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Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management



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ABSTRACT

The European Union (EU) Habitats Directive requires Member States to monitor and maintain at favourable conservation status those species identified to be in need of protection, including all cetaceans. In July 2005 we surveyed the entire EU Atlantic continental shelf to generate robust estimates of abundance for harbour porpoise and other cetacean species. The survey used line transect sampling methods and purpose built data collection equipment designed to minimise bias in estimates of abundance. Shipboard transects covered 19,725 km in sea conditions ≤Beaufort 4 in an area of 1,005,743 km². Aerial transects covered 15,802 km in good/moderate conditions (≤Beaufort 3) in an area of 364,371 km². Thirteen cetacean species were recorded; abundance was estimated for harbour porpoise (375,358; CV = 0.197), bottlenose dolphin (16,485; CV = 0.422), white-beaked dolphin (16,536; CV = 0.303), short-beaked common dolphin (56,221; CV = 0.234) and minke whale (18,958; CV = 0.347). Abundance in 2005 was similar to

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Harbour porpoise Bottlenose dolphin Common dolphin White-beaked dolphin Minke whale Bycatch Habitats Directive that estimated in July 1994 for harbour porpoise, white-beaked dolphin and minke whale in a comparable area. However, model-based density surfaces showed a marked difference in harbour porpoise distribution between 1994 and 2005. Our results allow EU Member States to discharge their responsibilities under the Habitats Directive and inform other international organisations concerning the assessment of conservation status of cetaceans and the impact of bycatch at a large spatial scale. The lack of evidence for a change in harbour porpoise abundance in EU waters as a whole does not exclude the possibility of an impact of bycatch in some areas. Monitoring bycatch and estimation of abundance continue to be essential.

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1. Introduction

Cetacean populations are affected globally by a range of human activities, including the direct impacts of hunting, bycatch in fishing gear and ship-strikes, and the indirect impacts of habitat destruction by fishing or construction, chemical and noise pollution, the overexploitation of prey resources and the effects of warming oceans (Harwood, 2001). The need to understand the severity of these impacts and to take action to mitigate them if necessary is widely recognised in the national legislation of many countries and in a number of international organisations: European Union, International Council for the Exploration of the Sea (http://www.ices.dk/), International Whaling Commission (http://www.iwcoffice.org/), Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR) (http://www.ospar.org/) and United Nations Environment Programme Convention on Migratory Species (http://www.cms.int/). Together with information on human activities and their effects, knowledge of species abundance and distribution is fundamental to understanding the extent to which cetacean populations are impacted by a particular threat.

Bycatch is the main direct threat to small cetaceans in European Atlantic waters (Read et al., 2006). The species most affected are the harbour porpoise, *Phocoena phocoena*, in bottom set gill and tangle net fisheries primarily in the North, Baltic and Celtic Seas and the short-beaked common dolphin, *Delphinus delphis*, in pelagic trawl and set net fisheries in the Channel, Celtic Sea and Bay of Biscay. In the early 1990s, an estimated 2200 harbour porpoise were taken annually by English and Irish hake fisheries in the Celtic Sea (Tregenza et al., 1997) and an estimated 6–7000 were bycaught annually in Danish gillnet fisheries in the central and southern North Sea (Vinther and Larsen, 2004).

In response to concerns about the impact of this bycatch, the European Commission supported a cetacean survey in 1994 (known as SCANS), which estimated for the first time the abundance of harbour porpoise, white-beaked dolphin (*Lagenorhynchus albirostris*), and minke whale (*Balaenoptera acutorostrata*) in the North Sea and Celtic Sea (Hammond et al., 2002). Results showed that, in some areas at least, bycatch of harbour porpoise was likely to be unsustainable.

Gill and tangle net fishing effort in monitored fisheries in the North Sea declined during the late 1990s/early 2000s and resulting estimates of harbour porpoise bycatch also declined (Northridge et al., 2003; Vinther and Larsen, 2004). In 2004, the European Council issued regulations 812/2004 and 814/2004, which made mandatory the monitoring of bycatch by observers in selected fleets and the use of acoustic devices ("pingers") to reduce bycatch by vessels greater than 15 m and 12 m in length, respectively. More recent developments in harbour porpoise bycatch are discussed below.

By comparison, common dolphin bycatch and abundance has received relatively little attention. Large numbers were taken in the drift net fishery for albacore tuna in the 1990s but this fishery has now ceased (Rogan and Mackey, 2007). Annual bycatch in the UK trawl fishery in the Channel in 2000–2006 has been estimated at around 150 dolphins and in UK gill and tangle net fisheries in the Celtic Sea in 2005–2008 at between 100 and 600 dolphins (ICES,

2009a). Bycatch has also been recorded in pair trawls operating in the Bay of Biscay (Fernández-Contreras et al., 2010). Current total annual bycatch of common dolphin in the NE Atlantic is unknown but likely to be at least 1000 animals (IWC, 2010).

The European Union Habitats Directive requires Member States to take action to maintain or restore, at favourable conservation status, natural habitats and species of wild fauna and flora specified as being in need of strict protection (Council Directive 92/43/EEC). Member States are also required to undertake surveillance of these habitats and species and to report every 6 years on whether their conservation status is favourable and on the implementation of measures taken to ensure this.

All species of cetacean are designated as being in need of protection. Conservation status is defined in the Habitats Directive as "the sum of the influences acting on the species that may affect the long-term distribution and abundance of its populations." It is considered favourable if the species is maintaining itself as a viable component of its natural habitats and if abundance and range are maintained. For EU Member States to discharge their responsibilities regarding cetaceans requires, at minimum, information on distribution and abundance to assess the impact of bycatch and allow safe limits to be determined, and to assess conservation status.

To meet this need, the European Commission and its Member States supported a cetacean survey in 2005 (known as SCANS-II) to estimate the abundance of cetacean species, particularly harbour porpoise and common dolphin, in all EU Atlantic continental shelf waters. Eleven years after the first SCANS survey, the SCANS-II survey provided an opportunity to follow up on the recommendations in Hammond et al. (2002), and to investigate any changes that may have occurred in the intervening decade. Here we present estimates of abundance and distribution from the SCANS-II survey and discuss the results in the context of informing conservation and management needs with robust science.

2. Methods

2.1. Study area and survey design

The study area was defined as all continental shelf waters (within the 200 m isobath) of the European Atlantic between 36°N and 62°N, including waters off Belgium, Denmark, France, Germany, Ireland, The Netherlands, Norway, Poland, Portugal, Spain, Sweden and the UK. The main survey area was divided into 17 blocks chosen primarily for logistical reasons, and surveyed by seven ships (29 June–28 July 2005) and three aircraft (27 June–4 August 2005) (Fig. 1). Transects were placed to provide equal coverage probability within each block using methods developed by Strindberg and Buckland (2004). Transects searched are incorporated in figures showing the distribution of sightings (Figs. 2–6).

2.2. Data collection

2.2.1. Shipboard survey

The method used was a double platform line transect survey with two teams of observers on each ship to generate abundance

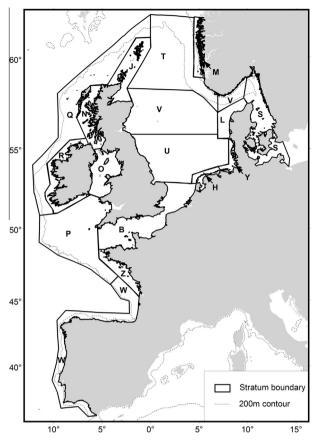


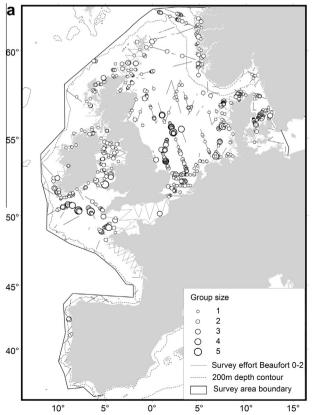
Fig. 1. Survey blocks defined for the SCANS-II surveys. Blocks P, Q, S, T, U, V, and W were surveyed by ship. Blocks B, H, J, L, M, N, O, R and Z were surveyed by aircraft. See Table 1 for details.

estimates that were corrected for animals missed on the transect line and also for the effects of movement of animals in response to the ship (Laake and Borchers, 2004); this approach had also been used on the 1994 SCANS surveys (Hammond et al., 2002).

