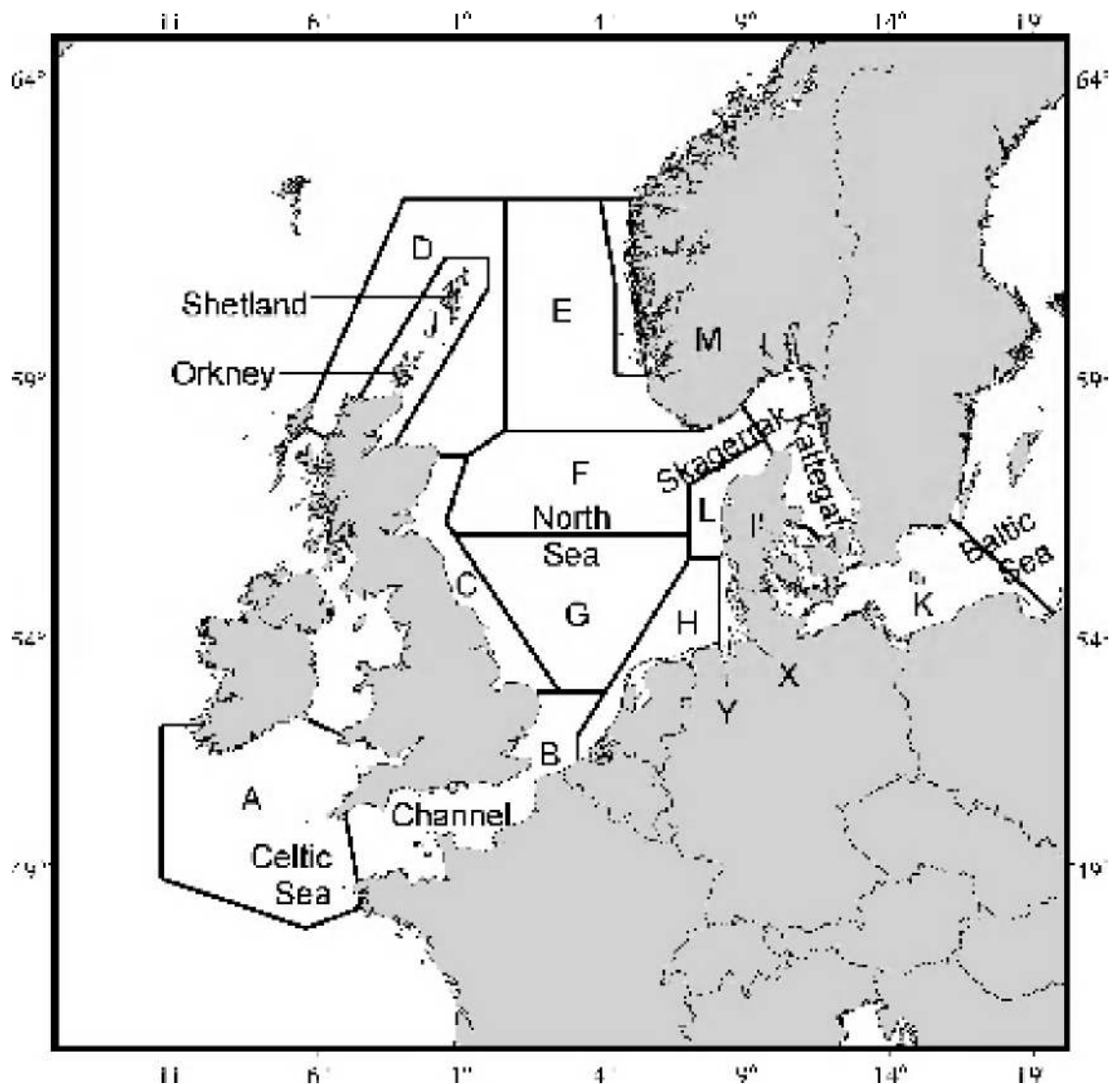


Fig. 1. Area covered during the SCANS survey in 1994. Blocks A–I were surveyed by ship. Blocks I' (a subset of block I), J–M, X and Y were surveyed by aircraft.

(Buckland *et al.* 1993; Hiby & Hammond 1989). In particular, they followed Buckland & Turnock (1992) and Borchers *et al.* (1998) and are highlighted below.

An experimental survey was conducted in April 1994 in part of Block I to test the proposed survey methods for the main survey, primarily data collection procedures, survey modes with secondary platforms and duplicate identification procedures (see below; Hammond *et al.* 1995). It gathered data to allow preliminary estimation of the proportion of schools detected on the transect line and a correction factor for responsive movement, and also provided staff training.

CRUISE TRACK DESIGN

Within each survey block, zigzag cruise tracks were selected to give a known, non-zero, coverage probability to each point in the survey block. This allowed a design-unbiased estimate of abundance to be calculated, regardless of the distribution of animals within the block.

DATA COLLECTION

The methods of Buckland & Turnock (1992) and Borchers *et al.* (1998) incorporate corrections for animals missed on the transect line and for responsive movement. They involve simultaneous survey from two independent observation platforms, one of which searches farther ahead of the vessel than the other, with the aim of detecting animals before they may respond to the approaching vessel. In the SCANS survey, two platforms (called primary and tracker) were located on each vessel.

The primary platform housed three observers (only two on the *Isis*) searching by naked eye in a standard way for line transect surveys. It was audibly and visually isolated from the tracker platform but its observers could communicate with the observer acting as duplicate identifier on the tracker platform by radio (see below). Observers on the primary platform searched as if it were the only platform on the vessel.

Table 1. Survey vessels, survey effort and surface areas for each survey block. Aerial survey block I' was a subset of shipboard survey block I. See text for description of good and moderate conditions for aerial survey

Block	Survey ship	Searching effort (km)	% sea state 4 or less	% sea state 2 or less	Surface area (km ²)
Shipboard surveys					
A	Dana	2 974	100	67	201 490
B	Henny	1 470	100	54	105 223
C	Henny	1 557	100	77	43 744
D	Abel-J	2 552	99	43	102 277
E	Gorm	2 556	96	49	109 026
F	Corvette	3 118	100	50	118 985
G	Holland + Tridens	3 372	99	65	113 741
H	Isis	854	100	80	45 515
I	Gunnar Thorsen	1 475	100	94	49 485
Total		19 927	99	61	889 486
Block	Aerial survey mode	Searching effort (km)	% good + moderate conditions	% good conditions	Surface area (km ²)
Aerial surveys					
I'	Tandem aircraft	1891	80	51	8 170
	Single aircraft	26	47	0	
J	Single aircraft	684	47	0	31 059
K	Single aircraft	685	90	51	65 369
L	Tandem aircraft	551	79	35	18 176
M	Single aircraft	1712	88	45	12 612
X	Tandem aircraft	200	87	77	5 810
	Single aircraft	705	91	64	
Y	Tandem aircraft	608	96	46	7 278
Total		7062	82	45	148 747

They were instructed to concentrate within 500 m of the vessel and to attempt to obtain data from two or three resightings of detected schools to facilitate duplicate identification. Primary observers co-operated in recording times, angles and radial distances to detected schools as accurately as possible, together with other relevant data (species, school size, orientation, etc.). Angles from the transect line to the detected schools were measured using angle-boards mounted on the platforms. Radial distances were estimated visually.

On the tracker platform, there were three observers (only two on the *Isis*): two trackers, searching far ahead of the vessel using 7 × 50 reticule binoculars, and one duplicate identifier. The trackers' responsibility was the detection of animals sufficiently far ahead of the vessel that they would not yet have reacted to the vessel's presence, and the tracking of these schools until they had either passed abeam or had been detected by the primary observers. Trackers were instructed to concentrate beyond 500 m ahead of the vessel. As soon as one tracker made an initial sighting of a school, the other tracker assisted him/her in obtaining and recording times, angles and radial distances for this and all repeat sightings as accurately as possible, together with other relevant data for a sighting as described above. Radial distances were estimated using the reticules in the binoculars, which were mounted on monopods passing through angle-boards on the platform.

The duplicate identifier received information from both the trackers and from the observers on the primary platform (by radio) immediately when sightings were made. His/her responsibility was the identification of duplicates, i.e. schools detected from both the tracker and primary platforms. In consultation with the two trackers, the duplicate identifier classified duplicates in real time as 'definite', 'likely' or 'possible' according to the degree of certainty that the pair were indeed duplicates, based primarily on times and locations of detected schools.

All data on detected schools were recorded by observers onto audio-tape and transcribed at the end of each day. Data on searching effort and sighting conditions were recorded in real time on a computer linked to the ship's global positioning system (GPS).

