

DISTRIBUTION AND ABUNDANCE OF CETACEANS IN ICELANDIC WATERS OVER 30 YEARS OF AERIAL SURVEYS

Daniel G. Pike^{1,2,3}, Thorvaldur Gunnlaugsson², Jóhann Sigurjónsson^{2,4} & Gísli A. Víkingsson²

¹ Esox Associates, 1210 Ski Club Road, North Bay, Ontario, Canada. Corresponding author: kinguq@gmail.com

² Marine and Freshwater Research Institute, P.O. Box 1390, IS-121 Reykjavík, Iceland

³ North Atlantic Marine Mammal Commission, Sykehusveien 21-23, N-9294 Tromsø, Norway

⁴ Ocean Affairs, Ministry for Foreign Affairs, 150 Reykjavík, Iceland

ABSTRACT

Beginning in 1986, 7 aerial surveys covering the coastal waters of Iceland have been conducted up to and including 2016. In addition, 7 partial surveys covering portions of the same area and at different times of the year have been flown in the same 30-year period. We present previously unpublished abundance estimates, corrected to the extent feasible for known biases, for common minke whales (*Balaenoptera acutorostrata*), humpback whales (*Megaptera novaeangliae*), white-beaked dolphins (*Lagenorhynchus albirostris*) and harbour porpoises (*Phocoena phocoena*) from some or all of the 2007, 2009 and 2016 surveys. We also examine the distribution of these and other species in Icelandic waters over the 30-year timespan of the surveys, as well as changes observed over the period. The relative abundance of common minke and humpback whales, and white-beaked dolphins, was comparatively low in the spring and fall, and peaked in June and July when all of the main surveys have been carried out. An analysis of changes in density as an index of relative abundance from all surveys (1986-2016) indicates that common minke whale abundance decreased by up to 75% after 2001 and has remained at a relatively low level since then. This decrease has been particularly apparent in the southwest and southeast of Iceland, areas that previously had very high densities. Relative abundance of humpback whales and white-beaked dolphins has increased over the period 1986-2016, particularly in the northern part of the survey area. Estimating harbour porpoise abundance and trend was considered unfeasible except from the surveys conducted in 2007 and 2016, which provide abundance estimates of similar magnitude. We place these observed changes in the context of oceanographic and ecosystem changes documented over the same period.

Keywords: common minke whale, humpback whale, white-beaked dolphin, harbour porpoise, abundance, population trend, aerial survey, Iceland

INTRODUCTION

The first full-scale aerial survey for cetaceans covering the Icelandic shelf and territorial waters during late June-July was carried out in 1986 and the most recent one, covering nearly the same survey area, was completed in 2016. Over this 30-year period, complete surveys have been attempted 7 times, usually as a component of the North Atlantic Sightings Surveys (NASS), in 1986, 1987 (incompletely), 1995, 2001, 2007, 2009, 2015 (incompletely) and 2016. In addition, 7 partial surveys covering portions of the same survey area, sometimes at different times of the year, have been flown.

The main target species of these surveys has been the common minke whale (*Balaenoptera acutorostrata*), with the harbour porpoise (*Phocoena phocoena*) and humpback whale (*Megaptera novaeangliae*) as secondary targets in some years. However, sightings of all species are registered using the same methodology, which provides data suitable for abundance estimation using cue-counting or line transect methods (Hiby & Hammond, 1989).

Previous estimates of common minke whale abundance using cue-counting have been provided for the 1987 and 2001 surveys (Borchers, Pike, Gunnlaugsson, & Víkingsson, 2009; Hiby, Ward, & Lovell, 1989). Problems with data recording precluded a cue counting analysis of data from the 1995 survey, although the data have been used in a line transect context. Line transect estimates, in some cases corrected for bias due to visible whales

missed by observers (perception bias), have been provided for humpback whales (1995, 2001) (Paxton et al., 2009; Pike, Paxton, Gunnlaugsson, & Víkingsson, 2009), white-beaked dolphins (*Lagenorhynchus albirostris*) (1986, 1995, 2001) and harbour porpoises (1986, 1995) (Pike et al., 2009). In addition, Gilles et al. (under revision) provide a fully-corrected estimate of harbour porpoise abundance from the 2007 survey.

In this paper, we provide fully corrected cue-count estimates of common minke whale abundance from the 2007, 2009 and 2016 surveys, as well as line transect estimates from surveys where sufficient sightings were realized and corrected for perception bias for humpback whales (2007, 2009), white-beaked dolphins (2007, 2009, 2016) and harbour porpoises (2016). The 30-year time span of the survey series provides a unique opportunity to look at trends in distribution and abundance at a temporal scale that is relevant to long-lived cetaceans. Pike et al. (2009) provided an analysis of trends up to and including the 2001 survey for minke whales, white-beaked dolphins, humpback whales and harbour porpoises, and here we extend that analysis to 2016 for the first 3 species.

MATERIALS AND METHODS

A full description of the methodology used in individual surveys is provided in the published and unpublished survey reports:

1986 (Gunnlaugsson, Sigurjónsson, & Donovan, 1988); 1987 (Donovan & Gunnlaugsson, 1989); 1995 (Sigurjónsson, Gunnlaugsson, Víkingsson, & Gudmundsson, 1996); 2001 (Borchers et al., 2009; Pike et al., 2009); 2007 (Pike, Gunnlaugsson, & Víkingsson, 2008); 2015 (Pike, 2015); and 2016 (Pike, 2016). They are also summarized below.

Surveys

Pike et al. (2009) detailed the history and development of the Icelandic aerial survey up to and including 2001. The first full survey (i.e. one with coverage in all or almost all strata) was carried out in 1986 (Gunnlaugsson et al., 1988). Later full surveys were part of the larger North Atlantic Sightings Surveys in 1987, 1995, 2001, 2007 and 2015 (Figure 1). An additional survey was done in 2009 primarily because the 2007 survey had revealed much lower densities of common minke whales than had been observed previously. Realized effort in the 2015 survey was very low and several strata were not sampled due to poor weather. The survey was therefore repeated in 2016.

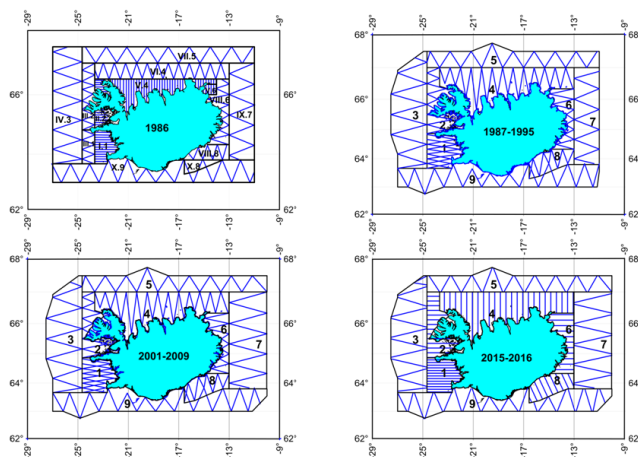


Figure 1. Stratification and transect designs used in Icelandic aerial surveys, 1986-2016.

Partial surveys using the same stratification and design were also carried out to address specific issues. Only block 1 (Figure 1) was surveyed in 1988. In September 2003, block 1 and parts of blocks 2, 8 and 9 were surveyed as part of an effort to calibrate an aerial photographic survey (Witting & Pike, 2009). Partial surveys carried out in April, June-July and September 2004, and May 2005 were intended to assess seasonal changes in distribution and abundance. Only block 1 was surveyed in July 2008 to determine if the low densities of minke whales observed in 2007 had been sustained.

Targeted species

The common minke whale has been the primary target species for all surveys. In 2007, secondary priority was given to the harbour porpoise and the survey was modified by reducing the survey altitude and including an observer with extensive experience in harbour porpoise aerial surveys.

Survey design

While the extent of the 1986 survey was similar to later ones, (covering Icelandic territorial waters corresponding roughly to the continental shelf), stratification and transect design differed from later surveys (Figure 1).

To obtain block estimates comparable with later surveys, a post-stratification to blocks identical to the 1987 and 1995 surveys was done as described in Pike et al. (2009). Because a single post-stratified block might consist of 2 or more sub-blocks with unequal coverage probability, post-strata estimates were obtained by combining individual estimates from sub-strata.

The survey design was largely standardized between 1987 and 2009 (Donovan & Gunnlaugsson, 1989), consisting of 6 inner blocks and 3 rectangular offshore blocks (Figure 1). Planned effort was generally higher in the inshore blocks and especially in areas where high densities of common minke whales were expected based on the results of the 1986 survey. The transect layout followed an equal-spaced zig-zag design, with a double set used in block 1. In 2001, strata 5, 7 and 9 were extended eastwards from 11°W to 10°W in order to better encompass the distribution of humpback whales in the area. Transect spacing in the stratum was left the same as previously. In 2007, additional effort was applied to the southern portion of block 2, designating it as block 2A and the northern part as block 2B, and these sub-strata were used in estimates of common minke whales only (Pike, Gunnlaugsson, & Víkingsson, 2008).

In 2015, the transect design in all inshore strata except block 9 was changed from the zig-zag design used in earlier surveys to an equal-spaced parallel line layout. This was done at the recommendation of the NAMMCO Scientific Committee to ensure even coverage in these areas, as the deeply indented coastline could result in uneven coverage using a zig-zag design (NAMMCO, 2015). The design in the rectangular outer strata and block 9 was left the same as in previous surveys.

Surveys were conducted mainly in passing mode, however, at the discretion of the flight leader the plane could go off-effort and circle cetacean groups if there was uncertainty in species identification and/or group size. Off-effort sightings made while transiting between transects were also recorded. However, these were not used in deriving the detection function or for abundance estimation.

In a few cases, transects were flown twice because of poor weather on the first pass or for other reasons (e.g. equipment issues). If a transect was flown more than once, it was recorded as one transect with the combined effort of the multiple passes.

Post-stratification

In the full surveys conducted in 2007, 2009 and 2016, contiguous areas of some strata were not surveyed because of poor weather and lack of time. In these cases, abundance was re-estimated using the revised surface areas of the blocks post-stratified to remove the un-surveyed portions.

Aircraft and configuration

A Partenavia Observer P-68 (Figure 2), with one bubble window on each side of the plane was used in all surveys up to and including 2015. A de Havilland DHC-6 Twin Otter (Figure 3), with 4 bubble windows was employed in the 2016 survey, which facilitated a full double platform for the first time. A satellite navigation system was used to fly the transects. Target altitude was 229 m, except in 2007 when the survey was flown at 183 m because of the inclusion of the harbour porpoise as a target species. Short term deviations from the survey altitude were allowed in order to fly under clouds or avoid fog banks. The target ground speed was 90 kn.



Figure 2. Survey aircraft of the type used in surveys prior to 2016, a Partenavia P-68 Observer, with 1 set of bubble windows at the rear of the plane, shown with the 2015 survey crew. (Photo by Daniel Pike)



Figure 3. Survey aircraft used in 2016, a de Havilland DHC-6 Twin Otter with 2 sets of bubble windows, one at the front and the other at the rear of the plane. (Photo by Rikke Guldborg-Hansen)

In the surveys conducted in the Partenavia, the crew consisted of 2 primary observers occupying the rear seats with the bubble windows, the survey leader in the front right seat, and the pilot. The rear primary observers had a clear view of the trackline, whereas the front observer could only see the trackline with difficulty. In most cases the observers had experience on previous aerial surveys. In surveys up to 2001, all crew including the pilot made whale observations. After 2001 the pilot no longer recorded sightings. For consistency we have therefore excluded sightings by the pilot from our analyses.

In the 1986 and most of the 1987 surveys, the front and rear seats were not visually or aurally isolated, so observations were not independent between the front and rear platforms. In subsequent surveys, isolation was maintained visually using a curtain and aurally by displacing the headset microphones as an experiment in 1987 and as a practice thereafter. Primary observers shifted seats on a daily basis so mark-recapture data could be obtained for each observer.