The survey ships included scientific research vessels and commercial vessels capable of accommodating a team of eight scientists and the observation platforms (see below). The heights of the primary observation platforms ranged from $5.4 \, \text{m}$ to $7.8 \, \text{m}$. Target survey speed was $10 \, \text{knots} \, (18.5 \, \text{km} \, \text{h}^{-1})$ on all ships.

Two observers on one platform, known as Primary, searched with naked eye a sector from 90° (abeam) starboard to 10° port or 90° port to 10° starboard out to 500 m distance. Two observers on the other, higher platform, known as Tracker, searched from 500 m to the horizon with high-power "big eye" (25×100) binoculars (80° sector centred around the transect line) and 7×50 binoculars (120° sector). Animals outside the sector searched by Tracker should not have been able to enter the region searched by Primary. Tracker observers tracked detected animals until they were aft of the vessel. Observers not searching acted as duplicate identifier on Tracker, or data recorder on Primary, or rested. The duplicate identifier assessed whether or not groups of animals detected by Tracker were re-sighted by Primary. Duplicates were classified as Definite (D: at least 90% likely), Probable (P: between 50% and 90% likely), or Remote (R: less than 50% likely). The data recorder recorded all sightings, effort and environmental data into a laptop computer running the LOGGER software, modified specifically for the survey (Gillespie et al., 2010). Environmental data included Beaufort scale, swell height and direction, glare, visibility and sightability, a subjective measure of conditions for detecting small cetaceans.

Data on sighting angle and distance for calculation of perpendicular distance were collected automatically, where possible, as well as manually (Gillespie et al., 2010). Sighting angles were measured from an angle board and on Tracker also using a small



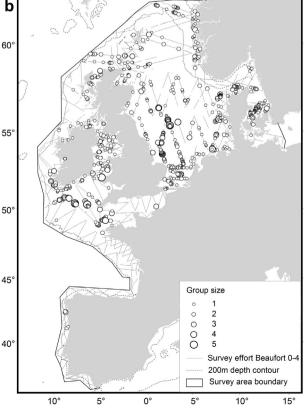


Fig. 2. Distribution of harbour porpoise sightings overlaid on transects searched: (a) sea conditions of Beaufort \leq 2; (b) sea conditions of Beaufort \leq 4.

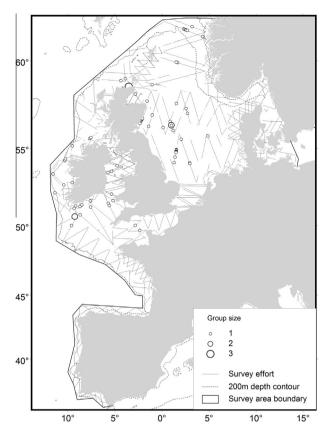


Fig. 3. Distribution of minke whale sightings overlaid on transects searched (sea conditions of Beaufort \leqslant 4).

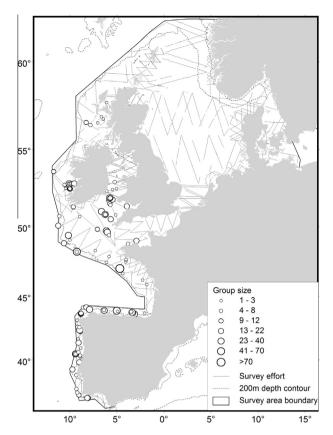


Fig. 5. Distribution of common dolphin sightings overlaid on transects searched (sea conditions of Beaufort $\leqslant\!4).$

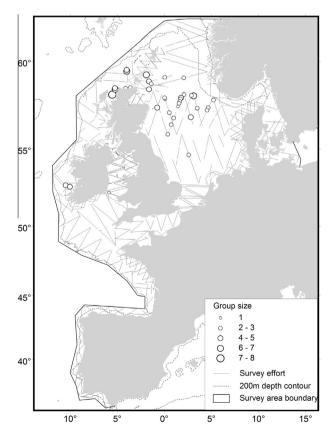


Fig. 4. Distribution of white-beaked dolphin sightings overlaid on transects searched (sea conditions of Beaufort \leq 4).

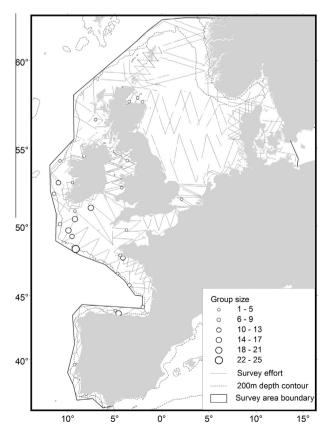


Fig. 6. Distribution of bottlenose dolphin sightings overlaid on transects searched (sea conditions of Beaufort \leqslant 4).

camera positioned on the underside of the binoculars that took snapshots of parallel lines on the deck (Leaper and Gordon, 2001). Distance to detected groups was measured on Primary using purpose-designed and calibrated measuring sticks and on Tracker as a binocular reticule reading and via a video-range technique (Gordon, 2001). Angles and distances were calculated from captured video frames using purpose-written software. Additional data collected from each detected group of animals included: cue, species composition, group size, swimming direction and behaviour. Data validation software was developed for checking all data at the end of each day. Data could also be recorded on pre-prepared paper data sheets in the event of data collection system failure. The effectiveness of the automatic data collection of distance and angle measurements and a comparison of estimated and measured values are described in Leaper et al. (2010).

2.2.2. Aerial survey

There were three scientific members of the crew in each aircraft, which flew at an altitude of 183 m and a speed of 90 knots (167 km h⁻¹). One acted as navigator and data recorder for environmental and sightings data, entered real-time into a laptop computer running purpose-written data collection software. Sighting conditions were classified as good, moderate or poor based primarily on sea conditions, water turbidity and glare. Conditions were typically good with Beaufort ≤ 2 or moderate with Beaufort ≤ 3 . The two observers sat at bubble windows on the right and left sides of the aircraft. The times when detected groups came abeam were given verbally over the intercom by the observers and recorded by the navigator. Other data recorded included declination angle to the detected animal or group (from which perpendicular distance was calculated), cue, presence of calves, behaviour, species composition and group size. Further details of field protocol are found in Gilles et al. (2009).

The problem of missing animals on the transect line is more acute for aerial surveys than for shipboard surveys because of the limited time that any animal is available for detection. However, responsive movement is not generally a problem. For the SCANS survey in 1994, the tandem aircraft method of Hiby and Lovell (1998) was used to collect data for analysis that accounted for animals missed on the transect line (Hammond et al., 2002). For the SCANS-II aerial survey, we employed the related circle-back or "racetrack" method of Hiby (1999) in which, on detecting a group of animals, a single aircraft circles back to resurvey a defined segment of transect. This method relies heavily on an adequate sample size of resurveyed segments; the "racetrack" procedure was therefore only implemented for harbour porpoise for which a large number of detections was expected. Further details are given in Scheidat et al. (2008). Exploratory analysis confirmed that the method continued to work well as local density increased, and that there was no evidence that detection probability was higher on the resurveyed (circle-back) segments of transect.

2.2.3. Pilot survey

A 2 week pilot survey was conducted in the Kattegat/Belt Seas 3 months prior to the main survey to test all field methodologies and equipment and to train all cruise leaders, who then trained observers on each ship and aircraft prior to the main survey. This ensured homogenous implementation of the survey methodology.