Experiments were conducted during the survey to allow estimation of the bias and variance of radial distances estimated by eye and using reticule binoculars, for each observer on each vessel. The experiments were conducted while the vessels were stationary, using dinghies as targets. One vessel used a polystyrene model porpoise as a target. While surveying, vessels towed a line with buoys attached every 100 m as a means for observers to practise and calibrate their distance estimations while off duty.

DATA ANALYSIS

Data analysis followed Borchers *et al.* (1998); the following summarizes relevant points for this survey.

Modelling school detection probability

The probability of detecting a school from the primary platform can be modelled as a function of any observable explanatory variable and not just perpendicular distance. This is important because methods that rely on duplicate detection data can be biased if detection probabilities vary among schools. Here, variables to include in estimating abundance were selected only if they had a significant effect on detection probability (see below).

Interval estimation

Coefficients of variation (CV) and confidence intervals (CI) were estimated using a non-parametric bootstrap procedure, which does not require the assumption of independence, in which transects were the sampling unit. Resampling was performed separately within each survey block, conditioning on the total searching effort in the block. Confidence limits were obtained as the 2.5 and 97.5 percentiles of the bootstrap distributions.

Data selection

Guidelines for truncating data with respect to perpendicular distance given by Buckland *et al.* (1993) were followed as far as possible, keeping in mind the need to keep the truncation distance sufficiently large so that the chance of a school moving into the detection area of the primary platform from outside the truncation distance was small. The data were also truncated at higher sea states. Detection probabilities of *P. phocoena* decline with sea state (Barlow 1988; Palka 1995a,b). Preliminary estimates indicated a sharp decline in their detectability between Beaufort 2 and 3. Consequently, for *P. phocoena*, data from sea states Beaufort 0–2 only were used in analyses. For all other species, data from Beaufort 0–4 were used.

Detection function estimation

There were sufficient data to estimate abundance for *P. phocoena*, *Balaenoptera acutorostrata* Lacepede and *Lagenorhynchus albirostris* Gray. Explanatory variables tested for inclusion in the model included: sea state; school size; vessel; aspect (a nominal variable indicating the orientation of the animal with respect to the observer's line of sight); cue (a nominal variable indicating the type of detection cue presented by the animal); behaviour (a nominal variable indicating behaviour type); glare (an ordinal variable indexing the degree to which glare interfered with detection); and swell height (a continuous variable measuring the height of ocean swell). For *B. acutorostrata* and *L. albirostris*, there was no evidence that any observed variables other than perpendicular distance affected detection probability, and this was

consequently modelled only as a function of perpendicular distance.

For *P. phocoena*, however, three explanatory variables other than perpendicular distance significantly affected detection probability: sea state, school size and vessel. For the vessel effect, precision was improved by limited pooling of data from vessels that had small sample sizes, using the similarity of the estimated vessel-effect parameters as the primary criterion for pooling. Separate vessel-effect parameters were estimated for the vessels *Abel-J*, *Gunnar Thorsen* and *Henny*; further vessel-effect parameters were estimated for *Corvette*, *Dana* and *Gorm*, combined, and *Holland*, *Tridens* and *Isis*, combined.

Mean school size

In Borchers *et al.* (1998), observed school sizes were incorporated directly into the estimation of animal abundance, avoiding the need to estimate mean school size as in conventional line transect methods. Mean school size can be estimated, however, as the ratio of the estimate of animal abundance to school abundance. Variances and confidence intervals of mean school size were estimated using the transect-based bootstrap procedure described above.

Estimated distance experiments

Only distance and angle data from the tracker platform were used in the analysis (Borchers *et al.* 1998). Bias in estimated distance was estimated using the slope and intercept of a linear regression of estimated reticule against true reticule. True reticule was obtained by converting the radar distance to the target object to a reticule reading, using the known angle of declination between reticules for the binoculars used. Bias in angle data was estimated in the same way.

In the case of angles, an additive error model was found to be adequate and no significant bias was found on any vessel. In the case of reticules, multiplicative error models, in which variance increases with increasing reticule, described the data better. No experimental data were available from the *Isis*, but some reticule estimation bias was found on all other vessels. A significant observer effect was found on the *Dana*, *Henny* and *Tridens*.

Bias in the observed reticules was corrected by subtracting from them the intercept of the regression line (if the intercept was significant) and/or dividing them by the slope of the regression line (if the slope was significant). This bias-corrected reticule was then converted to a distance, using the known angle of declination between reticules on the binoculars.

Sensitivity to duplicate identification

In this analysis, duplicates identified as definite and likely were considered to be true duplicates. The

sensitivity of the abundance estimates to this assumption was investigated by also estimating abundance: (i) taking only definite duplicates to be true duplicates; and (ii) taking definite, likely and possible duplicates to be true duplicates.

Aerial survey methods

Methods to estimate abundance from aerial surveys were based on standard line transect sampling techniques (Hiby & Hammond 1989; Buckland *et al.* 1993) but used the specific methods of Hiby & Lovell (1998); important points are highlighted below.

CRUISE TRACK DESIGN

Replicate zigzag tracks were constructed in each block by first defining a set of parallel lines perpendicular to a common axis, and then using the intersections of those lines with the block boundaries as successive waypoints for the track. Each set of parallel lines provided two replicate tracks; for example, one starting at the eastern end of the southern-most line and the other at the western end. Further tracks were constructed by shifting the set of parallel lines along the axis (Hiby & Lovell 1998).

The tracks were designed to give twice the mean coverage in block I' (the area of expected highest density) and half the mean coverage in block K (the area of expected lowest density) compared with the remaining blocks (J, M, L, X and Y). Inevitably, the coverage across a block varied in response to the shape of the block boundary, but the variation was minimized by adjusting the orientation of the common axis, and this remaining variation was allowed for by the method used to estimate abundance (Hiby & Lovell 1998).

DATA COLLECTION

Aircraft flew at 167 km h⁻¹ (90 knots) at 182 m (600 feet). In survey blocks I' L, X and Y, two aircraft were deployed in tandem formation (one flying about 9 km behind the other) to provide the potential for detection of the same school by both aircraft. The exact times and positions of sightings during these tandem phases of the survey were used to estimate the proportion of time *P. phocoena* was visible from the survey aircraft under different conditions.

Bubble windows allowed the two rear observers on each aircraft to search the sea area on their side of the aircraft, from the abeam line forward to the transect line with no blind area under the aircraft. All sighting information was recorded on acoustic tape. A continuous time signal was recorded on the same tape so that, on transcription, the time that each sighting was abeam of the aircraft could be determined to the nearest second. This was important for data collected during the tandem surveys because the times at which the aircraft drew abeam of detected schools provided

the most powerful indication of which schools were 'duplicates', i.e. were detected from both aircraft. Given the time the leading aircraft draws abeam of a detected school, the expected time the trailing aircraft will draw abeam of the same school can be calculated from the record of aircraft positions. These were logged from the GPS in each aircraft onto a computer that also relayed the GPS time signal to the acoustic tape, ensuring that time signals used in both aircraft were synchronous.

Species, school size and the declination angle to the school as it came abeam were recorded for each sighting. Declination angle was estimated using a hand-held declinometer and, in conjunction with aircraft altitude, provided an estimate of the perpendicular distance to each school. Altitude was continuously logged on the leading aircraft from the radar altimeter. The trailing aircraft used a pressure altimeter, which was calibrated before each flight.

Beaufort sea state, cloud cover, angle obscured by glare, turbidity, and an overall subjective assessment of sighting conditions of 'good', 'moderate' or 'poor', were recorded by one of the two observers in the leading aircraft at the commencement of each track leg and whenever any of these values changed.

The waypoint coordinates of each planned transect were stored in the aircraft GPS. During the flight, all recorded positions could therefore be related to the planned track line allowing the cross-track error, i.e. the perpendicular distance of the aircraft from the planned track line, to be calculated and the expected position for a school seen by the leading aircraft relative to the trailing aircraft to be calculated.

The same protocol was followed when the aircraft did not fly in tandem (in blocks J, K and M) except that observers on each aircraft were then responsible for recording sighting conditions.

DATA ANALYSIS

Data were analysed using the methods of Hiby & Lovell (1998). Reduction in detection probability with distance from the track line was estimated by fitting detection functions with the hazard rate form (Buckland 1985) to the perpendicular distance data for all schools detected on tandem and non-tandem effort, assuming that both aircraft had the same detection function. Because of the limited data available, stratification was limited to the overall subjective assessments of good and moderate sighting conditions. Searching effort under poor conditions yielded almost no sightings and was excluded from analysis.