In 2016, 4 observers were distributed in front and rear platforms onboard the Twin Otter, all using bubble windows with a clear view of the trackline. The seats were far enough apart such that visual and aural isolation was maintained,

making the platforms independent. The survey leader also acted as one of these observers.

Data collection

Data collection and recording techniques have evolved over the 30 years of surveys due to experience and technological innovations.

In the 1986 survey, data on sightings and effort were recorded on paper forms by the survey leader, who was in communication with the other observers by intercom. In 1987 and 1995, a 4-channel cassette tape recording system was used, and the time of the recording was used to retrieve position data from the GPS stream. From 2001 to 2009, data were recorded on laptop computers (1 per observer), which also recorded a time stamp and position from the GPS when the microphone was triggered. In 2015 and 2016, data were recorded on digital voice recorders, with positional data retrieved from the GPS stream by correlation with time.

In all surveys except 1986, observers recorded their own sightings vocally and sightings of all species were registered in all surveys. After 1986, additional data on sighting cues were taken for common minke, other baleen and sperm whale sightings. A cue was considered to be a dive by a common minke whale, defined as the moment the body submerges below the sea surface, or a blow by any other baleen whale or a sperm whale. The following data were recorded for every cetacean cue or sighting: time and position of sighting, angles of declination and from the head of the aircraft, time and position at which the angles were measured, cue type or behaviour, species with certainty (2 levels), school size and direction of travel. After 2001, most declination angles were measured when the sighting was abeam of the aircraft, eliminating the need to explicitly measure a lateral angle.

Prior to 2015, declination angles were measured with a hand-held inclinometer (Suunto PM5) and lateral angle from the nose of the airplane was estimated using an angle board mounted on the window frame. Beginning in 2015 and throughout later surveys, devices developed specifically for the NASS 2015 aerial surveys, called geometers, were used to record the times and declination angles to observations (Hansen et al., in prep). The geometers used 3D accelerometers, a 3D gyroscope, and a 3D magnetometer to measure the pitch, roll and yaw orientation of the device, and recorded these measurements, along with the clock time from the computer, to a text file when a button was pressed. The geometers were fitted with "Red Dot" gun sights (Bushnell First Strike <http://bushnell.com/all-products/rifle-scopes/trophy-red-dot/first-strike>) to enable the user to aim accurately at targets. The geometers were "sighted in" using targets at known declination angles and thoroughly tested for accuracy, angle drift and reproducibility before being used on the survey. During testing it was found that yaw measurements were not consistently accurate in the plane. We therefore elected to measure declination angles when the sighting was directly abeam.

In addition to recording cetacean sightings, the survey leader also monitored all changes in survey effort and environmental conditions. These included the beginning and end of each transect, interruptions in effort, weather conditions, changes in Beaufort Sea State (BSS), sightability (subjective scale, 3 levels) and glare (intensity and angles). In surveys up to 2001, these data were recorded on paper forms; in later surveys they were

recorded by voice so that the survey leader could maintain searching effort.

Data preparation

Data collected during BSS >3 were not used in the analyses. Both certainty classes (high and moderate) of species identification were included in data for species abundance estimates.

Radial, perpendicular and forward distances to the whale at the time the cue and/or animal was sighted were calculated as follows:

Where:

$$X = ALT \times \tan(90 - \alpha)$$

And:

$$Y = V \times ET$$

$$R = \sqrt{X^2 + Y^2}$$

Then

Where

X = perpendicular distance to sighting;

Y = distance ahead of the plane of the sighting at the time the sighting was made;

R = radial distance to sighting at the time the sighting was made;

α = declination angle to sighting;

V = ground speed;

ET = time elapsed between making the sighting and recording the angle measurements;

ALT = altitude.

In cases where the declination measurement was taken abeam of the aircraft, the putative head angle of 90° was corrected for aircraft drift angle and sighting distances were calculated as above.

Duplicate identification

Identification of duplicate sightings between the front and rear platforms was required to correct abundance estimates from the 2007, 2009 and 2016 surveys. In surveys using the Partenavia (2007 and 2009), which had a double platform on the right side only, duplicates were identified on the right side, while for the 2016 survey using the Twin Otter and double platforms on both sides, both right and left side duplicates were identified.

Duplicate cue or sighting identification followed the procedure used in previous surveys wherein duplicates between the front and rear right-side observers were identified through coincidence in the time and location of the sighting. Duplicates were identified as sighting pairs with 1) difference in sighting time 3 seconds or less, and 2) difference in radial or perpendicular distance to sighting 30% or less. In general, duplicate identification with surveys of this type is unambiguous.

Cue count estimates for common minke whales

Data analyses were carried out using the DISTANCE 6.2 (Thomas et al., 2010) software package and stratified cue counting methods (Borchers et al., 2009; Buckland et al., 2001; Hiby et al., 1989) to obtain an uncorrected estimate including rear seat cue sightings only (2007 and 2009) or unique (i.e. duplicates counted once) cue sightings (2016). Only common minke whales that exhibited a valid cue (i.e. body submerges below surface) were included in the analysis. This therefore excludes sightings in which the whale was submerged for the entire duration of the sighting. The cue rate was assumed to be 53 cues per whale per hour (Gunnlaugsson, 1989), the same rate used in previous analyses (Borchers et al., 2009; Hiby et al., 1989). No variance estimate was available for this cue rate so the variance of the abundance estimates does not include this source. The resulting estimates are uncorrected for visible cues missed by observers (perception bias).

Calculation of effective detection radius (*edr*) for cues was pooled over geographical strata, while encounter rate (n/T) was calculated separately for each stratum. Estimation of expected cluster (i.e., cue group) size ($E(s)$) was estimated at the stratum level. Radial distance data were truncated such that about 10% of the most extreme values were excluded from the analysis. The Hazard Rate and Half Normal models for the detection function were initially considered and the final model was chosen by minimisation of Akaike's information criterion (AIC) (Buckland et al., 2001), goodness of fit statistics and visual inspection of model fits. Covariates available for incorporation into the detection functions included observer identity, cue group size, cue type, side (R or L), platform (2016 only, front or rear), BSS, % cloud cover, fog (light, moderate, severe), glare intensity (light, moderate, severe), glare proportion in viewing field, rain (light, moderate, severe), and sightability (subjective, poor, moderate, good). For covariates related to glare and sightability, separate measurements were available from each side of the plane. Covariates were assumed to affect the scale rather than the shape of the detection function and were incorporated into the detection function through the scale parameter in the key function (Thomas et al., 2010). Covariates were retained only if the resultant AIC value was lower than that for the model without the covariate.

To estimate perception bias, duplicate and unique sightings from both platforms were analyzed using mark-recapture distance sampling (MRDS) techniques (Burt, Borchers, Jenkins, & Marques, 2014; Laake & Borchers, 2004). The average proportion of minke whale cues seen at radial distance 0 ($p(0)$) was estimated using logistic regression within DISTANCE with the covariates described above. For the 2007 and 2009 surveys, which had double platform effort on the right side only and a somewhat obstructed view from the front seat, we used a trial configuration in which the front platform provided duplicate trials to the rear (primary) platform and $p(0)$ was estimated for the primary platform only. For the 2016 survey, which used symmetrical platforms, we used the independent observer (IO) configuration (Laake & Borchers, 2004). The estimated average probability of detection at radial distance 0 ($p(0)$) was applied as a multiplier to the uncorrected estimates for the primary platform (2007 and 2009) or the combined platforms (2016) to derive the perception-bias corrected estimates. This is equivalent to MRDS estimation under the assumption of point independence (PI) (Burt et al., 2014; Laake & Borchers, 2004)

except that in this case a pooled value for $p(0)$ is estimated at the survey rather than the stratum level.

Line transect estimates for other species

Uncorrected estimates

For the 2007 and 2009 surveys, only sightings from the rear platform were used to estimate abundance prior to correction for perception bias. Unique sightings from both front and rear platforms were used in 2016. Estimation of effective search half-width (*esw*) was as described above for estimation of *edr* except that perpendicular rather than radial distances to sightings (rather than cues) were used. Estimation of *esw* was pooled over strata if the detection function incorporated no covariates; otherwise it was estimate at the stratum level. Similarly, estimation of mean group size was carried out at the stratum level.

Perception bias corrected estimates

Duplicate and unique sightings from both platforms were analyzed using MRDS methods as described above, using perpendicular distance rather than radial distance in the detection functions, and with the same covariates described above. As with the cue-count analysis described above, for the 2007 and 2009 surveys, the trial configuration was used, while for analysis for 2016 employed an IO configuration. Both full independence (FI), which assumes that sighting probability is independent at all distances (Laake & Borchers, 2004), and PI models were tried, with the best models selected by minimization of AIC.

Temporal trends

As described above, survey design and methodology evolved over the 30-year period between 1986-2016, and only surveys conducted after 1995 provide data suitable for bias correction for most species. Some additional surveys conducted over the period had reduced effort and covered only parts of the survey area (1988, 2003, 2004, 2015), did not use fully independent platforms, and did not result in sufficient sightings of most species to develop independent detection functions. In order to include all available survey data, we used the least biased estimator of relative abundance that was available from all surveys to elucidate trends in abundance across all survey years: uncorrected line transect density using data from the primary observers only. Only surveys conducted in the June/July period were included in this analysis, and for surveys up to and including 2015, only sightings from the primary platform (i.e., rear seats) were included. For the 2016 surveys, unique sightings from both platforms were used.

Because some partial surveys did not produce sufficient sightings to estimate separate detection functions, distance data were pooled across all surveys to derive common models for the species detection functions, while including a survey identity covariate to allow the scale of the detection functions to vary by survey. Group size and encounter rate were estimated at the stratum level by survey year. MCDS methods as described above were employed, however there was a more limited choice of covariates available for the combined dataset as not all covariates were collected consistently in all years. Group size, side, BSS, fog (3 levels), glare intensity (3 levels) and

sightability (subjective, 3 levels) were consistently available, as well as survey identity as described above.

The resulting estimates of line transect density from all surveys, including 95% confidence intervals, were plotted by species and stratum to visualize trends over time. For comparison, fully corrected (for common minke whales) or perception bias corrected (other species) density estimates from surveys from which they were available were also included. The statistical significance of changes in corrected estimates was determined using a parametric bootstrapping procedure, assuming a log-normal distribution for density estimates and generating a sample of 1,000 realizations of density across surveys and strata.

Seasonal changes in distribution and abundance

We analyzed the 2004 data separately by species, using the methods described above, to estimate density in April, June-July and September of that year, and estimates were compared using the parametric bootstrap procedure described above.

RESULTS

Coverage

Realized effort and sightings from all surveys is provided in Supplementary File 1, and illustrated in Figures 4, 5, 6, 7, and 8. Further details of the coverage realized in full surveys up to and including 2001 are provided in Pike et al. (2009). Effort in partial surveys in 1988 and September 2003 was restricted mainly to block 1 with minor effort in blocks 8 and 9 in 2003. In 2004, some effort was flown in 3 periods: April, June-July and September. Effort was flown in all strata in the June-July portion of the survey but was more restricted in April and September. In May 2005, all blocks except 6 and 7 off eastern Iceland received limited coverage. In 2008, effort was restricted to blocks 1 and 9.

Of the 30 days the plane was available in 2007, at least some effort was flown on 20 days (67%). Unlike in previous years, pack ice covered much of the northwestern part of the survey area, including the northern part of block 3 and the western parts of blocks 4 and 5. Pack ice coverage ranged from 0 to 90% in these areas. Near complete coverage was achieved in Blocks 1, 2, 3, 6 and 8. Block 8 was covered twice. Blocks 4 and 9 received moderate coverage, while the offshore blocks 5 and 7 were covered less than adequately and required post-stratification. The northeast and southeast extremes of the survey area were not covered. Total realized effort was 79% of planned effort.