2.3. Estimation of abundance

2.3.1. Shipboard survey

Analysis of the shipboard data followed the double-platform line transect methodology used in the SCANS survey (Borchers et al., 1998; Hammond et al., 2002; Laake and Borchers, 2004). Analyses were undertaken using software DISTANCE (Thomas

et al., 2010). To estimate the probability of detection, sightings made from the Tracker platform served as a set of binary trials in which success corresponded to detection by observers on the Primary platform. The probability that a group of animals, at given perpendicular distance x and covariates z, was detected from Primary is denoted $p_1(x, z)$ and modelled as a logistic function (see Eq. (9) in Borchers et al., 1998).

Although observers on Primary acted independently from those on Tracker, dependence of detection probability on unmodelled covariates may induce correlation in detection probabilities and potentially lead to bias. Estimators based on the assumption of independence of detections at zero perpendicular distance tend to be more robust than estimators assuming independence at all perpendicular distances (Borchers et al., 2006; Laake and Borchers, 2004). However, because we anticipated responsive animal movement for at least some species and the effects of responsive movement and unmodelled non-independence cannot be separated (Borchers et al., 2006), we used full independence estimators for all species. Specifically, we assumed that $p_{1|2}(x|z) = p_1(x|z)$ for all x, where $p_{1|2}(x|z)$ is the conditional probability of Primary detecting a group at distance x, given that it was first detected by Tracker, and estimated $p_{1|2}(x|z)$ from the binary data.

Explanatory covariates to model detection probability, in addition to perpendicular distance, included sea conditions as indicated by the Beaufort scale, glare, swell, sightability, visibility, group size and vessel. Models were selected using Akaike's Information Criterion (AIC). The extent of responsive movement was investigated by inspection of plots of Tracker and Primary perpendicular distance for duplicate detections (Supplementary Appendix, Fig. A1) and of data on direction of travel of detected groups following the methods described in Palka and Hammond (2001) (Supplementary Appendix, Table A1).

Perpendicular distance data for modelling detection probability were generally truncated at the largest value recorded by observers on Primary but for some species the data were truncated further to allow reliable models of detection probability to be fitted. For harbour porpoise, data obtained while surveying in sea conditions of Beaufort 2 or less were used; for other species data from sea conditions of Beaufort 4 or less were used. Duplicates classified as D and P were considered to be duplicates; those classified as R were not.

The abundance of groups was estimated using a Horvitz–Thompson-like estimator:

$$\widehat{N} = \sum_{j=1}^{n_1} \frac{1}{\int_0^W p_1(x, z_j | \hat{\theta}) \frac{1}{W} dx}$$

where n_1 is number of detections made from Primary, W is perpendicular truncation distance and $\hat{\theta}$ are the estimated parameters of the fitted detection function.

The abundance of individuals was estimated by replacing the numerator in the equation for estimating abundance of groups with s_{1j} , the group size of the jth group recorded from Primary. However, group sizes recorded on Tracker are typically larger and likely to be more accurate than on Primary because they were observed through binoculars and typically multiple times. Consequently, estimates of the abundance of individuals were corrected by the ratio of the sum of Tracker group sizes to the sum of Primary group sizes calculated from duplicate observations for each block or combination of blocks, depending on sample size. If the group size correction was estimated as <1, it was set to 1.

Estimates of mean group size were obtained by dividing abundance of individuals by abundance of groups.

Variance was estimated using a transect-based non-parametric bootstrap procedure in which the block structure of the data was preserved. Encounter rate variance was estimated using the method of Innes et al. (2002).

Investigation of the sensitivity of shipboard estimates to uncertainty in duplicate classification is described in Supplementary Appendix, Tables A2 and A3.

Where there were insufficient duplicate sightings to support double-platform methods, conventional line transect methods (assuming certain detection on the transect line) were used to obtain the detection function. For these analyses mean group sizes were estimated from detections made from the Tracker platform (see Hammond et al., 2002).

2.3.2. Aerial survey

Analysis of the "racetrack" data for harbour porpoise used the methods of Hiby (1999), and Hiby and Lovell (1998) to estimate total effective strip width (both sides of the transect) in good and moderate sighting conditions $\hat{\mu}_g$ and $\hat{\mu}_m$, respectively), taking account of detection probability less than 1 on the transect line. Abundance was estimated as:

$$\widehat{N} = \frac{A}{L} \left(\frac{n_{\rm g}}{\widehat{\mu}_{\rm g}} + \frac{n_{\rm m}}{\widehat{\mu}_{\rm m}} \right) \overline{s}$$

where A is area, L is length of transect searched in good or moderate conditions, n_g and n_m are number of sightings made in good and moderate conditions, respectively, and \bar{s} is mean observed group size

Variance was estimated by bootstrapping within blocks. A parametric bootstrap was used to generate effective strip width estimates, which were combined with encounter rates obtained from a non-parametric transect-based bootstrap procedure. The parametric bootstrap assumed that $\hat{\mu}_{g}$ and $\hat{\mu}_{m}$ were log-normally distributed random variables. For each bootstrap pseudo-sample of transect lines, a bivariate log-normal random variable was generated from a distribution with mean and variance–covariance matrix equal to those estimated from the data.

For species other than harbour porpoise, conventional line transect analysis was used to estimate abundance using software DISTANCE (Thomas et al., 2010). All sightings made in good and moderate conditions were used for estimating detection probability, including those during "racetrack" resurveys initiated by a sighting of harbour porpoise.

These estimates were then adjusted to account for availability bias by dividing by previously estimated correction factors: minke whale – 0.106 (CV = 0.66); bottlenose dolphin, *Tursiops truncatus* – 0.778 (CV = 0.04); striped dolphin, *Stenella coeruleoalba* (used for all "patterned" dolphins – see below) – 0.676 (CV = 0.24) (Forcada et al., 2004; Gómez de Segura et al., 2006; Witting, 2005).

2.4. Density surface modelling

Density surface modelling was used to generate broad scale predictions of how estimated abundance was distributed in space. The count method of Hedley and Buckland (2004) and Hedley et al. (1999) was used to model trend in spatial distribution. The number of animals in each of a series of small segments (lengths) of transect was estimated using a Horvitz–Thompson-like estimator as described above. Segments were delimited by changes in sighting conditions and were thus of variable length. Long segments were subdivided so no segment was greater than 15 km. Median segment length was 4.9 km.

The abundance of animals was modelled using generalised additive models (GAMs) with the general formulation

$$E[\widehat{N}_i] = \exp\left[\ln a_i + \beta_0 + \sum_{k=1}^K f_k(z_{ik})\right]$$

where a_i is the area of segment i (segment length multiplied by twice the truncation distance), β_0 is the intercept and the f_k are smooth functions of the K covariates z. This formulation assumes a logarithmic link function; we assumed the error distribution was an over-dispersed Poisson with mean-variance relationship $\mu = \varphi \sigma^2$ where φ is a scaling parameter estimated from the data. Available covariates were latitude, longitude, distance from the coast, seabed depth and slope.

The best fitting models were parameterised in all cells in a grid $(0.066^{\circ} \text{ latitude} \times 0.033^{\circ} \text{ longitude};$ similar resolution to segment length) to generate a density surface over the whole study area. These surfaces show broad scale variation in abundance; they should not be used to make inferences at fine spatial scales.

Density surface modelling was carried out in R (R Development Core Team, 2010) using package *mgcv* for modelling with GAMs (Wood, 2006).

3. Results

The large majority of survey effort was in sea conditions Beaufort 4 or less (ship survey) or in good or moderate conditions (aerial survey) (Table 1). The proportion of ship survey effort in sea conditions Beaufort 2 or less, used for analysis of harbour porpoise abundance, was variable over blocks but averaged almost 50%. Broad spatial coverage of survey effort was achieved (see Figs. 2–6).