The effective strip width also depended on the probability of detection of schools directly on the track line. Both this probability and the reduction in detection probability with perpendicular distance affected the proportion of duplicate sightings so that, given an estimate of the detection function, the observed duplicate proportion would allow the probability of detection on

the track line, and hence the effective strip width, to be calculated.

It was impossible to 'track' sightings from the leading aircraft back to the trailing aircraft. However, it was possible to predict at what time a sighting from the leading aircraft would come abeam of the trailing aircraft. Sightings from the trailing aircraft that occurred close to this predicted time were thus likely candidates for duplicates. Because it was difficult to know how close to the predicted time a sighting from the trailing aircraft should be in order to be classed as a duplicate, the sightings were not classified in this way. Instead, the likelihood of all intersighting intervals was calculated and maximized with respect to the probability of detection of a school on the track line and the parameters of a movement model for *P. phocoena*, which also incorporated the effect of positioning errors by the observers. The likelihood was calculated for all possible arrangements of leading and trailing sightings into duplicates and non-duplicates and summed over all the possibilities. The resulting estimate of detection probability was found to be insensitive to the type of movement assumed (diffusive or directed) and was consistent with telemetry estimates of time spent at or near the surface by *P. phocoena*, made by Westgate *et al.* (1995).

Abundance from a given track was estimated using the inverse selection probability method (Hansen & Hurwitz 1943). The cruise track design program was used to calculate coverage probabilities based on a nominal strip width of 1 km, for all locations along each track where schools were detected from both tandem and non-tandem effort. These were then multiplied by the average estimated effective strip width for that track to give the probabilities of detecting each school on the transect line required to estimate abundance. This method requires that every point of the survey area has a non-zero chance of being surveyed; the cruise track design program was used to verify this.

Analysis of replicate tracks within each survey block gave a mean abundance estimate with CV and confidence limits for each block.

Results

DISTRIBUTION OF SEARCHING EFFORT AND DETECTED SCHOOLS

Excellent coverage was achieved over most of the survey area (Fig. 2). Two blocks received substantially less effort than planned: aerial survey blocks J (Shetland and Orkney) and K (western Baltic), as a result of deteriorating weather towards the end of the survey period. Note that searching effort did not extend to coastal inlets in some areas. In particular, because of the complexity of the terrain, the fjord waters of western Norway were not covered by block M.

Phocoena phocoena were seen throughout most of the North Sea, Skagerrak and Kattegat and the Celtic Sea. None were seen in the Channel or the southern

part of the North Sea, and only a few were seen in the Baltic Sea (Fig. 3). Sightings were concentrated in the central North Sea, but it is important not to overinterpret the data presented in this way. The number of schools detected was a function of the distribution of effort and of the sighting conditions, which were accounted for in estimating abundance. Nevertheless, it was clear that during the survey period of July there were large numbers of *P. phocoena* offshore as well as in coastal waters.

Lagenorhynchus albirostris was concentrated in a band across the North Sea between 54° and 60°N, mostly to the west of 4°E (Fig. 4). Nine *Lagenorhynchus acutus* Gray schools were identified but there were 43 sightings of unidentified *Lagenorhynchus*, so it is likely that the large majority of these were *L. albirostris* and that the abundance for this species based on confirmed sightings alone was underestimated. For this reason, an estimate of all *Lagenorhynchus* sightings combined was also calculated.

Balaenoptera acutorostrata was also mostly detected in the north-western North Sea (north of 55°N and west of about 4°E) and in the Celtic Sea (Fig. 5).

Twenty-eight of 29 sightings of *Delphinus delphis* L. were made in the Celtic Sea.

ESTIMATES OF ABUNDANCE

Almost all (99%) searching effort on shipboard surveys was in sea state 4 or less; the percentage in sea state 2 or less varied between 43% in block D and 94% in block I (Table 1). Most (82%) aerial survey effort was categorized as moderate or good (Table 1). There were sufficient sightings from the shipboard surveys to estimate abundance for *P. phocoena*, *B. acutorostrata* and *L. albirostris* using the methods described above (Table 2). For the aerial survey, abundance could only be estimated for *P. phocoena* (Table 3); only one *B. acutorostrata* sighting and one *L. albirostris* sighting were made (in block J).

Duplicates as a percentage of tracker sightings, over all blocks, were 19% for *P. phocoena*, 49% for *B. acutorostrata*, 62% for *L. albirostris* and 49% for *Lagenorhynchus* spp. Duplicate percentages varied markedly among vessels, with ranges of 9–32% for *P. phocoena*, 23–67% for *B. acutorostrata*, 41–73% for *L. albirostris* and 30–63% for *L. albirostris*, for blocks with at least five tracker sightings (Table 2).

There were no unexpected patterns in detection probability as a function of perpendicular distance. In the shipboard surveys, detection probability declined steadily for *P. phocoena*, declined quite sharply in the first 100 m for *B. acutorostrata*, and was fairly flat out to 800 m for *L. albirostris*. In the aerial surveys, detection probability for *P. phocoena* was fairly flat out to about 200 m and then declined sharply.

Abundance of *P. phocoena* was estimated for all survey blocks except block K (because of insufficient coverage; Fig. 2). Total abundance in the survey area

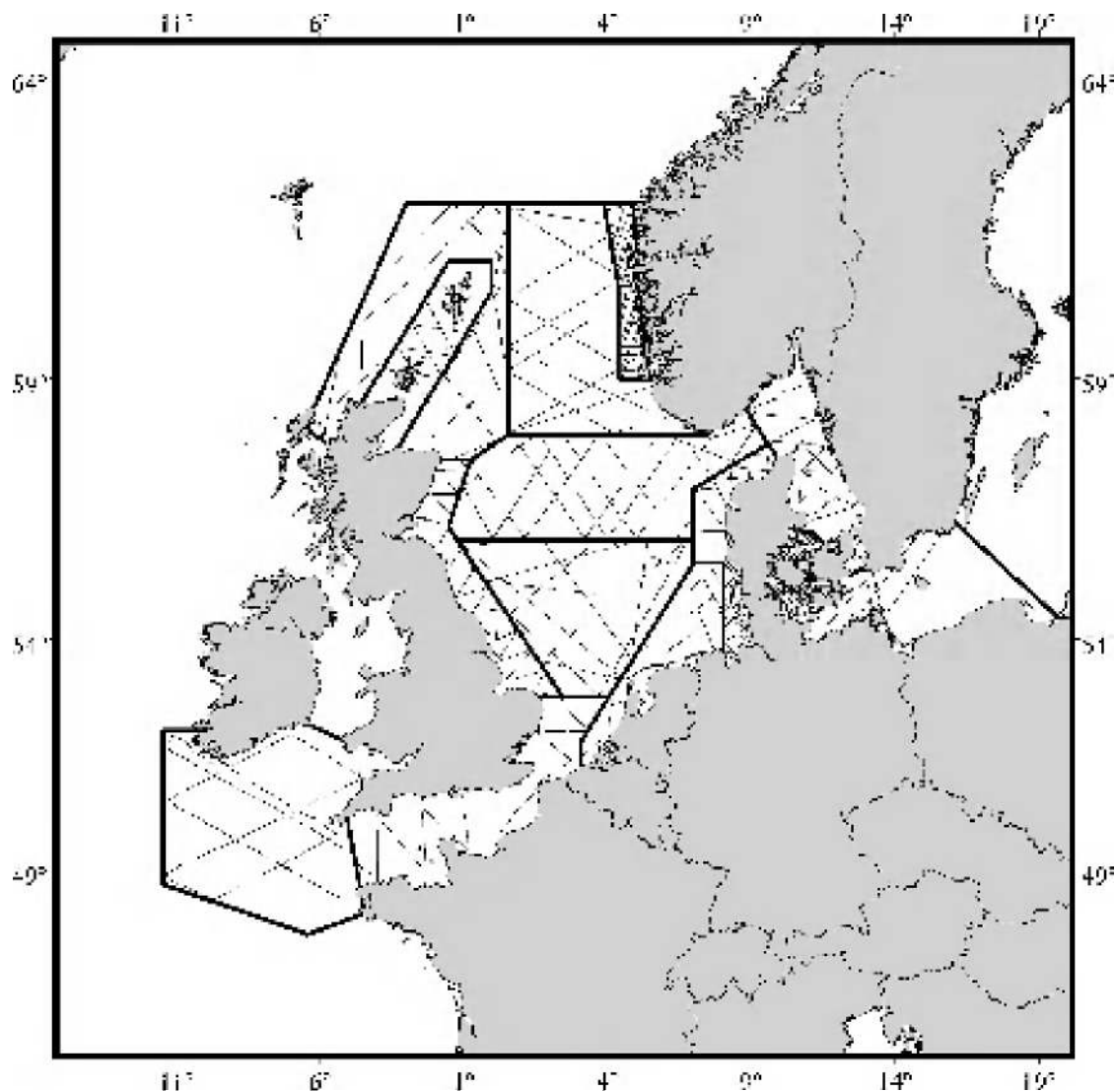


Fig. 2. Cruise tracks covered whilst searching: all survey ships and aircraft.