Of the 29 days the plane was available in 2009, at least some effort was flown on 17 days (59%). Coverage was over 80% complete in blocks 1, 4 and 8, and block 1 received substantial repeat coverage. Blocks 2, 3, 7 and 9 received moderate coverage, while block 6 was covered poorly. Unlike in most previous surveys the NW and NE extremes of the survey area were well covered, whereas the SE corner of the survey area was not covered. An undetected failure in the recording equipment led to the loss of primary platform data on one side of the plane for several transects. Realized effort was halved on these transects for analysis. Post-stratification removed the

southern portion of block 6 and the far-eastern portion of block 9. Total realized effort was 73% of planned effort.

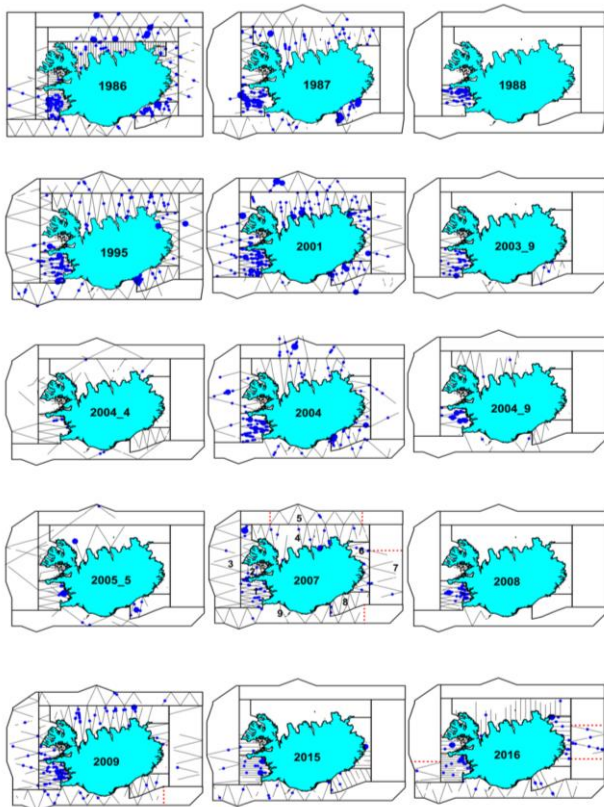


Figure 4. Realized survey effort and sightings of common minke whales by survey. Survey month is appended to year (numerical) if not June or July. Symbol size varies with group size from 1 to 3. Post-stratification borders are shown as red dotted lines.

Of the 27 days the plane was available in 2015, at least some effort was flown on 12 days (44%). The weather pattern in Iceland in 2015 was quite different than that encountered in other survey years and was characterized by a nearly constant strong easterly or northeasterly flow, caused by a stationary low pressure area to the south of the island. This led to a situation where the central west or southwest areas were in the wind shadow of the island and could have been surveyed repeatedly over the period. However, all other areas were usually too windy to survey. In the brief windows when other areas became open, they were usually covered by fog. Blocks 1 and 8 received nearly complete coverage, while over 70% coverage was achieved in block 9. Blocks 2, 3 and 6 received under 50% coverage, while blocks 4, 5 and 7 were not covered at all. First-pass (i.e., non-repeat) coverage for the entire survey was only 37%, the lowest of the 7 surveys attempted since 1986.

Of the 27 days the plane was available in 2016, at least some effort was flown on 13 days (48%). As in 2015, there were generally poor weather conditions particularly in the second half of July, with extensive fog and low cloud in most areas, followed by a persistent northerly flow that precluded survey in all areas except the south coast during the last week of the survey. Blocks 1, 6 and 9 were well-covered (over 70%) while block 4 was moderately covered. All other blocks received less than 50% coverage and no useable effort was flown in block 5.

Post-stratification removed the northern parts of blocks 2 and 3, and the northern and southern portions of block 7. Altogether, only 53% of planned effort was flown.

Distribution

Common minke whales occurred in all strata but were most frequently sighted in nearshore blocks 1, 4 and 8 (Figure 4). In surveys after 2005, common minke whales were rarely sighted in block 8 off southeastern Iceland, an area where they had previously been abundant. Common minke whales occurred most frequently as single animals (94%) and infrequently as pairs (5%) or larger groups (1%).

Humpback whales were infrequently sighted in the 1986 and 1987 surveys but were more often encountered from 1995 onwards. Distribution varied between surveys but humpback whales tended to be most frequently sighted in the northern half of the survey area, particularly in the northeast and northwest extremes, which were, unfortunately, rarely fully covered by the surveys (Figure 5). Single animals were sighted most frequently (71%) and groups of 4 or fewer comprised 98% of the sample, but larger groups of up to 14 were occasionally seen.

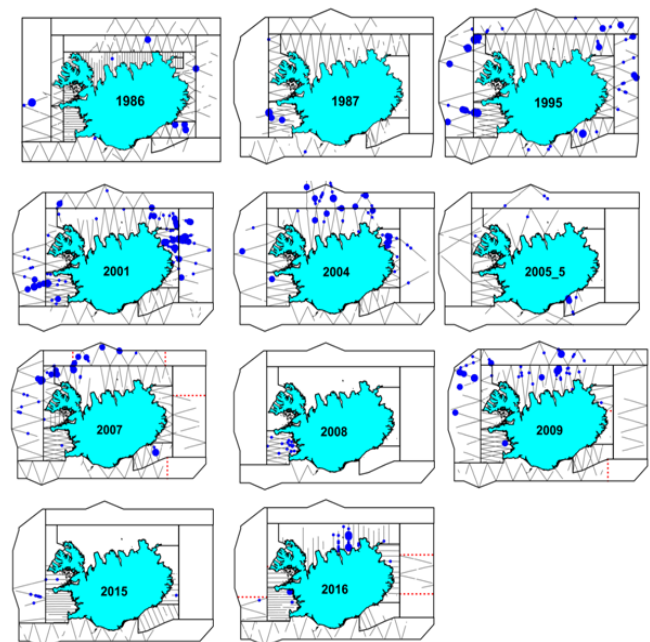


Figure 5. Realized survey effort and sightings of humpback whales by survey. Survey month is appended to year (numerical) if not June or July. No humpback whales were seen in surveys conducted in 1988, 2003_9, 2004_4, and 2004_9. Symbol sized varies with group size from 1 to 3. Post-stratification borders are shown as red dotted lines.

In full surveys attempted since 2001 (2007, 2009, 2015, 2016), white-beaked dolphins comprised 92% of all sightings identified as dolphins, with most of the remainder (7%) being unidentified to species. Very small numbers of white-sided (*Lagenorhynchus acutus*) and bottlenose (*Tursiops truncatus*) dolphins were also sighted (Figure 8). In the partial surveys carried out between 2003-2005, most dolphin sightings were not identified to species, apparently because the observers employed were not able to discriminate dolphin species. In those years, it is assumed that all of the sightings of unidentified dolphins were

white-beaked dolphins and they are included in estimates of abundance. Sightings of unidentified dolphins are not included in other years. White-beaked dolphins occurred in all strata but were most common off western and especially northern Iceland, where they were seen far offshore in some years (Figure 6). Modal group size was 1 to 3, and groups of up to 8 animals comprised 82% of the sample. Larger groups of up to 200 animals, sometimes associated with groups of long-finned pilot whales (*Globicephala melas*), were occasionally seen.

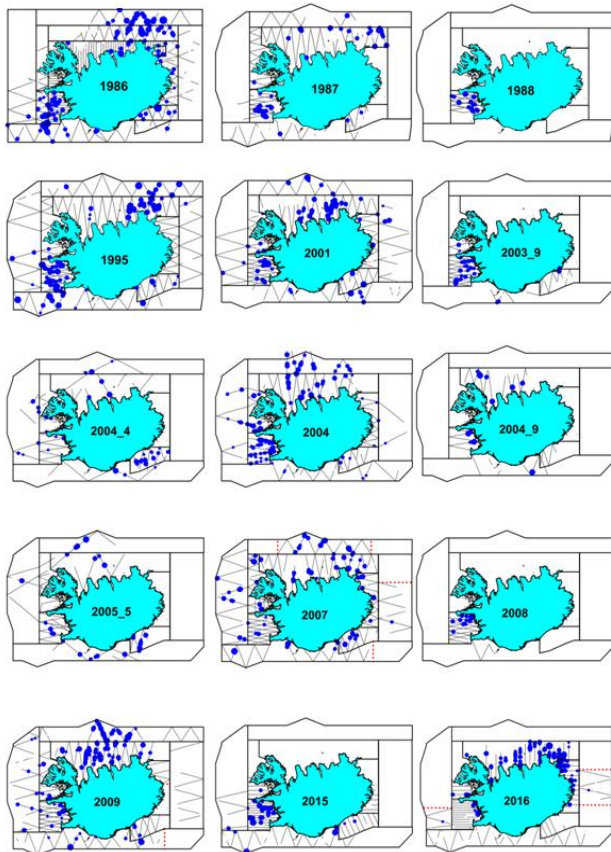


Figure 6. Realized survey effort and sightings of white-beaked dolphins by survey. Sightings of unidentified dolphins are included in 2003, 2004 and 2005 but not in other years. Survey month is appended to year (numerical) if not June or July. Symbol sized varies with group size from 1 to 30. Post-stratification borders are shown as red dotted lines.

Harbour porpoises occurred in all strata but were most frequently sighted in the nearshore blocks (Figure 7). They occurred most often as single animals or pairs, which together comprised 88% of the sample. The number of harbour porpoise sightings varied greatly between surveys and was greatest in 2007 when a specialist harbour porpoise observer was employed.

Sightings of other species were not sufficient to warrant abundance estimation (Figure 8). Fin whales (*Balaenoptera physalus*) were most frequently sighted far offshore western and southwestern Iceland. Long-finned pilot whales had a similar distribution and were seen in groups of up to 50 animals. Killer whales (*Orcinus orca*) were seen rarely throughout the survey area but were most frequently sighted off western Iceland. Scattered sightings of sperm whales (*Physeter*

macrocephalus) were made in deep waters off southern and far northern Iceland. Blue whales (*Balaenoptera musculus*) were sighted off the west coast of Iceland up until and including 2001 but have been largely absent from this area in more recent surveys. Northern bottlenose whales (*Hyperoodon ampullatus*) were sighted occasionally in the deep waters off southeast and eastern Iceland. White-sided dolphins were most commonly sighted off southwest Iceland, while sightings of common bottlenose dolphins were exceedingly rare.

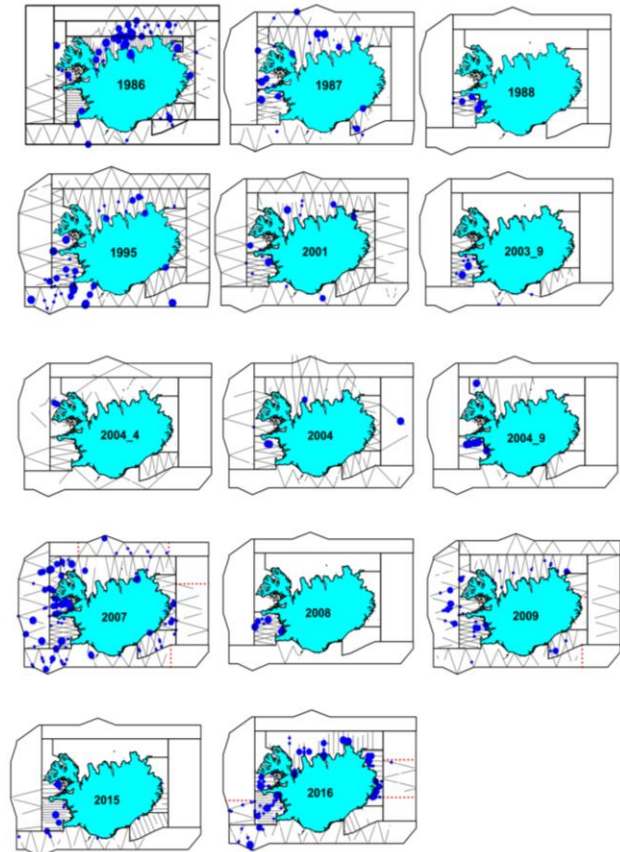


Figure 7. Realized survey effort and sightings of harbour porpoises by survey. Survey month is appended to year (numerical) if not June or July. No harbour porpoises were seen in the survey conducted in 2003_5. Symbol sized varies with group size from 1 to 3. Post-stratification borders are shown as red dotted lines.