The number of sightings of each of the main species sighted in each block is given in Tables 2 and 3. Figs. 2-6 show the distribution of these sightings for these species overlaid on the transects searched. The most commonly encountered and widely distributed species was harbour porpoise but there were few sightings south of 47°N. Minke whales were seen mostly in the central and northern North Sea and around Ireland and white-beaked dolphins were encountered primarily in the northern North Sea. Common dolphins were found west of Britain and Ireland, in the Channel and off France, Spain and Portugal. Bottlenose dolphins were seen along the coasts of Britain, Ireland, France, Spain and Portugal and in outer shelf waters off Ireland in the Celtic Sea and the Bay of Biscay. Other cetacean species sighted were: striped dolphin (S. coeruleoalba), white-sided dolphin (L. acutus), Risso's dolphin (Grampus griseus), long-finned pilot whale (Globicephala melas), killer whale (Orcinus orca), Cuvier's beaked whale (Ziphius cavirostris), fin whale (Balaenoptera physalus) and sei whale (Balaenoptera borealis).

3.1. Estimates of abundance

3.1.1. Harbour porpoise

For the shipboard analysis, the data were truncated at 1000 m perpendicular distance. The selected final model for detection probability included Beaufort and vessel as covariates, in addition to perpendicular distance (Supplementary Appendix, Fig. A2). Estimated detection probability on the transect line, conventionally known as g(0), for Primary was 0.216 (CV = 0.16). There was evidence of responsive movement (avoidance – Supplementary Appendix, Fig. A1, Table A1).

For analysis of aerial survey data, the total effective strip width was estimated to be 187 m (CV = 0.30) under good conditions and 107 m (CV = 0.31) under moderate conditions, incorporating g(0) values of 0.45 and 0.31, respectively. Visual inspection of the data indicated no dependence of group size on perpendicular distance nor was group size found to be a significant explanatory covariate in the estimation of effective strip width. The fitted detection function is given in Supplementary Appendix, Fig. A3.

Estimated abundance was 375,358 (CV = 0.197); estimates for each block are given in Table 4. Estimated densities were quite

Table 1Block sizes and survey effort searched by ship and aerial survey. For ship surveys, data collected in sea conditions Beaufort ≤ 2 were used for estimating the abundance of harbour porpoise; data collected in Beaufort ≤ 4 were used for all other species. For aerial surveys, all data were collected in good or moderate conditions (Beaufort ≤ 3) and were used for all species. Total surveyed area was 1,370,114 km². Total survey effort was 35,527 km.

| | Block | Surface area (km²) | Total survey effort (km) | Survey effort in Beaufort \leqslant 4 (%) | Survey effort in Beaufort \leqslant 2 (%) |
|----------------------------|-------|--------------------|--------------------------|---|---|
| Ship: Zirfaea | P | 197,400 | 3538 | 98.5 | 32.9 |
| Ship: Mars Chaser | Q | 149,637 | 3025 | 98.6 | 19.8 |
| Ship: Skagerak | S | 68,372 | 1762 | 100.0 | 72.6 |
| Ship: West Freezer | T | 134,206 | 2655 | 98.5 | 54.0 |
| Ship: Victor Hensen | U | 156,972 | 2195 | 98.2 | 54.3 |
| Ship: Gorm | V | 160,517 | 3020 | 100.0 | 67.6 |
| Ship: Investigador | W | 138,639 | 3530 | 95.8 | 37.3 |
| Total ship | | 1,005,743 | 19,725 | 98.4 | 45.8 |
| Aerial teams II and III | В | 123,825 | 3674 | | |
| Aerial team II | Н | 10,964 | 649 | | |
| Aerial team I | J | 37,477 | 1600 | | |
| Aerial team II | L | 20,844 | 1543 | | |
| Aerial team II | M | 12,931 | 1075 | | |
| Aerial team I | N | 30,626 | 730 | | |
| Aerial teams I, II and III | 0 | 45,417 | 2264 | | |
| Aerial teams I and III | R | 38,592 | 2168 | | |
| Aerial team II | Y | 11,776 | 577 | | |
| Aerial team III | Z | 31,919 | 1522 | | |
| Total aerial | | 364,371 | 15,802 | | |

Table 2Numbers of groups of the main species detected in each block surveyed by ship. The number of groups detected within the truncation distance from the Primary platform only, the Tracker platform only and duplicates (Definite and Probable) are given, except for bottlenose dolphin, for which there were too few duplicates for analysis.

| Species | Beaufort | Truncation distance (m) | | P | Q | S | T | U | V | W | Total |
|----------------------|------------|-------------------------|-----------|----|----|-----|----|-----|-----|----|-------|
| Harbour porpoise | €2 | 1000 | Tracker | 69 | 2 | 121 | 47 | 119 | 114 | 10 | 482 |
| | | | Primary | 53 | 7 | 96 | 51 | 108 | 45 | 4 | 364 |
| | | | Duplicate | 15 | 0 | 28 | 14 | 19 | 15 | 1 | 92 |
| Minke whale | ≪4 | 870 | Tracker | 7 | 2 | 0 | 4 | 4 | 41 | 0 | 58 |
| | | | Primary | 7 | 10 | 0 | 9 | 13 | 21 | 0 | 60 |
| | | | Duplicate | 4 | 1 | 0 | 2 | 2 | 9 | 0 | 18 |
| White-beaked dolphin | ≪4 | 1000 | Tracker | | 6 | 0 | 2 | 3 | 34 | 0 | 45 |
| | | | Primary | | 5 | 0 | 4 | 1 | 24 | 0 | 34 |
| | | | Duplicate | | 3 | 0 | 1 | 1 | 16 | 0 | 21 |
| Common dolphin | ≼ 4 | 2000 | Tracker | 31 | 8 | 0 | 0 | 0 | 0 | 61 | 100 |
| | | | Primary | 36 | 17 | 0 | 0 | 0 | 0 | 63 | 116 |
| | | | Duplicate | 18 | 2 | 0 | 0 | 0 | 0 | 33 | 53 |
| Bottlenose dolphin | ≪4 | 1500 | All | 13 | 10 | 0 | 1 | 0 | 1 | 13 | 38 |

Table 3Numbers of groups detected of the main species in each block surveyed by air. Patterned dolphin is one of common, striped, white-beaked or white-sided dolphin.

| Species | В | Н | J | L | M | N | 0 | R | Y | Z | Total |
|----------------------|-----|----|----|-----|----|----|----|----|---|---|-------|
| Harbour porpoise | 122 | 25 | 54 | 103 | 44 | 37 | 73 | 79 | 9 | 0 | 546 |
| Minke whale | 2 | 0 | 2 | 0 | 0 | 0 | 4 | 7 | 0 | 0 | 15 |
| White-beaked dolphin | 0 | 0 | 3 | 0 | 0 | 5 | 1 | 1 | 0 | 0 | 10 |
| Common dolphin | 3 | 0 | 0 | 0 | 0 | 8 | 5 | 19 | 0 | 4 | 39 |
| Bottlenose dolphin | 2 | 0 | 2 | 0 | 0 | 1 | 2 | 4 | 0 | 3 | 14 |
| Patterned dolphin | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 7 | 0 | 0 | 9 |

consistent among the majority of survey blocks, ranging mostly between 0.274 and 0.394 porpoises per km². Lowest estimated densities were offshore west of Scotland and Ireland (block Q) and around coasts of SW France, Spain and Portugal (block W). Highest estimated densities were in the south/central North Sea (block U) and off the west coast of Denmark (block L). Estimated abundance in the equivalent area surveyed in 1994 (2005 blocks B, H, J, L, M, P, S, T, U, V, Y) was 323,968 (CV = 0.22; 95% CI = 256,300–549,700), compared to 341,366 (CV = 0.14; 95% CI = 260,000–449,000) in 1994 (Hammond et al., 2002).