Table 2. Numbers of schools detected on effort within the truncation distance from the tracker and primary platforms, and duplicates (definite plus likely) for each shipboard survey block. Data for sea state 0–2 only for *P. phocoena* and for sea state 0–4 for other species

Species	Platform	Block									Total
		A	B	C	D	E	F	G	H	I	
<i>P. phocoena</i>	Tracker	46	0	101	65	53	143	92	6	113	619
	Primary	32	0	113	92	32	104	119	10	154	656
	Duplicates	6	0	32	19	5	17	18	2	19	118
<i>B. acutorostrata</i>	Tracker	9	0	13	21	4	16	9	0	1	73
	Primary	12	0	26	50	12	21	11	0	1	133
	Duplicates	6	0	8	12	0	6	3	0	1	36
<i>L. albirostris</i>	Tracker	0	0	15	8	2	17	19	0	0	61
	Primary	0	0	28	13	1	19	30	0	0	91
	Duplicates	0	0	11	4	1	7	15	0	0	38
<i>Lagenorhynchus</i> spp.	Tracker	2	0	30	8	2	23	24	0	0	89
	Primary	2	0	45	16	1	19	39	0	0	122
	Duplicates	2	0	15	5	1	7	15	0	0	45

was estimated as 341 366 animals (CV = 0.14; 95% CI = 260 000–449 000) (Table 4). Mean school size estimates varied little in blocks surveyed by ship (1.42–1.65) but were more variable in aerial survey blocks

(1.13–1.62). Estimated density was highest (0.6–0.8 animals km⁻²) in blocks F, I, J, L and Y, intermediate (0.3–0.5) in blocks C, D, E, G and M and lowest (0–0.2) in blocks A, B, H and X.

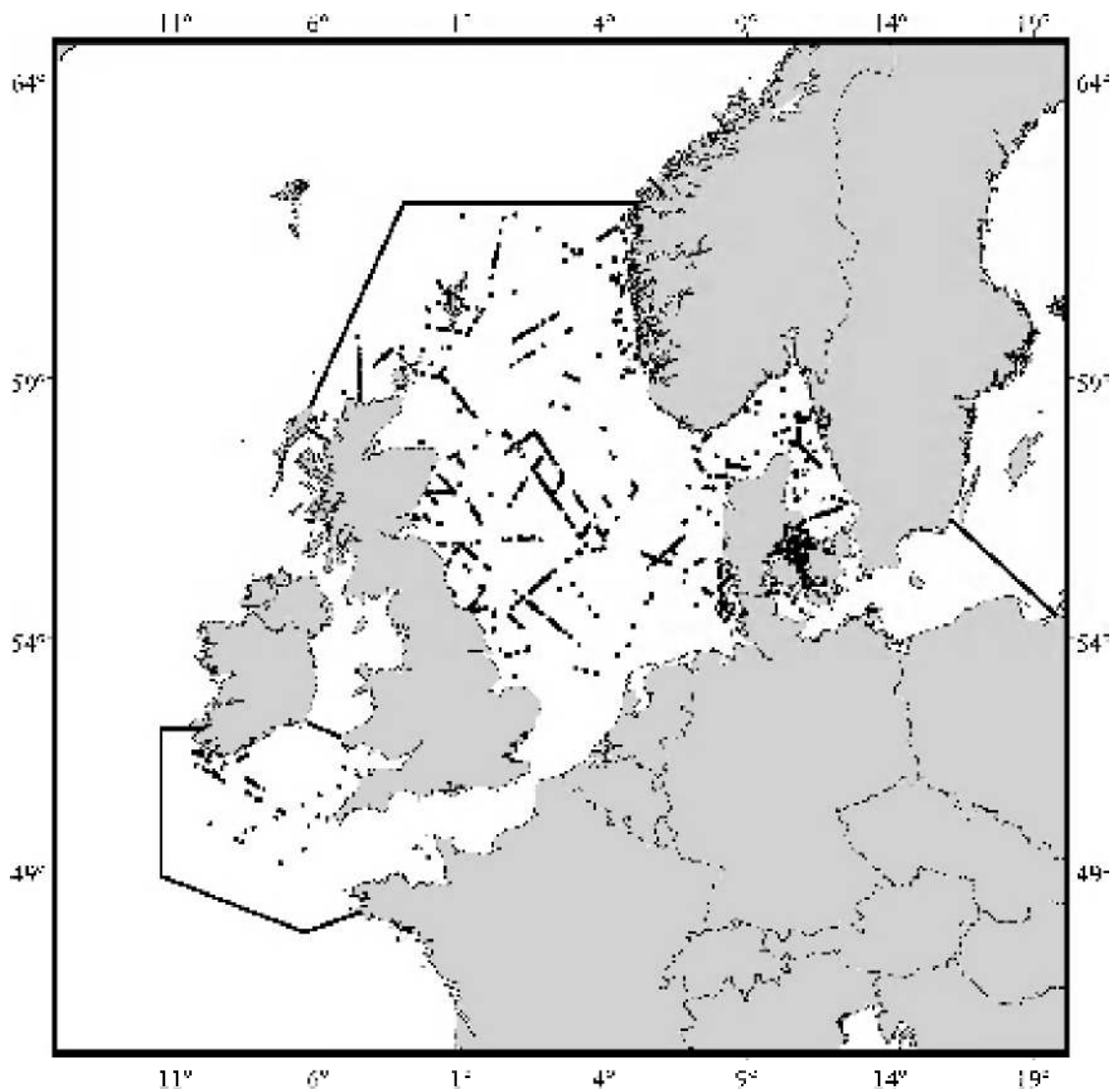


Fig. 3. Sightings of *Phocoena phocoena* made on effort during shipboard and aerial survey.

Abundance of *L. albirostris*, based on confirmed sightings of this species, was estimated as 7856 animals (CV = 0.30; 95% CI = 4000–13 300) (Table 5). Mean school size ranged from 3.4 to 4.5. The estimated number of *L. albirostris* plus *L. acutus* (including unidentified *Lagenorhynchus* spp.) was 11 760 (CV = 0.26; 95% CI 5900–18 900). Mean school size ranged from 3.7 to 9.5. Estimated density was highest (0.05–0.09 animals km⁻²) along the coast of Britain (block C).

Abundance of *B. acutorostrata* was estimated as 8445 animals (CV = 0.24; 95% CI = 5000–13 500) (Table 6). Mean school size ranged from 1.0 to 1.33. Estimated density was highest (0.025–0.03 animals km⁻²) in the north and along the coast of Britain (blocks C and D) and lower (around 0.01) in other areas of the central and northern North Sea (blocks E, F and G).

There were insufficient data to estimate abundance of *D. delphis* using the methods described above, but an estimate was made for block A using standard line transect methods; that is, with correction neither for animals missed on the transect line nor for responsive

Table 3. Sightings used in aerial abundance estimation for *P. phocoena*. Numbers of schools detected on effort from the leading and trailing aircraft under tandem effort and on single aircraft effort are shown for each survey block

Block	Number of sightings of <i>P. phocoena</i>		
	Tandem aircraft		Single aircraft
	Leading	Trailing	
I'	71	75	20
J	–	–	32
K	–	–	3
L	23	22	–
M	–	–	45
X	5	1	5
Y	31	21	–
Total	130	119	105

movement. The estimates were: school abundance 6986 (CV = 0.62; 95% CI 2100–23 300), mean school size 10.8 (CV = 0.25) and animal abundance 75 450 (CV = 0.67; 95% CI 23 000–249 000).