Abundance estimates

Numbers of sightings and duplicate sightings were sufficient to estimate abundance of common minke whales and white-beaked dolphins from full surveys conducted in 2007, 2009 and 2016. Abundance of humpback whales was estimated from the 2007 and 2009 surveys, but not for 2016 when large parts of the survey area where densities had been high in previous surveys (i.e., block 5, northern blocks 3 and 7) were not sampled. Abundance of harbour porpoises was estimated separately from the 2007 survey (Gilles et al., under revision) and data quality was sufficient to estimate abundance from the 2016 survey, but not the 2009 survey. Model specifications for all abundance estimates are provided in Table 1, and distance detection functions are provided in Figures 9 and 10. Estimates for the survey area by species and year are provided in Table 2, while stratum-level estimates and other details are provided in Supplementary Files 2-11.

Table 1. Model specifications for detection functions by survey and species. All DS (distance) and MRDS (mark-recapture) models include perpendicular distance (line transect = LT) or radial distance (cue counting = CC) as a covariate. BA – common minke whale; LL – white-beaked dolphin; MN – humpback whale; PP – harbour porpoise; HN – half normal; HZ – hazard rate; BSS – Beaufort sea state; OBS – observer identity; SIDE – side of plane; SPEC? – species identification certainty; YEAR – survey year; GLARE – glare severity; SIGHT – sightability; PLAT – platform; FI – assumed full independence; PI – assumed point independence.

SPECIES	YEAR	TYPE	TRUNCATION		DS MODEL		MR MODEL	
			L	R	KEY	Covariates/Adj	TYPE	Covariates
BA	2007	CC	0	1200	HN	/Cos	PI	
LL	2007	LT	0	350	HN	BSS	PI	GLARE
MN	2007	LT	0	1500	HN		FI	
BA	2009	CC	0	1600	HN	OBS	PI	
LL	2009	LT	100	600	HZ		PI	
MN	2009	LT	0	1200	HN	SIDE	PI	
BA	2016	CC	0	1800	HZ	SPEC?	PI	
LL	2016	LT	100	500	HN		PI	DIST:SIGHT
PP	2016	LT	100	400	HN	SIDE + SPEC?	PI	PLAT
BA	ALL	LT	0	1000	HZ	YEAR		
LL	ALL	LT	0	1000	HZ	YEAR		
MN	ALL	LT	0	2000	HN	YEAR		

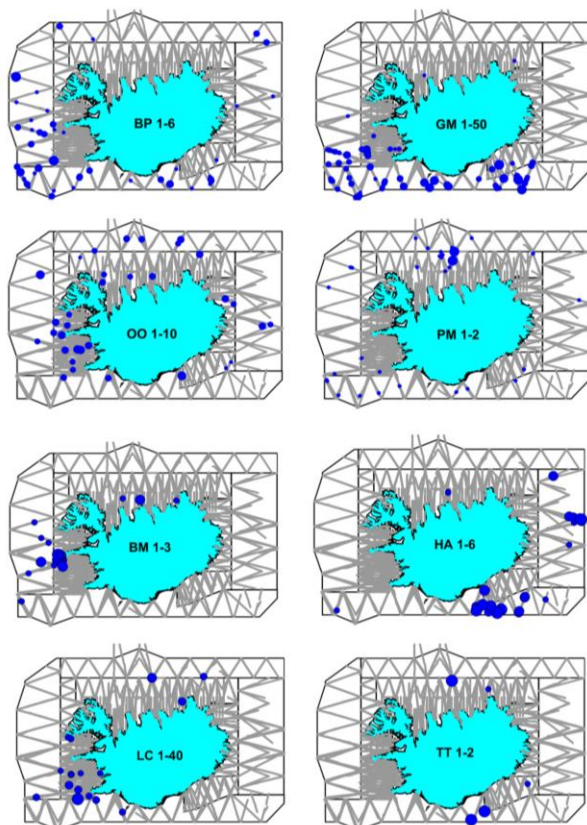


Figure 8. Realized survey effort from all surveys and sightings of cetaceans by species. Symbol size varies with group size in the number range given. BP – fin whale; GM – long-finned pilot whale; OO – killer whale; PM – sperm whale; BM – blue whale; HA – northern bottlenose whale; LC – white-sided dolphin; TT – common bottlenose dolphin.

2007

Common minke whales

A total of 71 unique (i.e., duplicates counted once) cues were sighted by the primary and secondary observers (Supplementary File 1). Of these, 9 were cues sighted by both the secondary observer and the primary observer on the right side of the plane (i.e., duplicate cues), and all of these were with one of the 2 primary observers (identified as P2).

A half-normal model with 1 cosine adjustment provided best fit to the primary platform cue sighting data (Figure 9). The total uncorrected abundance was 10,634 (CV=0.30, 95% CI: 5,459 – 18,262) (Supplementary File 2).

Because observer P2 sighted nearly twice as many cues (32 vs 17) as observer P1, and accounted for all duplicate sightings, we also estimated abundance using data from that observer only. The same model described above provided best fit to these data, resulting in an uncorrected abundance estimate of 15,055 (CV=0.36, 95% CI: 6,357 – 27,278) (Supplementary File 3).

The best MRDS model for the right side duplicate data, including sightings from both primary observers (who shifted sides regularly), included radial distance only and resulted in an estimated $p(0)$ of 0.71 (CV=0.25) for the primary platform. The fully corrected total estimate was 14,638 (CV=0.30, 95% CI: 7,381 – 24,919) (Table 2, Supplementary File 2). Post-stratification would decrease both the uncorrected and corrected estimates by 11%.

The best MRDS model including data from primary observer P2 only again included only radial distance and resulted in an estimated $p(0)$ of 0.72 (CV=0.24) for the primary platform. The fully corrected total estimate was 20,834 (CV=0.35, 95% CI:

9,808 – 37,042), with post stratification reducing the estimates by 15% (Table 2, Supplementary File 3).

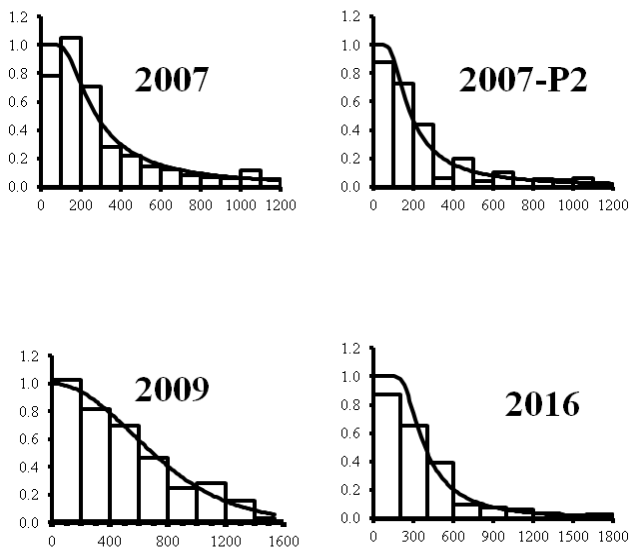


Figure 9. Detection functions (solid line) and cue sightings of common minke whales by survey. X-axis – radial distance (m); Y-axis – sighting probability, corrected for surface area.

Humpback whales

A total of 53 unique sightings were made by all observers (Supplementary File 1), of which 39 were sighted by the primary observers. Right truncation to 1,500 m reduced the number of primary sightings to 38.

A half-normal model with no covariates or series expansions provided best fit to the detection function (Figure 10), resulting in an *esw* of 969 m (CV=0.14) and total uncorrected abundance of 1,010 (CV=0.36, 95% CI: 483 – 2,110) (Supplementary File 4). Density and abundance were highest in stratum 5, which accounted for 56% of the total abundance. Post-stratification would decrease total abundance by 25%.

Of the 27 detections by the secondary platform within the truncation distance, 13 were missed by the primary platform. A full independence model using distance only as a covariate resulted in lowest AIC and an estimated *p*(0) for the primary platform of 0.87 (CV=0.13). Total abundance corrected for perception bias for the survey area was 1,518 (CV=0.38, 95% CI: 705 – 3,266) (Table 2, Supplementary File 4).

White-beaked dolphins

A total of 103 unique groups of white-beaked dolphins were sighted while on effort (Supplementary File 1), of which 86 were seen by the primary observers. Restriction to BSS≤3 and right truncation to 350 m reduced the number of primary sightings to 73. A half-normal model with BSS as a scale covariate provided best fit to the detection function (Figure 10), with *esw* negatively correlated with BSS. Density and abundance were highest in strata 4, 5 and 9, which together accounted for 78% of the total estimated uncorrected abundance of 45,497

(CV=0.37, 95% CI: 21,966 – 94,237) (Supplementary File 5). Post-stratification would decrease this estimate by 21

A total of 23 detections were made by the secondary observer on the right side within the truncation distance, of which 6 were missed by the primary observers. A point-independence model including distance and glare intensity as covariates provided best fit to the MRDS model, resulting in an estimated *p*(0) of 0.98 (CV=0.04) and an abundance estimate corrected for perception bias of 46,683 (CV=0.37, 95% CI: 22,409 – 97,251) (Table 2, Supplementary File 5).

Table 2. Abundance estimates (*N_c*) for the full (F) and post-stratified (P) survey area by survey year and species. Estimates are fully corrected for common minke whales and corrected for perception bias only for other species. BA – common minke whale; LL – white-beaked dolphin; MN – humpback whale; PP – harbour porpoise.

SURVEY	SPECIES	F/P	<i>N_c</i>	CV	LCL	UCL
2007	BA	F	20,834	0.35	9,808	37,042
2007	BA	P	17,650	0.34	7,220	30,695
2009	BA	F	9,588	0.24	5,274	14,420
2009	BA	P	9,129	0.24	5,084	13,766
2016	BA	F	13,497	0.5	3,312	55,007
2016	BA	P	9,885	0.45	3,132	31,197
2007	MN	F	1,518	0.38	705	3,266
2007	MN	P	1,142	0.35	569	2,293
2009	MN	F	2,261	0.35	1,142	4,477
2009	MN	P	2,235	0.35	1,124	4,442
2007	LL	F	46,683	0.37	22,409	97,251
2007	LL	P	36,929	0.36	18,037	75,607
2009	LL	F	75,959	0.56	26,366	218,834
2009	LL	P	74,878	0.56	25,790	217,400
2016	LL	F	59,966	0.44	24,907	144,377
2016	LL	P	58,919	0.45	24,191	143,499
2016	PP	F	22,806	0.48	9,166	56,746
2016	PP	P	18,527	0.49	7,395	46,414

2009

Common minke whales

A total of 136 unique cues were sighted by the primary (P) and secondary (S) observers (Supplementary File 1). Observer P1 made fewer sightings than P2 while acting as a primary observer. For example, P1 made 22 cue sightings in block 1 vs 42 made by P2. Observer S (secondary platform observer) made 43 cue sightings, 24 of which were unique (i.e. not duplicated by the primary observers). Observer P1 duplicated 7 of 22 sightings while P2 duplicated 12 of 21. Both observers missed at least some cues within 400 m of the plane.