3.1.2. Minke whale

For shipboard analysis, the data were truncated at 870 m perpendicular distance. The best model for detection probability included perpendicular distance only (Supplementary Appendix, Fig. A2). Estimated *g*(0) for Primary was 0.544 (CV = 0.29). There was some evidence of responsive movement (avoidance – Supplementary Appendix, Fig. A1, Table A1). For aerial survey data, the best model for detection probability also included perpendicular distance only (Supplementary Appendix, Fig. A3).

Table 4Estimates of harbour porpoise abundance. Animal density is given in individuals km⁻². Figures in square brackets are 95% confidence intervals. There were no sightings of harbour porpoise in block Z.

| Block | Group abundance | | Mean group s | ize | Animal abundance | | Animal densi | ty |
|-------|-------------------|-------|--------------|------|-------------------|-------|--------------|------|
| | Estimate | CV | Estimate | CV | Estimate | CV | Estimate | CV |
| В | 32,052 | 0.39 | 1.28 | 0.04 | 40,927 | 0.38 | 0.331 | 0.38 |
| Н | 3138 | 0.37 | 1.24 | 0.16 | 3891 | 0.45 | 0.355 | 0.45 |
| J | 8294 | 0.37 | 1.24 | 0.08 | 10,254 | 0.36 | 0.274 | 0.36 |
| L | 9152 | 0.43 | 1.26 | 0.04 | 11,575 | 0.43 | 0.555 | 0.43 |
| M | 3230 | 0.37 | 1.22 | 0.08 | 3948 | 0.38 | 0.305 | 0.38 |
| N | 9309 | 0.41 | 1.30 | 0.07 | 12,076 | 0.43 | 0.394 | 0.43 |
| 0 | 11,118 | 0.36 | 1.37 | 0.07 | 15,230 | 0.35 | 0.335 | 0.35 |
| P | 25,715 | 0.48 | 2.82 | 0.13 | 72,389 | 0.53 | 0.367 | 0.53 |
| Q | 8431 | 1.16 | 1.31 | 0.21 | 11,011 | 1.14 | 0.074 | 1.14 |
| R | 7685 | 0.35 | 1.39 | 0.10 | 10,716 | 0.37 | 0.278 | 0.37 |
| S | 13,049 | 0.32 | 1.47 | 0.11 | 19,129 | 0.36 | 0.280 | 0.36 |
| T | 9615 | 0.34 | 2.02 | 0.08 | 19,396 | 0.34 | 0.145 | 0.34 |
| U | 57,955 | 0.26 | 1.62 | 0.06 | 93,938 | 0.28 | 0.598 | 0.28 |
| V | 19,862 | 0.31 | 2.37 | 0.21 | 47,048 | 0.36 | 0.293 | 0.36 |
| W | 974 | 0.84 | 2.42 | 0.16 | 2357 | 0.92 | 0.017 | 0.92 |
| Y | 1473 | 0.47 | 1.00 | - | 1473 | 0.47 | 0.125 | 0.47 |
| Total | 221,052 | 0.187 | | | 375,358 | 0.197 | | |
| | [153,759–317,796] | | | | [256,304–549,713] | | | |

Table 5Estimates of minke whale abundance. Animal density is given in individuals km⁻². Figures in square brackets are 95% confidence intervals. Aerial survey estimates are corrected for availability bias but not for perception bias. There were no sightings of minke whale in blocks H, L, M, N, S, W, Y and Z.

| Block | Group abundance | | Mean group size | | Animal abundance | Animal density | | |
|-------|-------------------------|-------|-----------------|------|-------------------------|----------------|----------|------|
| | Estimate | CV | Estimate | CV | Estimate | CV | Estimate | CV |
| В | 883 | 0.97 | 1.36 | 0.12 | 1199 | 0.98 | 0.010 | 0.98 |
| J | 614 | 1.03 | 1.36 | 0.12 | 833 | 1.04 | 0.022 | 1.04 |
| 0 | 789 | 0.91 | 1.36 | 0.12 | 1070 | 0.91 | 0.024 | 0.91 |
| P | 1531 | 0.43 | 1.14 | 0.18 | 1749 | 0.44 | 0.009 | 0.44 |
| Q | 1938 | 0.46 | 1.00 | 0.03 | 1938 | 0.46 | 0.013 | 0.46 |
| R | 1633 | 0.85 | 1.36 | 0.12 | 2216 | 0.86 | 0.057 | 0.86 |
| T | 1783 | 0.60 | 1.00 | 0.42 | 1783 | 0.60 | 0.013 | 0.60 |
| U | 3655 | 0.69 | 1.00 | 0.00 | 3655 | 0.69 | 0.023 | 0.69 |
| V | 4310 | 0.50 | 1.05 | 0.34 | 4515 | 0.51 | 0.028 | 0.51 |
| Total | 17,136 [9015–32,568] | 0.337 | | | 18,958 [9798–36,680] | 0.347 | | |

Estimated abundance was 18,958 (CV = 0.347); estimates for each block are given in Table 5. Highest estimated densities were around Ireland (blocks O and R) and in the North Sea (blocks J, U, V). Estimated abundance was 13,734 (CV = 0.41; 95% CI = 9800-36,700) in the equivalent area surveyed in 1994 (2005 blocks B, J, P, T, U, V), compared to 8445 (CV = 0.24; 95% CI = 5000-13,500) in 1994 (Hammond et al., 2002).

3.1.3. White-beaked dolphin

For shipboard analysis, the data were truncated at 1000 m perpendicular distance. The best model for detection probability included perpendicular distance only (Supplementary Appendix, Fig. A2). Estimated g(0) for Primary was 0.565 (CV = 0.27). There was some evidence of responsive movement (avoidance – Supplementary Appendix, Fig. A1, Table A1). For aerial survey analysis, data for all "patterned" dolphins (white-beaked dolphin, white-sided dolphin, common dolphin, striped dolphin) were combined for the estimation of detection probability. The best model included sighting conditions as an explanatory variable as well as perpendicular distance (Supplementary Appendix, Fig. A3).

Estimated abundance was 16,536 (CV = 0.303); estimates for each block are given in Table 6. Highest estimated densities were in inshore waters west of Scotland (block N) and in the northern North Sea (block V). Estimated abundance in the equivalent area surveyed in 1994 (2005 blocks J, T, U, V) was 10,666 (CV = 0.38;

95% CI = 9200–29,600), compared to 7856 (CV = 0.30; 95% CI = 4000–13,300) in 1994 (Hammond et al., 2002).

3.1.4. Common dolphin

Common dolphins were sighted in shipboard blocks P, Q and W. Data were truncated at 2000 m perpendicular distance. The best model for detection probability included group size as well as perpendicular distance (Supplementary Appendix, Fig. A2). There was strong evidence of responsive movement (attraction – Supplementary Appendix, Fig. A1, Table A1). The estimated g(0) for Primary was 0.55 (CV = 0.17). The aerial survey analysis used estimates of detection probability for all "patterned" dolphins (see above).

Estimated abundance of common dolphin was 56,221 (CV = 0.234; 95% CI = 35,700–88,400); estimates for each block are given in Table 7. Highest estimated densities of common dolphin were west of Ireland (block R) and in coastal waters of SW France, Spain and Portugal (W). Shipboard estimates that did not take uncertain detection on the trackline or responsive movement into account (Supplementary Appendix, Fig. A4 for fitted detection functions) were 2.3 times higher than the corrected estimates: 83,616 (CV = 0.261) vs 36,225 (CV = 0.206).