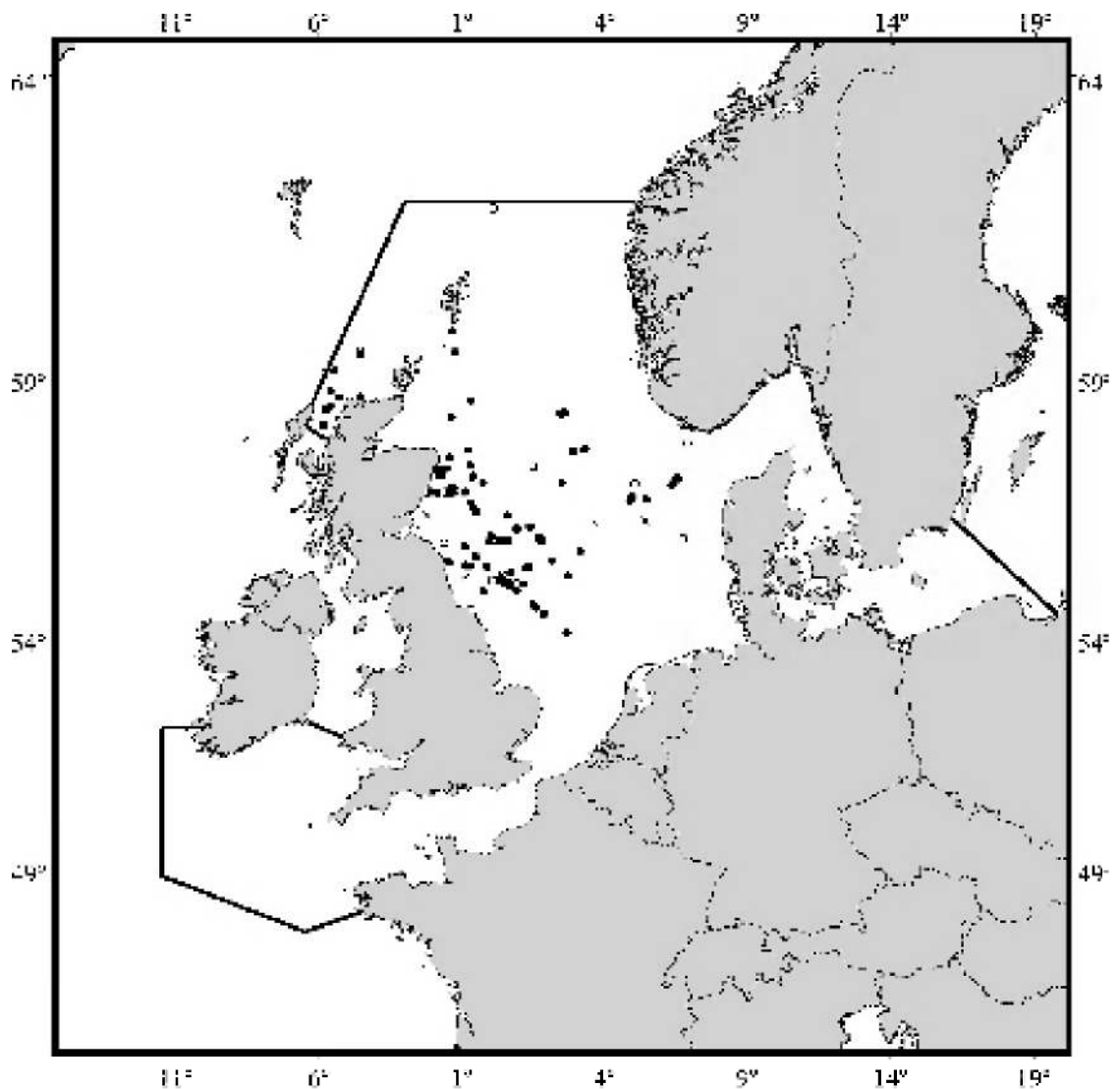


Fig. 4. Sightings of unidentified *Lagenorhynchus* spp. (open circles), *L. albirostris* (filled circles) and *L. acutus* (crosses) made on effort during shipboard and aerial survey.

Discussion

ABUNDANCE ESTIMATES

Bjørge & Øien (1995) presented estimates of *P. phocoena* abundance for the Norwegian and Barents Seas north of 66°N of 11 000 and for the northern North Sea of 82 600 in 1989. The latter estimate compares to an approximate equivalent of 190 000 (blocks D, E, F, J and M; Fig. 1) from our surveys. There are a number of possible reasons for the difference in these North Sea estimates. An important one is that Bjørge & Øien (1995) took no account of schools missed on the transect line and their estimate will be biased downwards because of this. In addition, because the data available to Bjørge & Øien (1995) were from a survey targeted at *B. acutorostrata* it is possible that the searching protocols used led to some undercounting of *P. phocoena*. In particular, surveying for whales typically continues in higher sea states than for *P. phocoena* and detection rates for the latter decline rapidly at sea states greater

than Beaufort 2 (see above). The distribution of *P. phocoena* extends beyond the area surveyed by Bjørge & Øien (1995), so another possible reason for the difference is interannual variability in abundance resulting from variation in prey distribution from year to year.

Schweder *et al.* (1997) presented estimates of *B. acutorostrata* abundance in the north-eastern Atlantic. Of particular interest are the estimates for the northern North Sea, which are 5400 for 1988–89 and 20 300 for 1995, compared with our estimate of 7200 (blocks C–G; Fig. 1) for 1994. Different analytical methods were used to calculate these estimates but this considerable interannual variability is present even though all these estimates take account of animals missed on the transect line. Most *B. acutorostrata* are distributed north of this area during the summer (Schweder *et al.* 1997) and interannual variability in prey availability may be an important contributing factor to the wide variation in abundance estimates, at the southern edge of the species' range.

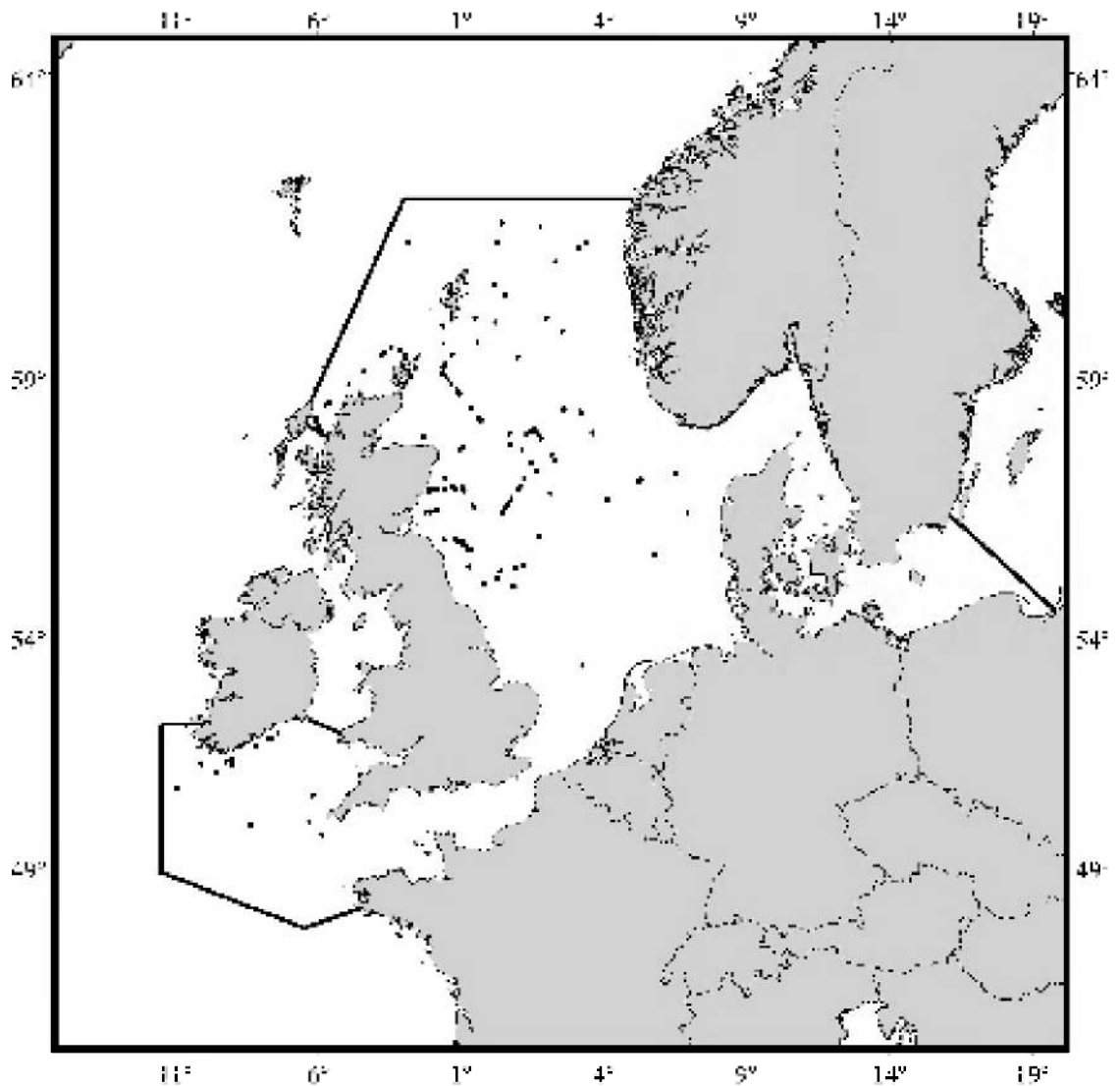


Fig. 5. Sightings of *B. acutorostrata* made on effort during shipboard and aerial survey.