A truncation distance of 1,600 m was chosen for these data, reducing the number of primary sightings to 88. A half-normal function with no adjustment terms and including a covariate for observer identity, combining observer P3, who made only 4 sightings, with observer P1 to make a 2-level covariate (i.e., P1+P3, P2), resulted in the lowest AIC. This model resulted in an

edr of 849 m (Figure 9) and a total uncorrected estimate of 5,284 (CV= 0.24, 95% CI: 2,915 – 7,822) (Supplementary File 6).

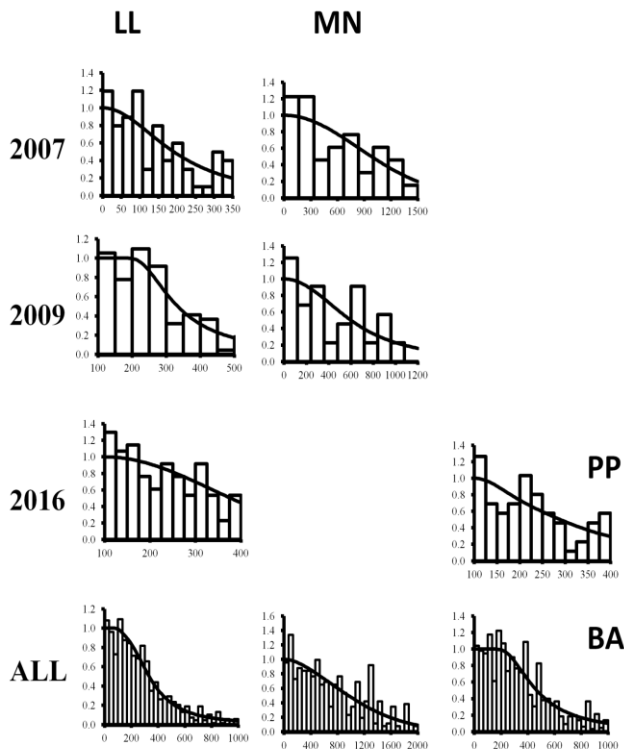


Figure 10. Detection functions (solid line) and sightings by species and survey, and for all surveys combined (ALL). X-axis – perpendicular distance (m); Y-axis – sighting probability. LL – white-beaked dolphin; MN – humpback whale; PP – harbour porpoise; BA – common minke whale.

The best MRDS model for the right side duplicate data included only radial distance as a covariate and resulted in an estimated $p(0)$ of 0.55 (CV=0.10) for the primary platform. The fully corrected total estimate was 9,588 (95% CI: 5,274 – 14,420), with post-stratification reducing both the corrected and uncorrected estimates by 5% (Table 2, Supplementary File 6).

Humpback whales

A total of 69 unique humpback whale groups were sighted by all observers (Supplementary File 1), of which 56 were seen by the primary observers. Restriction to $BSS \leq 3$ and right truncation at 1,200 m reduced the number of primary sightings to 48. A half-normal model including the factor covariate for the side of the plane provided best fit to the detection function (Figure 10), with detection distances on the right being generally shorter than those on the left. Density and abundance were highest in blocks 3, 4 and 5, which together accounted for 96% of the total uncorrected abundance estimate of 2,002 (CV= 0.30, 95% CI: 1,096 – 3,655) (Supplementary File 7). Post-stratification would reduce this estimate by 1%.

Of the 12 sightings made by the secondary right-side platform, 5 were also sighted by observers on the primary platform. A model assuming point-independence using the distance detection function described above and including only distance in the MRDS detection function was chosen based on minimization of AIC, resulting in an estimated average $p(0)$ of 0.89 (CV=0.18). This correction for perception bias increased

estimated abundance to 2,261 (CV=0.35, 95% CI: 1,142 – 4,477) (Table 2, Supplementary File 7).

White-beaked dolphins

A total of 206 unique sightings of white-beaked dolphin groups were made (Supplementary File 1), of which 160 were seen by the primary observers. The number of sightings was lower than expected between perpendicular distances of 0 m and 100 m, requiring left truncation at 100 m and right truncation at 600 m. This, along with restriction to $BSS \leq 3$, reduced the number of primary sightings for abundance estimation to 117. A hazard rate model with no covariates provided best fit to the detection function (Figure 10). Density and abundance were highest in strata 4 and 5 (north Iceland), which accounted for 88% of the total uncorrected abundance estimate of 38,136 (CV=0.44, 95% CI: 15,499 – 93,831) (Supplementary File 8). Post-stratification would reduce this estimate by 1%.

Of the 42 detections by the secondary platform observer, 34 were missed by the primary observer on the same side of the plane. AIC was minimized using a model assuming point-independence and including distance only in the MRDS detection function, resulting in an estimated average $p(0)$ (actually $p(100)$ in this case) of 0.50 (CV=0.35). This increased estimated abundance, corrected for perception bias, to 75,959 (CV=0.56, 95% CI: 26,366 – 218,834) (Table 2, Supplementary File 8).

2016

Common minke whales

Not all minke whales exhibited valid cues; 25% were seen underwater and did not surface while in view. Of the 46 unique cues detected (Supplementary File 1), 13 (29%) were seen by both platforms. Observers staffing the rear platform sighted about twice as many cues as those in the front.

Radial distances were right truncated at 1,800 m, reducing the number of sightings to 36. A hazard rate model with no adjustment terms incorporating the covariate for certainty in species identification produced the lowest AIC, with lower certainty detections having a wider detection field. Average *edr* was 577 m (CV=0.09) (Figure 9). Total uncorrected abundance was 12,966 (CV=0.47, 95% CI: 3,384 – 49,688) (Supplementary File 9). Density and abundance were highest in blocks 6 and 7, with block 7 accounting for 61% of the total estimate. Post-stratification would reduce estimated abundance by 27%.

An MRDS model including radial distance and no other covariates produced the lowest AIC, estimating $p(0)$ as 0.96 (CV=0.19) for the combined platforms. This produced a fully corrected total abundance estimate of 13,497 (CV=0.50, 95% CI: 3,312 – 55,007) (Table 2, Supplementary File 9).

White-beaked dolphins

A total of 221 unique sightings of white-beaked dolphins were made by the combined platforms (Supplementary File 1), of which 63 were duplicate sightings. The frequency of white-beaked dolphin sightings was lower than expected within about 100 m of the transect line, so a left truncation distance of 100 m in the detection function was used, which, along with restriction to $BSS \leq 3$, resulted in a loss of 33 sightings. A right truncation distance of 500 m eliminated the need for adjustment terms and resulted in a further loss of 44 sightings. A half normal model incorporating no covariates provided best

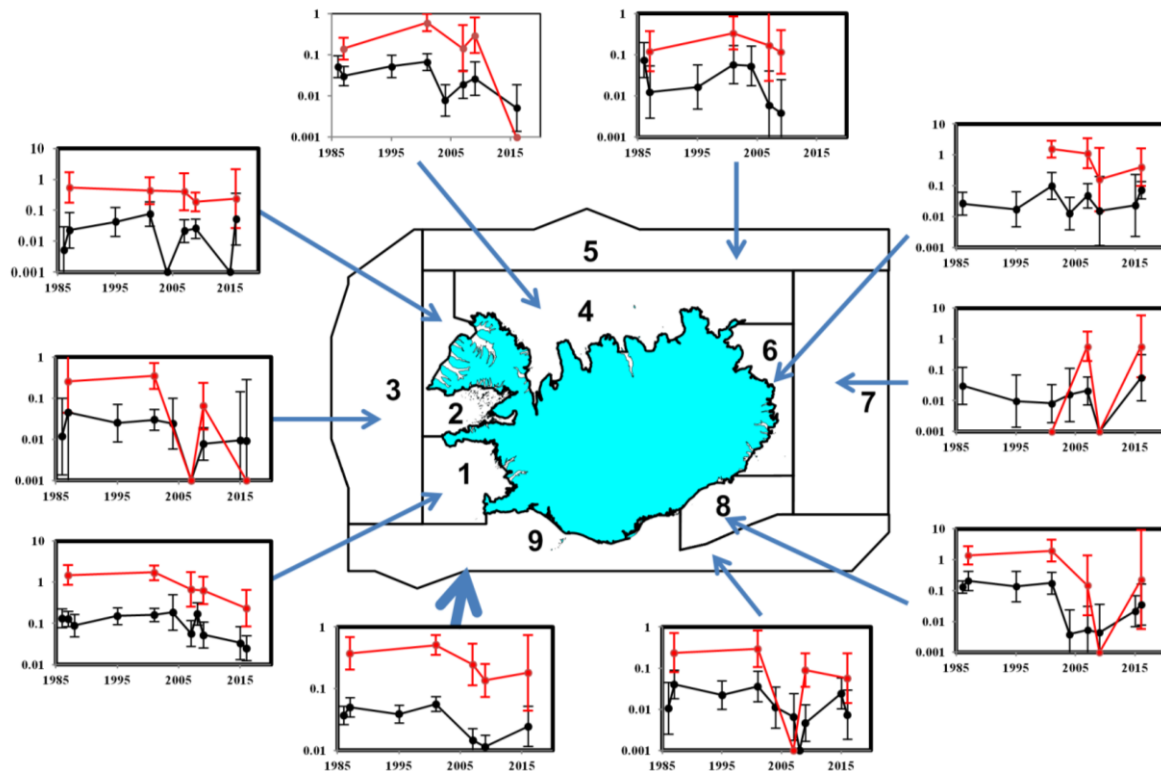


Figure 11. Trends in the relative abundance (black line, uncorrected line transect density, whales nm^{-2}) and fully corrected density (red line) of common minke whales by stratum and for the entire survey area (thick arrow). Zero values of density are shown as the lowest value on the Y-axis. 95% confidence intervals are shown.

fit as determined by minimization of AIC, resulting in an overall effective strip half-width of 269 m (i.e. from the left truncation distance of 100 m out to 369 m from the transect) (Figure 10). Total uncorrected estimated abundance was 42,908 (CV=0.42; 95% CI: 18,536 – 99,328) (Supplementary File 10). Density and abundance were highest in block 4, which accounted for 83% of the total estimate. Post-stratification would reduce this estimate by 2%.

Similar numbers of sightings were made by the front and rear platforms, with 46 duplicate sightings within the truncation distances. Some nearby sightings were missed by both platforms. Point independence models incorporating the model described above consistently produced lower magnitude AIC than did full independence models in the MRDS detection function. A point independence model incorporating the interaction term between perpendicular distance and sightability as a covariate in the MRDS detection function minimized AIC and was therefore chosen, estimating $p(0)$ as 0.72 (CV=0.13) for the combined platforms.

Total abundance corrected for perception bias was 59,966 (CV=0.44; 95% CI: 24,907 – 144,377) (Table 2, Supplementary File 10).

Harbour porpoises

A total of 90 unique sightings of harbour porpoise groups were sighted by the combined platforms (Supplementary File 1), of which 7 were duplicate sightings.

The number of harbour porpoise sightings was lower than expected within about 100 m from the transect line, so a left truncation of 100 m was used, thereby discarding 16 sightings, for the purpose of estimating esw . A right truncation distance of 400 m resulted in a further loss of 8 sightings. A half-normal model with no adjustment terms incorporating (in addition to perpendicular distance) factor covariates for side of the plane and species identification certainty provided the best fit to the data, resulting in an effective strip half-width of 187 m (i.e., from the left truncation distance of 100 m out to 287 m from the transect line) (Figure 10). Total uncorrected estimated abundance was 10,506 (95% CI: 6,120 – 18,036) (Supplementary File 11). Post-stratification would reduce this estimate by 20%.