3.1.5. Bottlenose dolphin

There were insufficient shipboard sightings of bottlenose dolphin to estimate abundance using double-team analysis methods

Table 6Estimates of white-beaked dolphin abundance. Animal density is given in individuals km⁻². Figures in square brackets are 95% confidence intervals. Aerial survey estimates are corrected for availability bias but not for perception bias. There were no sightings of white-beaked dolphin in blocks B, H, L, M, P, S, W, Y and Z.

| Block | Group abundance | | Mean group si | Mean group size | | Animal abundance | | |
|-------|---------------------|-------|---------------|-----------------|-------------------------|------------------|----------|------|
| | Estimate | CV | Estimate | CV | Estimate | CV | Estimate | CV |
| J | 263 | 0.84 | 4.10 | 0.18 | 1078 | 0.85 | 0.029 | 0.85 |
| N | 785 | 0.75 | 4.10 | 0.18 | 3219 | 0.77 | 0.105 | 0.77 |
| O | 75 | 0.80 | 4.10 | 0.18 | 307 | 0.82 | 0.007 | 0.82 |
| Q | 342 | 0.68 | 6.06 | 1.92 | 2071 | 0.62 | 0.014 | 0.62 |
| R | 67 | 0.85 | 4.10 | 0.18 | 273 | 0.86 | 0.007 | 0.86 |
| T | 280 | 0.64 | 5.47 | 0.44 | 1530 | 0.67 | 0.011 | 0.67 |
| U | 99 | 0.99 | 5.05 | 1.50 | 501 | 0.97 | 0.003 | 0.97 |
| V | 1738 | 0.46 | 4.35 | 0.21 | 7557 | 0.47 | 0.047 | 0.47 |
| Total | 3649 [2031–6557] | 0.306 | | | 16,536 [9245–29,586] | 0.303 | | |

Table 7Estimates of common dolphin abundance. Animal density is given in individuals km⁻². Figures in square brackets are 95% confidence intervals. Aerial survey estimates are corrected for availability bias but not for perception bias. There were no sightings of common dolphin in blocks H, J, L, M, S, T, U, V and Y.

| Block | Group abundance | | Mean group size | | Animal abunda | nce | Animal density | |
|-------|-----------------------|-------|-----------------|------|--------------------------|-------|----------------|------|
| | Estimate | CV | Estimate | CV | Estimate | CV | Estimate | CV |
| В | 378 | 0.73 | 13.0 | 0.36 | 4919 | 0.82 | 0.040 | 0.82 |
| N | 1256 | 0.58 | 1.75 | 0.14 | 2199 | 0.60 | 0.072 | 0.60 |
| 0 | 375 | 0.69 | 2.20 | 0.36 | 826 | 0.78 | 0.018 | 0.78 |
| P | 1058 | 0.33 | 11.6 | 0.30 | 15,957 | 0.31 | 0.081 | 0.31 |
| Q | 558 | 0.98 | 3.08 | 0.32 | 2230 | 0.87 | 0.015 | 0.87 |
| R | 1266 | 0.70 | 9.21 | 0.19 | 11,661 | 0.73 | 0.302 | 0.73 |
| W | 1470 | 0.29 | 12.3 | 0.27 | 18,039 | 0.23 | 0.130 | 0.23 |
| Z | 314 | 0.84 | 1.25 | 0.20 | 392 | 0.86 | 0.012 | 0.86 |
| Total | 6675 [3969–11,230] | 0.270 | | | 56,221 [35,748–88,419 | 0.234 | | |

Table 8Estimates of bottlenose dolphin abundance. Animal density is given in individuals km⁻². Figures in square brackets are 95% confidence intervals. Ship survey estimates are uncorrected for animals missed on the transect line or for any responsive movement. Aerial survey estimates are corrected for availability bias but not for perception bias. There were no sightings of bottlenose dolphin in blocks H, L, M, S, U and Y.

| Block | Group abundar | nce | Mean group siz | Mean group size | | nce | Animal density | |
|-------|---------------|-------|----------------|-----------------|---------------|-------|----------------|------|
| | Estimate | CV | Estimate | CV | Estimate | CV | Estimate | CV |
| В | 146 | 0.65 | 2.71 | 0.35 | 395 | 0.74 | 0.0032 | 0.74 |
| J | 152 | 0.79 | 2.71 | 0.35 | 412 | 0.87 | 0.0110 | 0.87 |
| N | 91 | 0.99 | 2.71 | 0.35 | 246 | 1.05 | 0.0080 | 1.05 |
| 0 | 87 | 0.66 | 2.71 | 0.35 | 235 | 0.75 | 0.0052 | 0.75 |
| P | 604 | 0.59 | 12.70 | 0.24 | 7665 | 0.64 | 0.0388 | 0.64 |
| Q | 411 | 0.53 | 3.60 | 0.22 | 1481 | 0.58 | 0.0099 | 0.58 |
| R | 116 | 0.73 | 2.71 | 0.35 | 313 | 0.81 | 0.0081 | 0.81 |
| T | 42 | 1.03 | 3.60 | 0.22 | 151 | 1.05 | 0.0011 | 1.05 |
| V | 44 | 1.12 | 3.60 | 0.22 | 157 | 1.14 | 0.0010 | 1.14 |
| W | 437 | 0.49 | 11.58 | 0.29 | 5061 | 0.57 | 0.0365 | 0.57 |
| Z | 136 | 0.73 | 2.71 | 0.35 | 369 | 0.81 | 0.0116 | 0.81 |
| Total | 2266 | 0.322 | | | 16,485 | 0.422 | | |
| | [1224-4197] | | | | [7463-36,421] | | | |

so data from Tracker and Primary were pooled, truncated at 1500 m and analysed using conventional line transect methods. The best model included perpendicular distance only (Supplementary Appendix, Fig. A4), as it also did for the aerial survey data (Supplementary Appendix, Fig. A3). Estimated abundance was 16,485 (CV = 0.422; 95% CI = 7500–36,400); estimates for each block are given in Table 8. Highest estimated densities were in coastal waters of SW France, Spain and Portugal (block W) and in the Celtic Sea (block P).

3.2. Model-based density surfaces

There were sufficient data for analysis of three species: harbour porpoise, minke whale and common dolphin. Results for common dolphin, which primarily occurs in waters off the continental shelf, will be presented elsewhere in combination with results from offshore surveys (see below). Data from the SCANS survey (Hammond et al., 2002) were reanalysed to generate density surfaces for harbour porpoise and minke whale for 1994. Best-fitting models are given in Supplementary Appendix Table A4.

The predicted density surfaces for 1994 and 2005 are shown for harbour porpoise in Figs. 7 and 8, and for minke whale in Figs. 9 and 10. A marked difference in harbour porpoise distribution between 1994 and 2005 is evident with higher densities in northern areas in 1994 shifting south in 2005. Although less clear, there is a suggestion of this same pattern for minke whale.

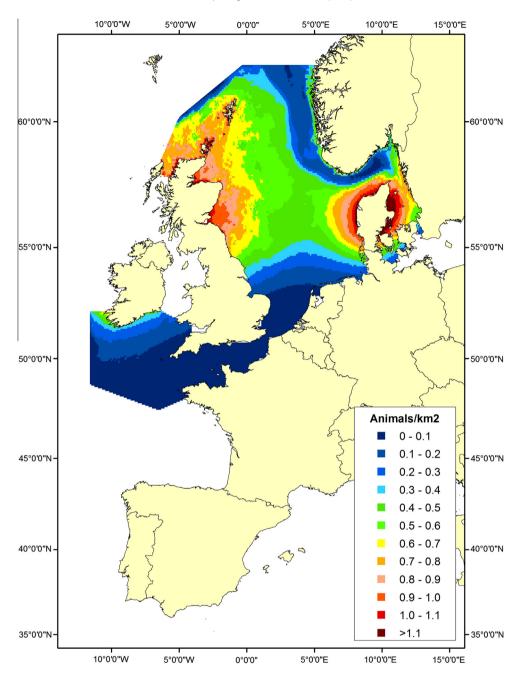


Fig. 7. Predicted density surface for harbour porpoise in 1994

4. Discussion

We present new robust estimates of abundance for the main species of cetacean inhabiting European Atlantic shelf waters. These results are essential for assessing the conservation status of these species at a large spatial scale and for informing options for management of those human activities that impact them; in particular, they allow estimates of fisheries bycatch to be put into a population context. The estimates also form part of a time series that will provide added value as it grows in decades to come.