Northridge *et al.* (1997) examined the available data for *L. albirostris* in the North Sea and around the British Isles and concluded that the observed distribution suggested that these animals may form a separate population from those found further north and west. The summer distribution comprised the survey area covered by SCANS (Fig. 1) and the shelf waters to the west of Scotland. Our estimate can therefore be viewed as a first estimate of the size of this putative population, albeit biased downwards through not including animals west of Scotland. It is also biased downwards because many of the unidentified *Lagenorhynchus* sightings are likely to have been of *L. albirostris*.

METHODOLOGICAL CONSIDERATIONS

The two central assumptions of conventional line transect theory that are most likely to be violated when surveying small cetaceans are that all animals on the transect line are detected and that animals remain

stationary or move little before they are detected. Another important factor is that detection probabilities may be influenced by factors other than perpendicular distance. The new methods developed as part of project SCANS and used to estimate abundance here (Borchers *et al.* 1998; Hiby & Lovell 1998) were designed to improve significantly previously available methods of data collection and analysis. The methods were successfully implemented and we believe they do constitute an improvement to cetacean survey methodology.

Data collection

Measuring distance at sea remains difficult but is a critical determinant of accurate data for line transect sampling, including the determination of duplicates (see below). Recent developments in the use of photographic and video images for distance measurement (Gordon 2001) may help to improve shipboard survey data in the future.

Table 4. Estimates of school abundance, mean school size, animal abundance and animal density for *P. phocoena*. Figures in square brackets are 95% CIs calculated using the log-based method of Burnham *et al.* (1987) rounded to the nearest thousand. CVs for animal density are the same as for animal abundance. Aerial subtotal and grand total do not include block I', which was a subset of block I

Block	School abundance (CV)	Mean school size (CV)	Animal abundance (CV)	Animal density (animals km ⁻²)
A	22 050 (0.58)	1.64 (0.09)	36 280 (0.57)	0.180
B	0	–	0	–
C	10 255 (0.19)	1.65 (0.07)	16 939 (0.18)	0.387
D	26 154 (0.27)	1.42 (0.07)	37 144 (0.25)	0.363
E	20 658 (0.54)	1.52 (0.24)	31 419 (0.49)	0.288
F	63 542 (0.26)	1.46 (0.04)	92 340 (0.25)	0.776
G	26 685 (0.36)	1.45 (0.10)	38 616 (0.34)	0.340
H	2 850 (0.35)	1.48 (0.14)	4 211 (0.29)	0.095
I	24 677 (0.35)	1.46 (0.06)	36 046 (0.34)	0.725
Shipboard subtotal	196 898 (0.17)	1.49 (0.04)	292 995 (0.16)	
I'	4 385 (0.25)	1.20 (0.03)	5 262 (0.25)	0.644
J	21 535 (0.33)	1.13 (0.08)	24 335 (0.34)	0.784
L	7 327 (0.46)	1.62 (0.08)	11 870 (0.47)	0.635
M	4 497 (0.26)	1.26 (0.08)	5 666 (0.27)	0.449
X	392 (0.46)	1.50 (0.15)	588 (0.48)	0.101
Y	4 077 (0.26)	1.45 (0.10)	5 912 (0.27)	0.812
Aerial subtotal	37 828 (0.21)		48 371 (0.30)	
Grand total	234 726 (0.13) [182 000–303 000]		341 366 (0.14) [260 000–449 000]	

Table 5. Estimates of school abundance, mean school size, animal abundance and animal density for *L. albirostris* and *Lagenorhynchus* spp. Figures in square brackets are 95% CIs calculated from bootstrap percentiles, rounded to the nearest hundred. CVs for animal density are the same as for animal abundance

Block	School abundance (CV)	Mean school size (CV)	Animal abundance (CV)	Animal density (animals km ⁻²)
<i>L. albirostris</i>				
A	0	–	0	0.0
B	0	–	0	0.0
C	526 (0.56)	4.47 (0.22)	2351 (0.52)	0.0538
D	341 (0.43)	3.40 (0.31)	1157 (0.56)	0.0113
E	29 (1.09)	4.00 (–)	115 (1.09)	0.0011
F	505 (0.36)	3.67 (0.12)	1790 (0.42)	0.0150
G	679 (0.49)	3.56 (0.08)	2443 (0.54)	0.0215
H	0	–	0	0.0
I	0	–	0	0.0
Total	2080 (0.26) [1200–3200]	3.78 (0.12)	7856 (0.30) [4000–13 300]	
<i>Lagenorhynchus</i> spp.				
A	88 (1.02)	9.50 (0.26)	833 (1.02)	0.0041
B	0	–	0	0.0
C	836 (0.51)	4.86 (0.16)	4063 (0.50)	0.0929
D	420 (0.44)	3.73 (0.24)	1569 (0.51)	0.0153
E	29 (1.03)	4.00 (–)	116 (1.03)	0.0011
F	494 (0.39)	3.92 (0.14)	1937 (0.36)	0.0163
G	880 (0.46)	3.68 (0.08)	3242 (0.47)	0.0285
H	0	–	0	0.0
I	0	–	0	0.0
Total	2747 (0.23) [1700–4100]	4.28 (0.11)	11 760 (0.26) [5900–18 500]	

Responsive movement

In earlier simple analyses of the data, Hammond *et al.* (1995) showed substantial attraction of *L. albirostris* to ships. For *P. phocoena* and *B. acutorostrata*, the

evidence was equivocal and the extent and direction of responsive movement remains uncertain for both species.

It is important to note that the estimation methods were designed to correct for responsive movement,

Table 6. Estimates of school abundance, mean school size, animal abundance and animal density for *B. acutorostrata*. Figures in square brackets are 95% CIs calculated from bootstrap percentiles, rounded to the nearest hundred. CVs for animal density are the same as for animal abundance

Block	School abundance (CV)	Mean school size (CV)	Animal abundance (CV)	Animal density (animals km ⁻²)
A	1195 (0.49)	1.00 (0.005)	1195 (0.49)	0.0059
B	0	–	0	0.0
C	1032 (0.40)	1.04 (0.03)	1073 (0.42)	0.0245
D	2920 (0.41)	1.00 (0.01)	2920 (0.40)	0.0286
E	787 (0.35)	1.08 (0.08)	853 (0.37)	0.0078
F	1354 (0.36)	1.00 (0.01)	1354 (0.36)	0.0114
G	751 (0.62)	1.33 (0.14)	1001 (0.70)	0.0088
H	0	–	0	0.0
I	49 (0.87)	1.00 (–)	49 (0.87)	0.0010
Total	8088 (0.23) [5000–12 700]	1.04 (0.03)	8445 (0.24) [5000–13 500]	

Table 7. Numbers and percentages of duplicate sightings (D = definite; L = likely; P = possible) within the truncation distance and abundance estimates for combinations of duplicate classes. Data for sea state 0–2 only for *P. phocoena* and for sea state 0–4 for other species

Species	Duplicate class	Number recorded	Percentage of total	Abundance estimate	% Difference from D + L
<i>P. phocoena</i>	D	99	73	366 000	+25
	D + L	118	86	293 000	0
	D + L + P	136	100	242 000	–17
<i>B. acutorostrata</i>	D	28	70	11 000	+13
	D + L	36	90	8 000	0
	D + L + P	40	100	7 000	–16
<i>L. albirostris</i>	D	37	95	8 000	+1
	D + L	38	98	8 000	0
	D + L + P	39	100	8 000	–4
<i>Lagenorhynchus</i> spp.	D	43	93	12 000	+1
	D + L	45	97	12 000	0
	D + L + P	46	100	12 000	–2

and the presence of attraction to or avoidance of the vessel should not have caused a bias in our results. However, if responsive movement routinely occurred before schools were detected by the tracker team, bias as a result of responsive movement is possible. Methods that use the orientation of animals at first sighting to account more fully for responsive movement have recently been published (Palka & Hammond 2001).

Sensitivity of the estimates to duplicate classification

The data collection protocols were designed to minimize the uncertainty of duplicate identification in the field as well as allowing post-survey identification of duplicates. Sensitivity of estimates of total abundance to variation in the classification of duplicate sightings is shown in Table 7. In the case of *P. phocoena*, and to a lesser extent *B. acutorostrata*, uncertainty in duplicate identification appears to contribute substantially to the overall uncertainty in shipboard abundance estimation. This is an area that would benefit from further methodological development, and will be important to address when ASCOBANS has in place a management procedure that incorporates uncertainty explicitly.