Only 7 duplicate sightings were available to estimate perception bias. Point independence models incorporating the model described above consistently produced lower values for AIC than did full independence models in the MRDS detection function. A point independence model incorporating the covariate perpendicular distance and the factor covariate for platform identity in the MRDS detection function minimized AIC and was therefore chosen. Inclusion of platform identity as a covariate produces separate estimates of $p(0)$ for each platform: 0.45 (CV=0.41) for the combined platforms, 0.23 (CV=0.51) for the front platform and 0.30 (CV=0.47) for the rear platform. Total abundance corrected for perception bias was 22,806 (CV=0.48; 95% CI: 9,166 – 56,746) (Table 2, Supplementary File 11).

Table 3. Comparison of corrected abundance estimates of common minke whales for all strata and the entire survey area. Estimates for 1987 and 2001 are from Borchers et al. (2009). Cells list proportional change from first year to second. Plus or minus sign indicates change to or from abundance of zero. * = $P < 0.05$, ** = $P < 0.01$.

BLOCK	YEAR	2001	2007	2009	2016	
1	1987	0.17	-0.56	-0.58	-0.84	**
1	2001		-0.62	* -0.64	* -0.86	**
1	2007			-0.05	-0.63	
1	2009				-0.62	
2	1987	-0.19	-0.24	-0.64	-0.54	
2	2001		-0.06	-0.56	-0.44	
2	2007			-0.54	-0.41	
2	2009				0.13	
3	1987	0.34	** -1.00	** -0.79	-1.00	**
3	2001		-1.00	** -0.83	** -1.00	**
3	2007			+	** -1.00	**
3	2009				-1.00	**
4	1987	3.28	** 0.01	1.14	-1.00	**
4	2001		-0.76	* -0.50	-1.00	**
4	2007			1.11	-1.00	**
4	2009				-1.00	**
5	1987	1.73	0.41	-0.01		
5	2001		-0.48	-0.63		
5	2007			-0.30		
5	2009					
6	2001		-0.02	-0.17	-0.13	
6	2007			-0.21	-0.16	
6	2009				0.05	
7	2001		+ **	0.00	+ **	
7	2007			-1.00	** 0.02	
7	2009				+ **	
8	1987	0.39	-0.89	** -1.00	** -0.83	*
8	2001		-0.91	** -1.00	** -0.87	*
8	2007			-1.00	** 0.50	
8	2009				+ **	
9	1987	0.43	-0.91	** -1.00	** -0.99	**
9	2001		-0.95	** -1.00	** -1.01	**
9	2007			-1.00	** -0.06	
9	2009				+ **	
TOTAL	1987	0.38	-0.33	-0.63	* -0.50	
TOTAL	2001		-0.52	* -0.74	** -0.64	*
TOTAL	2007			-0.45	-0.26	
TOTAL	2009				0.34	

Trends in relative and corrected abundance

Common minke whales

The complete dataset from all surveys included 1,227 primary platform sightings of common minke whale groups. Truncation to 1,000 m perpendicular distance reduced the number of available sightings by 15%. Best fit to the detection function was achieved using a hazard rate model including a factor covariate for survey year, resulting in an estimated average *esw* of 531 m (CV=0.02) (Table 1, Figure 10). This ranged from 381 m in 2015 to 766 m in 2009. Mean group size across all surveys was 1.07 (CV=0.32) and there was no significant difference ($P > 0.05$) between survey years.

Relative density in the survey area was relatively stable from 1986 until 2001, after which it dropped by about 75% in 2007 and remained at similarly low levels through 2016 (Figure 11). The decline in the survey area as a whole was driven by declines in blocks 1, 4, 5 and 8. The declines in these areas began sometime after 2001, and relative density was still high in blocks 1 and 5, but not 4 and 8, as late as 2004 (Figure 11).

Relative density recovered to higher levels in block 1 in 2008 but declined again thereafter. Similarly, fully corrected density in the entire survey area was significantly lower after 2001, declining by 52% to 74% and again remaining at low levels up to 2016 (Table 3). Significant declines compared to 2001 were observed in blocks 1, 4 and 8, areas which had held the highest densities of common minke whales in previous surveys, and also in blocks 3 and 9, areas which had previously had low densities. Common minke whales have been nearly absent from block 8 off southeast Iceland (formerly an area of high density) in surveys conducted since 2001. Density in block 7 off eastern Iceland has undergone substantial fluctuations but was higher in 2016 than in any previous survey.

Humpback whales

A total of 458 humpback whale groups were seen from the primary platform over all survey years. Right truncation to 2,000 m reduced the number of sightings by 12%. The detection function was modeled using a half-normal key function with a factor covariate for survey year (Figure 10). Estimated *esw* was 1,116 m (CV=0.04) averaged over all surveys and ranged from a low of 405 m in 2008 to a high of 1,529 m in 2005. Mean group size was 1.5, (CV=0.04) ranging from 1.23 in 2015 to 2.38 in 1986, with no significant differences ($P > 0.05$) between survey years.

Relative density in the survey area increased from 1986 to 2001, then declined thereafter (Figure 12). This pattern was driven primarily by density changes in strata 3 and 7, where high relative densities were observed in some years. In more recent surveys (after 2001), higher relative densities have been observed in the northern blocks 4 and 5. Density estimates corrected for perception bias, available from 2001, 2007 and 2009, declined significantly ($P < 0.05$) by 69% from 2001 to 2007, then recovered somewhat by 2009 (Table 4). This pattern was driven primarily by changes in block 4, which held the highest densities of humpback whales in the survey area during this period.

White-beaked dolphins

Primary platform observers identified 1,103 groups as white-beaked dolphins over all surveys. In the partial surveys

conducted in 2003, 2004 and 2005, in which dolphins were usually not identified to species, an additional 216 sightings of unidentified dolphins were assumed to be white-sided dolphins for this analysis. Truncation to 1,000 m perpendicular distance reduced the number of sightings by 13%. Best fit of the detection function was achieved using a hazard rate key function with a factor covariate for survey year (Figure 10). Effective strip half-width was estimated as 387 m (CV=0.03) and ranged from 213 m in 2007 to 558 m in 1995. Mean group size over all surveys was 6.6 (CV=1.86).

Table 4. Comparison of perception bias corrected abundance estimates of humpback whales for selected strata and the entire survey area. Estimates from 2001 are from Pike et al. (2009). Only strata where significant ($P<0.05$) changes to or from non-zero values occurred are shown. Cells list proportional change from first year to second. * = $P<0.05$.

BLOCK	YEAR	2007	2009
4	2001	-0.69	0.08
4	2007		2.38 *
5	2001	0.97	0.47
5	2007		-0.25
TOTAL	2001	-0.66 *	-0.51
TOTAL	2007		0.50

There was an overall increasing trend in relative density in the survey area from 1986 to 2016, due primarily to increases in the large northern blocks 4 and 5, which had the highest densities of white-beaked dolphins in the survey area in most years (Figure 13). Density estimates corrected for perception bias available for surveys conducted in 2001, 2007, 2009 and 2016 also showed significant increases in the northern blocks 4 and 5, and decreases in the southern blocks 1 and 8 (Figure 13, Table 5). Overall corrected density in the entire survey was highest in 2016, but not significantly higher than other years for which estimates are available (Table 5).

Seasonal distribution

Sufficient effort and sightings were realized in strata 1, 4, 8 and 9 in 2004 to assess seasonal changes in density for common minke and humpback whales and white-beaked dolphins. Effort was also conducted outside of the normal June/July survey period in September 2003 and May 2005.

Common minke whales

Density was highest in the summer in all strata sampled, but the differences were not significant in most cases except when density in other periods was 0 (Figure 14). In block 1 where observed densities were highest in all periods, summer and fall densities were significantly higher ($P<0.05$) than that observed in April, while density in September was nearly the same as that during the summer. Density observed in block 1 in September 2003 was 37% of that seen in summer 2001, a difference that was significant ($P<0.05$). Density in block 1 in May 2005 was 5% and 13% of that seen in summer 2001 and 2007, respectively, and the difference was significant ($P<0.05$) in both cases.

Common minke whales were not observed in block 8 in April or September 2004, while density in September 2003 was significantly lower than that observed in prior years during the summer months.

Table 5. Comparison of perception bias corrected abundance estimates of white-beaked dolphins for selected strata and the entire survey area. Estimates from 2001 are from Pike et al. (2009). Only strata where significant ($P<0.05$) changes to or from non-zero values occurred are shown. Cells list proportional change from first year to second. Blank cells not sampled in one of years. Proportion of -1 indicates that abundance was zero in the second year. * - $P<0.05$, ** - $P<0.01$.

BLOCK	YEAR	2007	2009	2016
1	2001	-0.91 **	-0.74 *	0.42
1	2007		2.60	20.31 **
1	2009			5.01 *
4	2001	-0.48	1.01	2.86 *
4	2007		2.76 *	6.16 **
4	2009			0.91
5	2001	5.42 **	17.69 **	
5	2007		1.91	
5	2009			
8	2001	-0.89 *	-0.97 **	-1.00 **
8	2007		-0.67	-1.00 **
8	2009			-1.00 **
TOTAL	2001	0.46	1.40	0.89
TOTAL	2007		0.63	0.29
TOTAL	2009			-0.21

Humpback whales

Humpback whales were not sighted in blocks 8 or 9 in the surveys conducted in 2004. In blocks 1 and 4, density was highest in the summer (Figure 14), but the difference between June/July and September in block 1 was not significant ($P>0.05$).

Density was 0 in April in both strata and in September in block 4. Humpback whales were not sighted in block 1 in May 2005 or in September 2003.

White-beaked dolphins

Density was highest in the summer in blocks 1 and 4 (Figure 14), but the difference was significant only between spring and summer in block 1 ($P<0.05$). Density in block 8 was significantly higher ($P<0.05$) in April than in other months, while in block 9 density in the summer was significantly lower ($P<0.05$) than that seen in April or September. Density in block 1 was 0 in May 2005, while in September 2003 it was 56% of that observed in summer 2001 in the same area; however, this difference was not significant.

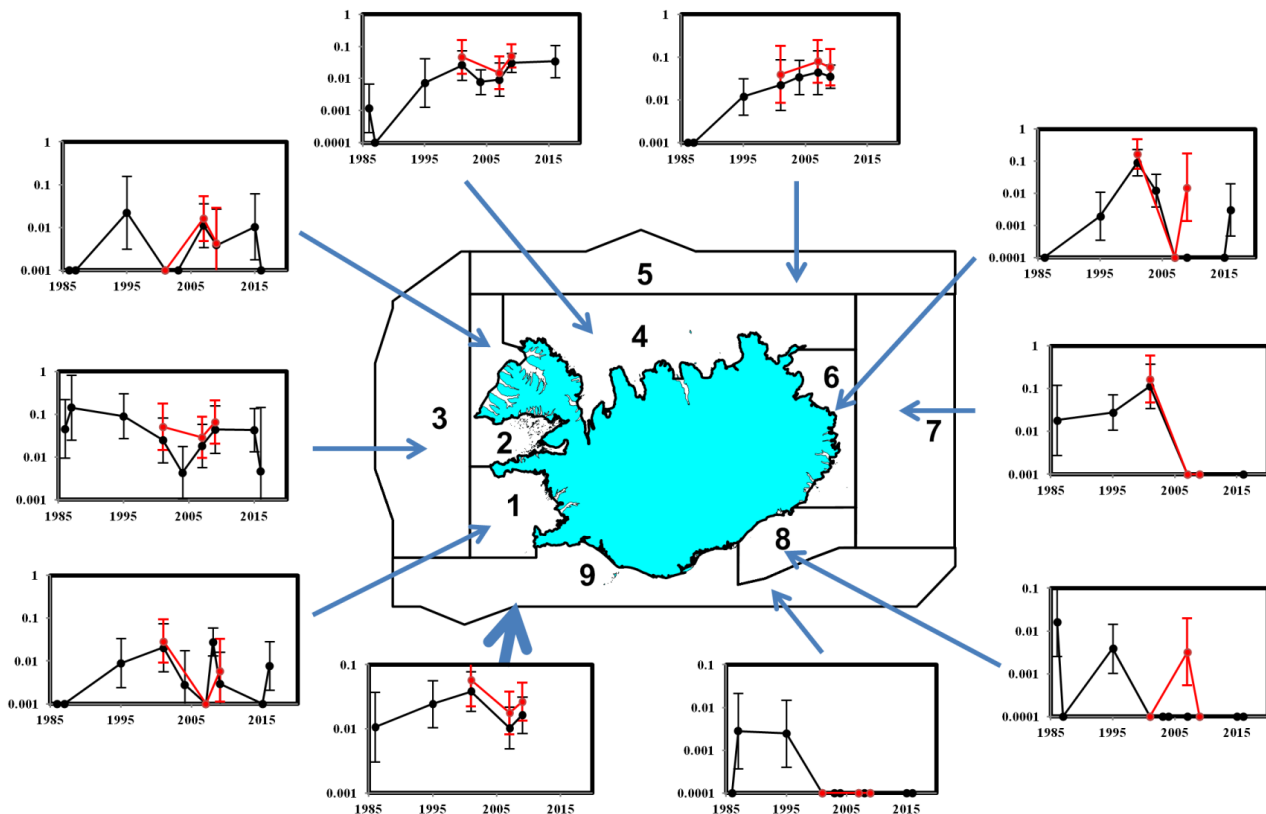


Figure 12. Trends in the relative abundance (black line, uncorrected line transect density, whales nm^{-2}) and density corrected for perception bias of humpback whales by stratum and for the entire survey area (thick arrow). Zero values of density are shown as the lowest value on the Y-axis. 95% confidence intervals are shown.