Spatial modelling suggested a shift in distribution of harbour porpoise and perhaps minke whale between the 2005 and 1994 surveys. Shifts in prey availability may be responsible but abundance may also have been affected by fisheries bycatch in some parts of the study area. The results from this survey are the primary

instrument for assessment of these species' conservation status and demonstrate the need for continued bycatch monitoring and estimation of abundance.

In publishing the results from the first SCANS survey in 1994, Hammond et al. (2002) made a number of observations and recommendations regarding future work, including that the interval between that first survey and future surveys "should probably not exceed 10 years". We missed this timing by a year but the addition of another set of estimates for 2005 is an important step towards the continuation of this series. We maintain that the interval for obtaining estimates of abundance at a large spatial scale should be decadal and recommend that the next such major survey should take place by 2015.

By covering all continental shelf waters of the Atlantic from 62°N to the Strait of Gibraltar, our 2005 survey achieved an almost

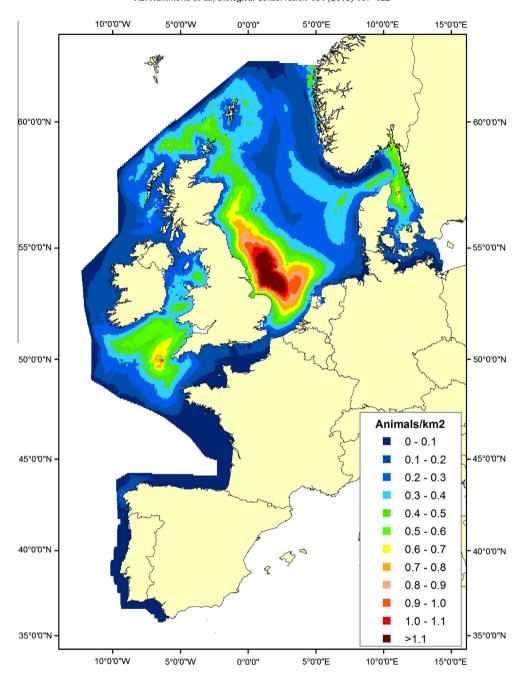


Fig. 8. Predicted density surface for harbour porpoise in 2005

complete assessment of harbour porpoise abundance in EU waters and is a marked improvement on the survey in 1994. This is also the case for white-beaked dolphin. Minke whales also occur offshore in deeper waters but shelf waters form an important part of their habitat in the EU Atlantic. For these species, in an area comparable to that surveyed in 1994 and 2005, we found no evidence of a change in abundance over the intervening 11 years. However, the statistical power of these data to show anything other than major changes is low, and testing this as a hypothesis was not an objective.

The estimates also help partly fulfil another recommendation (Hammond et al., 2002), which was to continue monitoring of abundance and levels of bycatch "to enable further assessments of the impact of bycatch on harbour porpoise populations in particular". Bycatch monitoring in the area has been patchy (ICES, 2009a) but there have been developments in a framework for setting safe

bycatch limits using management strategy evaluation modelling (SCANS-II, 2008; Winship, 2009). This framework uses the new abundance results but, before it can be implemented, formal quantitative conservation objectives need to be defined for use throughout the EU. An example is the interim conservation objective used by ASCOBANS: 'To allow populations to recover to and/or maintain 80% of carrying capacity in the long term'.

To reduce potential for bias and to maximise value for the resources committed to the survey, we updated and developed data collection and analysis methods to ensure our estimates were as robust as possible. This included the new data collection methods described in Gillespie et al. (2010) and the first large-scale implementation of the "racetrack" aerial survey method (Hiby, 1999). These shipboard methods have since been used in other large scale surveys for cetaceans in the Southern Ocean (Leaper et al., 2010) and the North Atlantic (CODA, 2009; Pike et al., 2010).

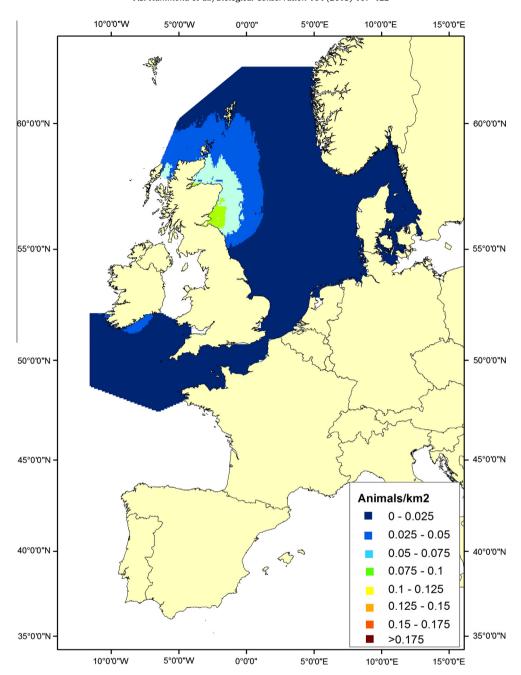


Fig. 9. Predicted density surface for minke whale in 1994

Although estimates of "absolute" abundance are required to assess the impact of bycatch, assessing trends in population size can use an appropriate index of relative abundance. Furthermore, information on trends in time and space may be valuable at time scales shorter than a decade. Therefore, we used the survey as an opportunity to develop and evaluate methods for monitoring trends in abundance of small cetacean species between large-scale decadal surveys (SCANS-II, 2008); Results of this work will be published elsewhere.

4.1. Harbour porpoise

Although we found no evidence that total harbour porpoise abundance in the North Sea/Celtic Sea changed between 1994 and 2005, we did find a marked difference in summer distribution. The main concentration in the North Sea had shifted from the northwest in 1994 to the southwest in 2005, the high densities

around coastal Denmark in 1994 had dissipated in 2005, and densities in the Celtic Sea were higher in 2005 than 1994 (Figs. 7 and 8).

Part of the difference could simply be inter-annual variation in the spatial distribution of abundance. However, that there has been a systematic change in distribution over this period is corroborated by the increases in sightings and strandings of porpoises in French, Belgian, Dutch and German waters over the last decade (Camphuysen, 2004; Gilles et al., 2009, 2011; Haelters et al., 2011; Jauniaux et al., 2008; Scheidat et al., 2012). Data from Norwegian surveys in the North Sea show an approximate 20-fold decline in sighting rates of harbour porpoise in the northern North Sea (56–62°N) between 1998/2004 and 2009 (Øien, 1999, 2005, 2010) suggesting that low porpoise density in this area persists. Another large-scale SCANS-type survey is needed to confirm this trend at a larger temporal and spatial scale.