CONSERVATION AND MANAGEMENT APPLICATIONS

The abundance estimates presented here have been used by the IWC Scientific Committee to assess the status of *P. phocoena* 'stocks' in the North Atlantic (IWC 1996). In considering estimates of the level of bycatch in fishing gear as part of that assessment, the Committee agreed that 'a figure of 1% of estimated abundance represented a reasonable and precautionary level beyond which to be concerned about the sustainability of anthropogenic removals' (IWC 1996).

Concern about bycatch in fisheries and other anthropogenic threats to small cetaceans in northern European seas led to the establishment of ASCOBANS. Obtaining abundance estimates was identified as one of the first priorities to allow for the assessment of the conservation status of small cetaceans present in the ASCOBANS area. Moreover, the conservation objective that 'Populations should be kept at or restored to 80% of their carrying capacity' has been established (ASCOBANS 1997). The abundance estimates presented here will assist in conducting the assessments required by the conservation objectives.

In recent years, levels of *P. phocoena* bycatch in bottom set gillnet fisheries have been estimated in the Celtic Sea (Tregenza *et al.* 1997), the North Sea (Northridge & Hammond 1999; Vinther 1999) and the Skagerrak Sea (Carlström & Berggren 1996; Harwood *et al.* 1999). Using the 1% criterion agreed by the IWC, bycatches estimated in all these areas are considered to be unsustainable. Continued monitoring of abundance, bycatch rates and levels of fishing effort are necessary to enable further assessments of the impact of bycatch on *P. phocoena* populations in particular.

In summary, the results presented here fill one of the key information gaps hindering assessment of the impact of threats to small cetacean populations in the North Sea and adjacent waters. The main reason for undertaking this work was to provide the data on abundance to complete one of the essential first steps in the formulation of a conservation and management plan for small cetaceans in this area. In this primary aim, the work has been successful. Similarly, assessments of the impact of bycatch would not have been possible without the estimates of abundance calculated from this work. There now exist baseline estimates of abundance for the main species of cetacean in the North Sea and adjacent waters that will serve as a reference point for the future and upon which a framework for a management and monitoring programme can be founded.

TOWARDS DETERMINING STATUS

The surveys covered a large area, but there are significant parts of the range of *P. phocoena* in European waters that were not surveyed. One such area is the Baltic Sea, where *P. phocoena* used to be common (Skora, Pawliczka & Klinowska 1988; Berggren 1994; Berggren & Arrhenius 1995a) but is now scarce. Additional surveys were conducted in the Baltic Sea in 1995 that resulted in an abundance estimate of about 600 (CV = 0.57) animals in the southern Baltic Sea excluding Polish coastal waters (P. Berggren *et al.*, unpublished data). It is important that a future survey be conducted that covers the entire known range of *P. phocoena* in the Baltic Sea to allow for a complete assessment of the species in this area.

Another important area encompasses the waters to the west and north of the British Isles where *P. phocoena* are known to be abundant (Leopold, Wolf & van der Meer 1992; Pollock *et al.* 1997; Weir *et al.* 2001; Skov *et al.* 2002; Reid *et al.*, in press). It is important that these areas are surveyed so that a more complete picture of *P. phocoena* abundance in European waters can emerge.

Our results provide baseline estimates of abundance but tell us nothing about whether or not any of the species are increasing, decreasing or are stable in numbers. There are a number of ways to determine this status. Recent analytical developments (Bravington 2000) for data collected from so-called platforms of opportunity (Northridge *et al.* 1995) may allow useful information on temporal and spatial changes in relative abundance

to be gleaned in some areas. The SCANS survey was intended to provide the first of a series of absolute abundance estimates. The interval between such surveys depends on a number of factors both scientific and political, but the interval should probably not exceed 10 years. Future dedicated surveys will eventually provide data for the estimation of a long-term rate of population change.

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References

- ASCOBANS (1997) *Report of the Second Meeting of Parties to ASCOBANS, 17–19 November 1997*. ASCOBANS Secretariat, Bonn, Germany.
- Barlow, J. (1988) Harbour porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon and Washington. I. Ship surveys. *Fishery Bulletin (US)*, **86**, 417–432.
- Barlow, J., Oliver, C.W., Jackson, T.D. & Taylor, B.L. (1988) Harbour porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon and Washington. II. Aerial surveys. *Fishery Bulletin (US)*, **86**, 433–444.
- Berggren, P. (1994) Bycatches of the harbour porpoise (*Phocoena phocoena*) in the Swedish Skagerrak, Kattegat and Baltic Seas 1973–1993. *Reports of the International Whaling Commission, Special Issue*, **15**, 211–215.
- Berggren, P. & Arrhenius, F. (1995a) Sightings of harbour porpoises (*Phocoena phocoena*) in Swedish waters before 1990. *Reports of the International Whaling Commission, Special Issue*, **16**, 99–107.
- Berggren, P. & Arrhenius, F. (1995b) Densities and seasonal distribution of harbour porpoises (*Phocoena phocoena*) in the Swedish Skagerrak, Kattegat and Baltic Seas. *Reports of the International Whaling Commission, Special Issue*, **16**, 109–121.
- Berggren, P., Ishaq, R., Zebühr, Y., Näf, C., Bandh, C. & Broman, D. (1999) Patterns and levels of organochlorine contaminants (DDTs, PCBs, non-ortho PCBs and PCDD/Fs) in male harbour porpoises (*Phocoena phocoena*) from the Baltic Sea, the Kattegat–Skagerrak Seas and the West Coast of Norway. *Marine Pollution Bulletin*, **12**, 1070–1084.
- Bjørge, A. & Øien, N. (1995) Distribution and abundance of harbour porpoise, *Phocoena phocoena*, in Norwegian waters. *Reports of the International Whaling Commission, Special Issue*, **16**, 89–98.
- Borchers, D.L., Buckland, S.T., Goedhart, P.W., Clarke, E.D. & Hedley, S.L. (1998) Horvitz–Thompson estimators for double-platform line transect surveys. *Biometrics*, **54**, 1221–1237.