DISCUSSION AND CONCLUSIONS

Potential biases

Incomplete coverage and post stratification

The full surveys attempted in 2007, 2009, 2015 and 2016 did not fully achieve their planned coverage and parts of some strata were not surveyed. Coverage was insufficient in 2015 to derive an estimate for the entire survey area. In the 2016 survey, 5 strata received less than 50% coverage and block 5 was not surveyed at all. While this does not necessarily introduce bias to the resulting abundance estimates for the strata that were sampled, there is a risk that animal distribution within strata will be correlated with realized coverage, which would cause a positive or negative bias. If the un-surveyed area comprised a contiguous portion of a stratum, we modified the affected stratum to remove un-surveyed areas and presented a post-stratified estimate using the revised surface areas (Figures 4, 5 6, and 7). The resulting estimates are regarded as negatively biased for the affected strata and the full survey area as the underlying assumption is that density in the un-surveyed areas is 0, which we have no reason to expect in most cases.

The post-stratified estimates should therefore be regarded as minimum estimates for these areas. The likely effect of incomplete coverage will vary by species and is addressed below. In comparing estimates between surveys, the original stratification was always used.

Cue count estimates

Cue rate

The cue rate of 53 cues per hour for common minke whales used here is based on work reported by Gunnlaugsson (1989) from the coastal areas of Iceland. However, this estimate was based on limited data and may be biased to an unknown degree. No variance for cue rate was included in the abundance estimate, nor was this source of variance included in previous estimates (Borchers et al., 2009; Hiby et al., 1989); therefore, total variance is underestimated. A slightly lower cue rate of 46.3 cues per hour ($CV=0.11$) was estimated for West Greenland waters by Heide-Jørgensen and Simon (2007). Using this cue rate would increase our abundance estimates for common minke whales by 14%. However, we retain the earlier cue rate estimate for comparability with previous estimates and because it is specific to Icelandic waters.

Measurement error

Since the area searched by observers is semi-circular, the surface area of the search area increases as a squared function of the radial distance from the search platform. Because of this, random error in the measurement of radial distance results in a net transfer of sightings towards distance 0. Borchers et al. (2009) developed maximum-likelihood estimators for distance sampling surveys in the presence of measurement error. Conventional distance sampling estimators were found to be positively biased by measurement errors when the CV of measurement error is greater than about 10%. As the CV for

measurement error was <10% for all available duplicates from the 2007, 2009 and 2016 surveys, measurement error is likely not a substantial source of bias for these data.

Line transect estimates

Availability bias

Line transect methods assume that all animals on the trackline are available to be seen, but this is clearly not the case for cetaceans. Some unknown proportion of whales were under water during the passage of the aircraft and therefore not available to be seen by observers (availability bias), causing the resultant estimates to be negatively biased. Cue counting does not suffer from this problem and could potentially be implemented for species other than common minke whales that exhibit an easily-visible cue, such as a blow for large baleen or sperm whales. However, we lack information on blow rates for humpback whales in this area and blows were not well-recorded in the surveys, particularly for groups larger than 2 animals. Other means of correction for availability bias require local information on diving frequency and profiles, usually obtained through satellite-tagging experiments (Hansen et al., 2019). Unfortunately, such information is not yet available for most species in Icelandic waters. The magnitude of availability bias will vary by species and is addressed below.

Trends in abundance

We used uncorrected line transect density from primary observations only as a proxy for abundance in examining trends, because correction for perception bias was not possible for all surveys. An underlying assumption is that perception and availability biases do not have a temporal trend. Since the same

aircraft and platform configuration was used for all but the 2016 survey, the magnitude of perception bias will be primarily dependent on the aptitude, training and experience of the observers, and different observers were used for almost every survey. As observer training and field methods have not changed over the course of the surveys (except for the 2016 survey when a different aircraft and full double platforms were employed), we would not expect a temporal trend in perception bias. The proportion of time an air-breathing whale spends at or near the surface is likely largely determined by physiological requirements, so again we would not expect to see a temporal trend in availability bias.

We pooled distance data by species from all surveys to estimate detection functions, using a scale covariate for year to account for survey differences. The resulting detection functions may not be optimal for any one survey, but pooling avoids the potential bias introduced by model selection and truncation distance for individual surveys. It also allowed us to estimate density for partial surveys that produced too few sightings to estimate a survey-specific detection function.

Common minke whales

Abundance 2007

Realized effort in 2007 left the far NW, NE and SE parts of the survey area uncovered. These “corners” of the survey area have proven consistently difficult to cover because of weather and logistics, so little information is available on the density of common minke whales in these areas. The NE and NW were well-covered in 1995 and 2009 and density in these areas was very low (Figure 4). The far SE has not been well-covered by any survey, however the density of common minke whales in

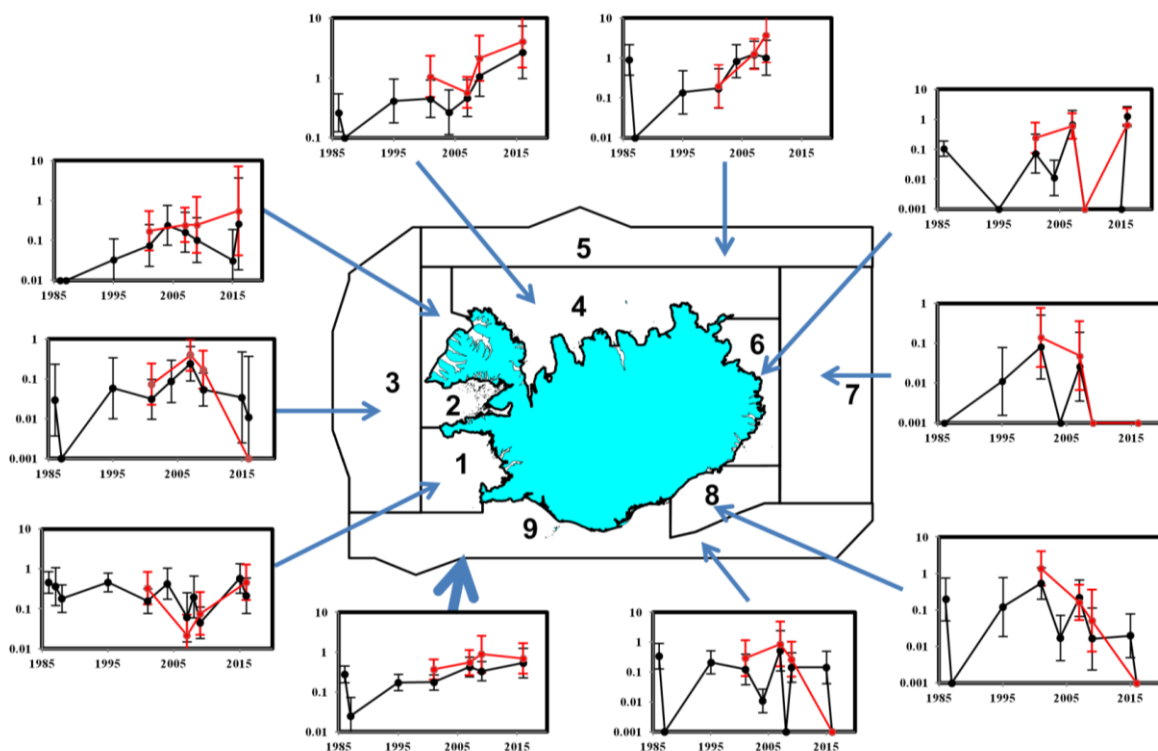


Figure 13. Trends in the relative abundance (black line, uncorrected line transect density, whales nm⁻²) and density corrected for perception bias (red line) of white-beaked dolphins by stratum and for the entire survey area (thick arrow). Zero values of density are shown as the lowest value on the Y-axis. 95% confidence intervals are shown.

adjoining areas in recent surveys has been low. Given that density was likely very low in the un-sampled areas, the post-stratified estimate, which is 11% lower than the full estimate, may provide a better approximation of abundance in the survey area.

We provide 2 corrected estimates for common minke whales from this survey: one using data from both primary observers (Table 2, Supplementary File 2), and the other using sightings from the more effective primary observer (P2) only (Table 2, Supplementary File 3). The 2007 uncorrected estimate for the single primary observer is 42% greater than that for the full primary platform. Observer P1 made very few minke whale sightings while on the right side of the plane and duplicated none of the sightings made by the secondary platform. Therefore, there are no data with which to estimate $p(0)$ for this observer, which must be lower than that for observer P2. For this reason, the estimate using both primary observers is regarded as negatively biased, and the single observer corrected estimate of 20,834 (CV=0.35, 95% CI: 9,808 – 37,042) (Supplementary File 3) is considered to be the more accurate of the 2 provided.

Abundance 2009

Coverage in 2009 was the best of all surveys since 1995 and only the far SE corner of the area was left unflown. The coverage is therefore considered sufficient to produce an accurate estimate for the full survey area for this species.

Both primary observers sighted common minke whales at longer distances than those used in previous surveys, which resulted in an estimate of *edr* that was 102% and 41% higher than those estimated in 2007 and 2016, respectively, and substantially higher than that realized in any other survey (Borchers et al., 2009; Hiby et al., 1989). Different observers were used in almost every survey and the individual observation patterns of observers certainly play a role in the observed differences. Given that survey specific detection functions were used, these differences should not introduce bias. In contrast, little difference in sighting distances between surveys was noted for humpback whales or white-beaked dolphins.

An equipment failure meant not only that sightings data was lost from 1 channel for several flights, but also that environmental data were lost during the period when the cruise leader was in the affected position, affecting 10% of the total effort of the survey. Environmental covariates could therefore not be included in the estimation of detection functions for this survey (this applies to all species). The effect of this loss on the estimation of the detection function is unknown but likely small given experience with similar datasets. For example, inclusion of a covariate in the 2016 detection function resulted in a 5% change in estimated abundance compared to that using a detection function without covariates. The loss of sightings data from 1 side was fully corrected by adjusting realized effort and would therefore not affect estimated abundance. The loss of data would, however, result in a decrease in precision because survey effort is effectively lowered.