Could bycatch have contributed to the observed reduced abundance in northern areas? Porpoise bycatch in Norwegian coastal

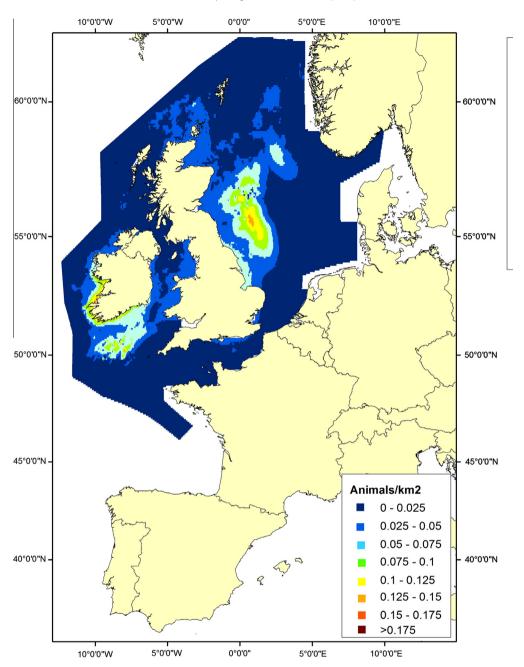


Fig. 10. Predicted density surface for minke whale in 2005

waters has been estimated at 20,720 (CV = 0.36) for the period 2006-2008 (i.e. an annual bycatch of 6900) but only a small proportion occurred south of 62°N (~800 per annum) (Bjørge et al., 2011). However, much of the porpoise bycatch in Danish set net fisheries occurs in the northern half of the North Sea (Vinther and Larsen, 2004), so without estimates of Danish bycatch in the last decade we cannot be specific about how much bycatch may have contributed to the change in estimated abundance in this area. Danish gill/tangle net effort in the North Sea did decline between the two surveys: recorded days at sea (vessels >15 m) in 2005 were less than half of the peak effort in 1994 (Lotte Kindt-Larsen, DTU, personal communication). Harbour porpoise bycatch in Swedish fisheries occurs mainly in the Skagerrak/Kattegat Seas where recorded levels were previously thought likely to have had a negative effect on porpoise abundance (Berggren et al., 2002); this is also an area where the point estimate of abundance was lower in 2005 than 1994.

In contrast, porpoise bycatch in UK and Irish fisheries is primarily in the central North Sea and/or Celtic Sea (ICES, 2008a; Northridge et al., 2003; Tregenza et al., 1997), areas where estimated harbour porpoise abundance was higher in 2005 than 1994. UK gill/tangle net fishing effort in the North Sea has also fallen by >50% since 1995, yielding an average annual bycatch estimate of 370 porpoises in 2003–2007 (http://archive.defra.gov.uk/environment/biodiversity/documents/indicator/200812m6.pdf). Further south in the North Sea, porpoise bycatch in French, Belgian and Dutch coastal waters has increased in the last decade (Haelters and Camphuysen, 2009; Jauniaux et al., 2008). Recent bycatch estimates in the Celtic Sea are about 800 porpoises per annum (ICES, 2008a, 2009a).

Even though set net effort has decreased in some areas, monitoring bycatch and estimation of abundance continue to be essential. Much attention is being focussed on recovering cod and other fish stocks in the North Sea and elsewhere in European waters. Set

nets or fish traps could be considered favourable gears for future sustainable exploitation because they are relatively selective and fuel-efficient compared to other non-static gears. However, an increase in set net effort will likely lead to an increase in porpoise and other cetacean bycatch unless mitigation methods are applied.

A likely cause of the observed difference in harbour porpoise distribution in 1994 and 2005 is a change in the distribution and/or availability of prey. Harbour porpoise diet is varied (Santos et al., 2004; S.P. Northridge, unpublished data) but primarily comprises sandeel, whiting and herring. The structure of the food web in the North Sea has changed markedly in recent decades because of large scale fisheries removals and the influence of decadal scale oceanic changes (Heath, 2005; Christensen and Richardson, 2008). Between 1994 and 2005, whiting and sandeel biomass in the North Sea declined but relative abundance of whiting appeared to increase in the southwest North Sea (ICES, 2008b), Seabird breeding failure in the northwest North Sea has been linked to a reduction in the availability of sandeels (Wanless et al., 2004) and to reduced sandeel recruitment in warm winters (Frederiksen et al., 2004). During this period, herring abundance increased markedly (ICES, 2009b), although there is no evidence that the relative abundance of herring increased in the southern North Sea (ICES FishMap http://www.ices.dk/marineworld/ices-fishmap.asp). It is therefore not unreasonable to suggest that the change in porpoise distribution may be in response to declines in prey availability in the north (whiting and sandeel) but sustained availability in the south (whiting and herring). This requires further investigation.

4.2. Minke whale

European shelf waters are only a relatively small part of the range of minke whales in the northeast North Atlantic. Nevertheless, our results add to knowledge of this species, suggesting that the weak concentration of summer distribution in the north-western North Sea in 1994 had shifted to the central North Sea in 2005 (Figs. 9 and 10). High densities of minke whales were also found in the central North Sea (Dogger and Fisher Banks) in spring 2007 (de Boer, 2010). Minke whales presumably enter the North Sea in spring/summer from the north because they are not found in the southern North Sea and eastern Channel (Reid et al., 2003). Distribution and abundance in the North Sea might therefore be expected to vary from year to year, depending on prey availability there and further north. Estimates of abundance in the North Sea include: 5429 (CV = 0.34) in 1989; 7250 (CV = 0.21) in 1994; 20,294 (CV = 0.26) in 1995; 11,713 (CV = 0.29) in 1998; 6246 (CV = 0.48) in 2004 (Hammond et al., 2002; Schweder et al., 1997; Skaug et al., 2004; Bøthun et al., 2009). The 2005 estimate for the North Sea (Blocks J, T, U, V) was 10,786 (CV = 0.49). These results may reflect changes in prey availability in recent years (see above) but the substantial inter-annual variability in estimated abundance in summer over the last two decades means that caution is needed in this interpretation.

4.3. Common dolphin, bottlenose dolphin and white-beaked dolphin

For common and bottlenose dolphin, our estimates of abundance are the first at a large scale for European Atlantic shelf waters. The estimate for common dolphin covers all continental shelf waters west of Europe and is corrected for responsive movement. Common dolphin abundance was estimated for the Celtic Sea in 1994 (Hammond et al., 2002) but this estimate is subject to considerable positive bias because responsive movement could not be accounted for and it should thus not be considered further. That our uncorrected shipboard estimate for 2005 was 2.3 times higher than our corrected estimate illustrates how large this source of bias can be. Our estimate for bottlenose dolphin includes all

coastal populations for which estimates have been made from photo-identification data, which typically have fewer than 200 animals (e.g. Wilson et al., 1999; Ingram, 2000; Cheney et al., 2013) as well as part of the much larger populations living further offshore, particularly to the southwest of Britain and Ireland.

These two species also occur in deeper waters to the west of the continental shelf study area; 273,159 (CV = 0.26) common dolphins (corrected for responsive movement) were estimated in an approximately 100,000 km² survey block (52–57.5°N, 18–28°W) in 1995 (Cañadas et al., 2009). Additional knowledge of abundance in offshore waters of the European Atlantic is necessary to allow more complete assessments of conservation status.

The distribution of the white-beaked dolphin is limited to high latitudes in the North Atlantic and the species is generally rather poorly known. Compared to the other main species encountered which have a wide distribution globally, the survey covered a substantial proportion of the known range of white-beaked dolphin. The abundance estimates presented are thus particularly informative in terms of the global numbers of this species.

5. Conclusions

This study was conducted to provide scientific information to underpin national and international conservation and management responsibilities. The new estimates of abundance extend the baseline established in 1994 to all shelf waters and cover almost all of the range of the harbour porpoise and white-beaked dolphin in EU waters. For common dolphin, bottlenose dolphin and minke whale the estimates in shelf waters extend knowledge for that part of their range. This information is the most extensive and robust yet available and will stand as a reference point for decades to come. Our results inform the reporting by EU Member States under the Habitats Directive and also the deliberations of international organisations that have a responsibility for and/or interest in the conservation of cetaceans in European Atlantic shelf waters (ASCOBANS, 2008; ICES, 2008a; IWC, 2010).

The model-based density surfaces showed a marked difference in harbour porpoise distribution between 1994 and 2005, a pattern weakly reflected by the minke whale, but no evidence of a change in abundance in EU shelf waters as a whole was found. The most likely cause of this difference in distribution is a change in prey availability but we cannot exclude the possibility of an impact of bycatch on harbour porpoise in some parts of the study area. Monitoring bycatch and estimation of abundance continue to be essential to inform conservation and management of cetaceans in European Atlantic waters.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.

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