- Bravington, M.V. (2000) *Covariate Models for Continuous-Time Sightings Data*. Document SC/52/RMP14. Scientific Committee of the International Whaling Commission, Cambridge, UK.
- Buckland, S.T. (1985) Perpendicular distance models for line transect sampling. *Biometrics*, **41**, 177–195.
- Buckland, S.T. & Turnock, B.J. (1992) A robust line transect method. *Biometrics*, **48**, 901–909.
- Buckland, S.T., Anderson, D.R., Burnham, K.P. & Laake, J.L. (1993) *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman & Hall, London, UK.
- Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. & Pollock, K.H. (1987) *Design and analysis methods for fish survival experiments based on release–recapture*. American Fisheries Society Monograph 5, Bethesda, Maryland, USA.
- Camphuysen, C.J. & Leopold, M.F. (1993) The harbour porpoise *Phocoena phocoena* in the southern North Sea, particularly the Dutch sector. *Lutra*, **36**, 1–24.
- Carlström, C. & Berggren, P. (1996) *Bycatch Estimates of Harbour Porpoises (Phocoena phocoena) in the Swedish Skagerrak Sea Obtained from Independent Observer Data*. Document SC/48/SM25. The Scientific Committee of the International Whaling Commission, Cambridge, UK.
- Clausen, B. & Andersen, S. (1988) Evaluation of bycatch and health status of the harbour porpoise (*Phocoena phocoena*) in Danish waters. *Danish Review of Game Biology*, **13**, 1–20.
- Collet, A., Gourvenec, A., Firmin, V. & Le Boulanger, F. (1994) *Harbour Porpoises and other Small Cetaceans off the French Channel coasts*. Internal Report. Centre de Recherche sur les Mammifères Marins, Musée Océanographique, La Rochelle, France.
- Evans, P.G.H. (1990) *Harbour Porpoises (Phocoena phocoena) in British and Irish Waters*. Document SC/42/SM49. The Scientific Committee of the International Whaling Commission, Cambridge, UK.
- Evans, P.G.H., Canwell, P.J. & Lewis, E.J. (1992) An experimental study of the effects of pleasure craft noise upon bottlenosed dolphins in Cardigan Bay, West Wales. *European Research on Cetaceans*, **6**, 43–46.
- Evans, P.G.H., Harding, S., Tyler, G. & Hall, S. (1986) *Analysis of Cetacean Sightings in the British Isles, 1958–1985*. Nature Conservancy Council, Peterborough, UK.
- Gordon, J. (2001) Measuring the range to animals at sea from boats using photographic and video images. *Journal of Applied Ecology*, **38**, 879–887.
- Hammond, P.S., Benke, H., Berggren, P., Borchers, D.L., Buckland, S.T., Collet, A., Heide-Jørgensen, M.P., Heimlich-Boran, S., Hiby, A.R., Leopold, M.F. & Oien, N. (1995) *Distribution and Abundance of the Harbour Porpoise and other Small Cetaceans in the North Sea and Adjacent Waters*. Final Report under European Commission, Project LIFE 92-2/UK/027. Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews, Fife, UK.
- Hansen, M.M. & Hurwitz, W.N. (1943) On the theory of sampling from finite populations. *Annals of Mathematical Statistics*, **14**, 333–362.
- Harwood, J., Andersen, L.W., Berggren, P., Carlström, J., Kinze, C.C., Mcglade, J., Metzuzals, K., Larsen, F., Lockyer, C.H., Northridge, S., Rogan, E., Walton, M. & Vinther, M. (1999) *Assessment and Reduction of the Bycatch of Small Cetaceans (BY-CARE)*. Final Report under European Commission, Project FAIR-CT05-0523. Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews, Fife, UK.
- Heide-Jørgensen, M.P., Mosbech, A., Teilmann, J., Benke, H. & Schulz, W. (1992) Harbour porpoise (*Phocoena phocoena*) densities obtained from aerial surveys north of Fyn and in the Bay of Kiel. *Ophelia*, **35**, 133–146.
- Heide-Jørgensen, M.P., 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. *Helgoländer Meeresuntersuchungen*, **47**, 335–346.
- Hiby, A.R. & Hammond, P.S. (1989) Survey techniques for estimating the abundance of cetaceans. *Reports of the International Whaling Commission, Special Issue*, **11**, 47–80.
- Hiby, L. & Lovell, P. (1998) Using aircraft in tandem formation to estimate abundance of harbour porpoise. *Biometrics*, **54**, 1280–1289.
- IWC (1992) Report of the Scientific Committee. *Reports of the International Whaling Commission*, **42**, 210.
- IWC (1996) Report of the Scientific Committee. *Reports of the International Whaling Commission*, **46**, 160–171.
- Jepson, P.D., Bennett, P.M., Allchin, C.R., Law, R.J., Kuiken, T., Baker, J.R., Rogan, E. & Kirkwood, J.K. (1999) Investigating potential associations between chronic exposure to polychlorinated biphenyls and infectious disease mortality in harbour porpoises from England and Wales. *Science of the Total Environment*, **243/244**, 339–348.
- Kuiken, T., Hofle, U., Bennett, P.M., Allchin, C.R., Kirkwood, J.K., Baker, J.R., Appleby, E.C., Lockyer, C.H., Wotton, M.J. & Sheldrick, M.C. (1993) Adrenocortical hyperplasia, disease and chlorinated hydrocarbons in the harbour porpoise (*Phocoena phocoena*). *Marine Pollution Bulletin*, **26**, 440–446.
- Law, R.J. & Whinnett, J.A. (1992) Polycyclic aromatic hydrocarbons in muscle tissue of harbour porpoises (*Phocoena phocoena*) from UK waters. *Marine Pollution Bulletin*, **24**, 550–553.
- Law, R.J., Jones, B.R., Baker, J.R., Kennedy, S., Milne, R. & Morris, R.J. (1992) Trace metals in the livers of marine mammals from the Welsh coast and the Irish Sea. *Marine Pollution Bulletin*, **24**, 296–304.
- Leopold, M.F., Wolf, P.A. & van der Meer, J. (1992) The elusive harbour porpoise exposed: strip transect counts off southwestern Ireland. *Netherlands Journal of Sea Research*, **29**, 395–402.
- Lowry, N. & Teilmann, J. (1995) Bycatch and bycatch reduction of the harbour porpoise (*Phocoena phocoena*) in Danish waters. *Reports of the International Whaling Commission, Special Issue*, **15**, 203–209.
- Morris, R.J., Law, R.J., Allchin, C.R., Kelly, C.A. & Fileman, C.F. (1989) Metals and organochlorines in dolphins and porpoises in Cardigan Bay, West Wales. *Marine Pollution Bulletin*, **20**, 512–523.
- Northridge, S.P. & Hammond, P.S. (1999) *Estimation of Porpoise Mortality in UK Gill and Tangle Net Fisheries in the North Sea and west of Scotland*. Document SC/51/SM42. The Scientific Committee of the International Whaling Commission, Cambridge, UK.
- Northridge, S.P., Tasker, M.L., Webb, A., Camphuysen, K. & Leopold, M. (1997) White-beaked *Lagenorhynchus albirostris* and Atlantic white-sided dolphin *L. acutus* distributions in northwest European and US North Atlantic waters. *Reports of the International Whaling Commission*, **47**, 797–805.
- Northridge, S.P., Tasker, M.L., Webb, A. & Williams, J.M. (1995) Distribution and relative abundance of harbour porpoises (*Phocoena phocoena*, L.), whitebeaked dolphins (*Lagenorhynchus albirostris*, Gray) and minke whales (*Balaenoptera acutorostrata*, Lacepede) around the British Isles. *ICES Journal of Marine Science*, **52**, 55–66.
- Palka, D. (1995a) Abundance estimate of the Gulf of Maine harbor porpoise. *Reports of the International Whaling Commission, Special Issue*, **16**, 27–50.
- Palka, D. (1995b) Influences on spatial patterns of Gulf of Maine harbor porpoises. *Whales, Seals, Fish and Man* (eds A.S. Blix, L. Walløe & Ø. Ulltang), pp. 69–75.

- Developments in Marine Biology No. 4. Elsevier Science BV, Amsterdam, the Netherlands.
- Palka, D.L. & Hammond, P.S. (2001) Accounting for responsive movement in line transect estimates of abundance. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 777–787.
- Pollock, C.M., Reid, J.B., Webb, A. & Tasker, M.L. (1997) *The Distribution of Seabirds and Cetaceans in the Waters around Ireland*. JNCC Report No. 267. Joint Nature Conservation Committee, Peterborough, UK.
- Reid, J.B., Evans, P.G.H. & Northridge, S.P. (in press) *Atlas of Cetacean Distribution in Northwest European Waters*. Joint Nature Conservation Committee, Peterborough, UK, in press.
- Schweder, T., Skaug, H.J., Dimakos, X.K., Langaas, M. & Oien, N. (1997) Abundance of northeastern Atlantic minke whales, estimates for 1989 and 1995. *Reports of the International Whaling Commission*, **47**, 453–483.
- Simmonds, M.P. (1992) Cetacean mass mortalities and their potential relationship with pollution. *Whales: Biology, Threats and Conservation* (ed. J.J. Symoens), pp. 217–245. Royal Academy of Overseas Sciences, Brussels, Belgium.
- Skora, K.E., Pawliczka, I. & Klinowska, M. (1988) Observations of the harbour porpoise (*Phocoena phocoena*) on the Polish Baltic coast. *Aquatic Mammals*, **14**, 113–119.
- Skov, H., Upton, A.J., Reid, J.B., Webb, A., Taylor, S.J. & Durinck, J. (2002) *Dispersion and Vulnerability of Marine Birds and Cetaceans in Faroese Waters*. Joint Nature Conservation Committee, Peterborough, UK, 106pp.
- Smeenk, C. (1987) The harbour porpoise *Phocoena phocoena* (L., 1758) in the Netherlands: stranding records and decline. *Lutra*, **30**, 77–90.
- Trezenza, N.J.C., Berrow, S.D., Hammond, P.S. & Leaper, R. (1997) Harbour porpoise (*Phocoena phocoena* L.) by-catch in set gillnets in the Celtic Sea. *ICES Journal of Marine Science*, **54**, 896–904.
- Verwey, J. & Wolff, W.J. (1983) The common or harbour porpoise (*Phocoena phocoena*). *Ecology of the Wadden Sea, Vol. 2, Part 7: Marine Mammals*. (ed. W.J. Wolff), pp. 51–58. A.A. Balkema, Rotterdam, the Netherlands.
- Vinther, M. (1999) Bycatches of harbour porpoises *Phocoena phocoena* (L.) in Danish set-net fisheries. *Journal of Cetacean Research and Management*, **1**, 123–135.
- Weir, C.R., Pollock, C., Cronin, C. & Taylor, S. (2001) Cetaceans of the Atlantic Frontier, north and west of Scotland. *Continental Shelf Research*, **21**, 1047–1071.
- Westgate, A., Read, A., Berggren, P., Koopman, H. & Gaskin, D. (1995) Diving behaviour of harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 1064–1073.

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