Abundance 2016

Block 7, which received only 37% of planned effort on 4 of 10 transects, accounted for over 60% of the total estimated abundance of common minke whales in the survey area (Supplementary File 9). This stratum has had low densities of

minke whales in previous surveys (Figure 11) (Borchers et al., 2009; Pike et al., 2009), and this is the highest abundance observed in the block in any survey. Post-stratification of block 7 alone reduced estimated abundance by 23%. We cannot be certain whether or not the observed densities in central block 7 were present throughout the stratum. However, ship surveys conducted in 2015 and 2016 showed relatively large numbers of minke whales within and east of this stratum (Pike, Gunnlaugsson, Mikkelsen, & Víkingsson, 2019; Solvang & Oien, 2017). Similarly, little or no effort was realized in offshore strata 3 and 5. However, these strata, relative to others, have not had high numbers of minke whales in previous surveys.

This was the first survey in which the Twin Otter rather than the Partenavia was used as a survey platform. This allowed the use of 2 fully independent platforms for the first time. This configuration results in more sightings, more duplicate sightings and potentially better precision in the estimation of density and perception bias. This was also the first full survey in which geometers were used. The devices functioned well and offer many advantages over the previously used analogue forestry inclinometers (Hansen et al., in prep).

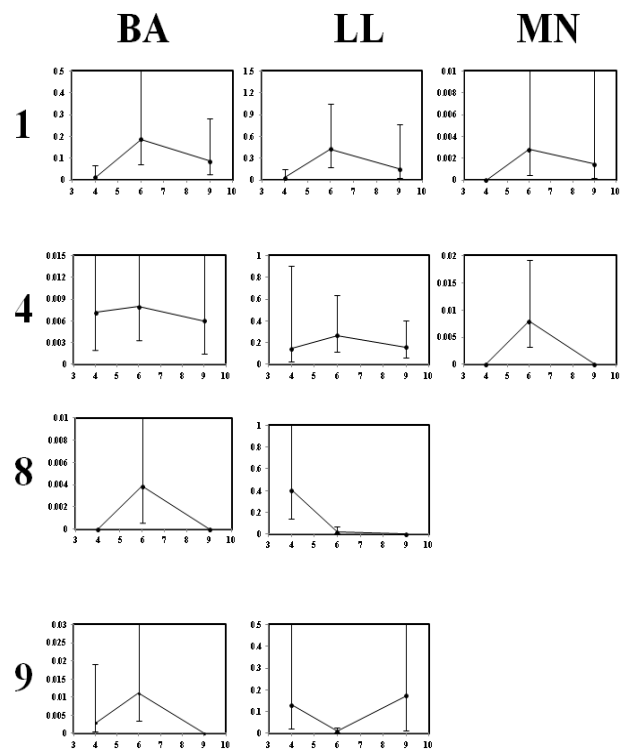


Figure 14. Seasonal change in relative abundance (uncorrected line transect density, whales nm^{-2}) by stratum and species. Survey month on X-axis. BA – common minke whale; LL – white-beaked dolphin; MN – humpback whale.

Trend in abundance

Recent surveys suggest that the abundance of common minke whales in the Icelandic shelf area has undergone a substantial decrease since 2001. Corrected estimates from 2007, 2009 and 2016 are 52% to 74% lower than that from 2001 and the differences are significant ($P < 0.05$) (Table 3). Changes in relative density (Figure 11) reveal a similar pattern but the inclusion of partial surveys provides some further insight into the timing of the decrease. Relative density remained stable in block 1 as late as 2004, but decreased by 2007, followed by a rebound in 2008,

followed by another decrease in 2009. In contrast, density had already decreased in blocks 4 and 8 by 2004. This suggests that the decline in common minke whale abundance in the survey area occurred over a few years and may not have been a single event across the area. Surveys conducted in 2015 and 2016 indicate that common minke whale density remains comparatively low in Icelandic coastal waters.

Víkingsson et al. (2015) present a complete discussion of recent changes to the marine ecosystem around Iceland, including the distribution and abundance of cetaceans from the NASS ship and aerial surveys. Temperature and salinity have increased substantially since 1995 due to increased inflow of Atlantic waters into the area, likely as a result of climate change. This is correlated with changes in the distribution of forage fish and euphausiids on which many cetaceans are dependent. Since 2005, sandeel (*Ammodytes spp.*) recruitment and abundance has declined drastically in western and southern Iceland. Over roughly the same period the distribution of capelin (*Mallotus villosus*) has shifted away from northern Iceland towards the East Greenland coast, and Atlantic mackerel (*Scomber scombrus*) has moved in from east to become much more abundant in Icelandic waters during the summer and fall (Asthórsson, Valdimarsson, Gudmundsdóttir, & Óskarsson, 2012).

These changes have been correlated with concomitant shifts in the diet of common minke whales in the area. In the period 1977-1997, sandeel formed the largest part of the common minke whale diet in southern and western Iceland, while capelin and euphausiids were more important off northern Iceland (Sigurjónsson, Galan, & Víkingsson, 2000). After 2003, Víkingsson et al. (2014) observed changes in the diet, including a drastic reduction in the proportion of sandeel by 2007, and smaller reductions in the proportions of capelin and euphausiids. Over the same period, the importance of larger gadoids and herring (*Clupea harengus*) increased in the diet.

As these changes correspond temporally with the reduction in abundance of common minke whales in Icelandic coastal waters, we consider it likely that they are related. Common minke whales may have shifted their distribution in response to changes in the availability of favoured prey. Recent ship surveys (Pike et al., 2020; Pike et al. 2019) have shown relatively high densities of common minke whales off East Greenland; however, this area is usually poorly covered because of the prevalence of pack ice. Similarly, an aerial survey conducted in 2015 found relatively high densities of minke whales in East Greenland coastal waters (Hansen et al., 2019.). A Norwegian survey in 2016 registered a large increase in abundance of minke whales in the Jan Mayen area north of Iceland compared to previous surveys in the series (Solvang, Skaug, & Oien, 2017). In some years (e.g. 2007, (Pike et al., 2020)), common minke whales have been abundant off northern Iceland, while in other years (2015, (Pike et al., 2019)) they have not. Similarly, distribution shifts of common minke whales have been observed to the east and southeast of Iceland and around the Faroes (Pike et al., 2019) and in the Norwegian and Barents Seas (Skaug et al., 2004). In contrast, there is little evidence of changes in distribution or abundance in more southerly European waters (Hammond et al., 2017). Taken together, this suggests that the distribution of common minke whales in the Central North Atlantic is quite dynamic and that they may not exhibit strong philopatry to specific areas. This has also been

suggested by photographic marking studies in Iceland and other locations (IWC, 2015).

There is little evidence for the existence of distinct stocks of common minke whales in the North Atlantic from genetic or other data sources (IWC, 2015). Management of whaling has been based on operational rather than biological stock boundaries (Donovan, 1991; IWC, 2015). Catching of common minke whales in Icelandic coastal waters resumed in 2003 after a hiatus of 17 years (NAMMCO, 2019). Recent catch quotas in the area have been around 200 but actual harvests have been lower, averaging 41 since hunting resumed (NAMMCO, 2019). Given that this comprises less than 0.1% of the estimated abundance in 2001 of 43,600 (95% CI: 30,150 – 63,150) (Borchers et al., 2009), it is highly unlikely that a direct take of this magnitude has played any role in the decline in numbers of more than 50% since then.

Seasonal distribution

Common minke whales are known from whaling records to be present in Icelandic coastal waters between March and November, with catches peaking in July (Sigurjónsson & Víkingsson, 1997). Our data from off-season surveys conducted in 2003, 2004 and 2005 (Figure 13) generally confirm this pattern, with highest densities observed in June and July when all of the complete surveys were carried out. Density was particularly low in April and May in strata that were surveyed. It therefore appears that the survey series has captured the period of peak common minke whale occupation in the area.

Humpback whales

Abundance estimates

The distribution of humpback whales has varied between surveys (Figure 6). Humpback whales have been concentrated in the NW corner of the survey area in those years (1995, 2007, 2009) when it has been adequately covered. In 2007, much of this area was covered by ice but humpback whales were abundant to the south and east of the edge of the pack ice. The northeast corner received adequate coverage only in 1995 and held high densities then, and probably also in 2001. Numbers off northern Iceland were high in 2004, 2009 and 2016 but not in other years. Because humpback whales tend to be concentrated in particular portions of strata that are frequently inadequately covered by the surveys (e.g. the northern parts of blocks 3 and 7), abundance estimates tend to be variable and likely strongly affected by coverage. For example, post-stratification would reduce abundance in 2007 by 25%, solely because of the reduced area of block 5. However, the northern part of block 7, where high densities were observed in 1995 and 2001, was not surveyed and density was nil elsewhere in the block. We have no way of knowing whether humpback whales occupied the area in 2007, but if they did, the estimate for 2007 will be negatively biased, perhaps substantially. Coverage was better in 2009 and this is likely the more reliable estimate for the survey area. For similar reasons, we did not attempt to estimate humpback whale numbers in 2016 because the far north, northeast and northwest parts of the survey area, all of which have held high densities in some past surveys, were not covered at all.

While no data on humpback whale diving is available from Icelandic waters, Heide-Jørgensen and Laidre (2015) found that humpback whales off West Greenland spent on average 33.5%

(CV=0.10) of their time in the 0-2 m depth interval during daylight hours. Assuming that humpback whales were visible to observers in this interval, they derived an availability bias estimate of 0.37 for an aerial survey conducted there in 2007. The same diving data were used to estimate availability bias as 0.43 (CV=0.27) for a similar survey conducted in 2015 (Hansen et al., 2019). Given that our surveys used a similar configuration, we would expect them to have a bias of similar magnitude, a correction that would more than double our estimates. This suggests, based on the 2009 survey with an estimated abundance of 2,261 (CV=0.35, 95% CI: 1,142 – 4,477), that humpback whale abundance in Icelandic coastal waters may exceed 5,000 animals in some years.

Trends in abundance

Interpretation of apparent trends in the abundance of humpback whales in the survey area is complicated by their contagious and temporally dynamic distribution. The numbers of sightings in the 1986 (16) and 1987 (4) surveys were insufficient to estimate abundance (Pike et al., 2009). However, the NW corner of the survey area was not covered in 1986, and neither the NW nor the NE were covered in 1987. Both areas were adequately covered in 1995 and abundance that year, uncorrected for perception and availability biases, was estimated as 1,674 (95% CI: 656 – 4,629) (Pike et al., 2009). Despite limited coverage in the NW and NE in 2001, uncorrected abundance in that year was higher at 2,937 (95% CI: 1,665 – 5,182). Using these data, Pike et al. (2009) estimated a rate of increase of 0.12 (CV=0.29) in the survey area for the period 1986-2001. Since 2001, total abundance in the survey area has shown little trend. We consider that the 2009 survey had adequate coverage for this species and our estimate from that year (Table 2) is similar to that from 2001.

A more detailed examination of changes in relative abundance (Figure 12, Table 4) leads to a similar conclusion, with a rapid growth in numbers from 1986 to 2001, and a decline or stabilization thereafter. There has been an increase in the northern blocks 4 and 5 over the entire period, but there has been no identifiable trend elsewhere.

NASS ship surveys have shown that humpback whales have a continuous distribution from our survey area farther offshore, particularly to the north and west of Iceland (Paxton et al., 2009; Pike et al., 2020; Pike et al., 2019). Humpback whales in our survey area are part of a larger feeding stock that spends a large proportion of the year in the area before migrating to breeding areas in the Caribbean, near the Cape Verde Islands and possibly other areas in the spring (Smith, 2010; Smith et al., 1999; Smith & Pike, 2009; Wenzel et al., 2009). Estimates from NASS ship surveys, which cover a much larger area around Iceland and the Faroe Islands and includes the aerial survey area in some years, increased from 1987 to 2001 with a leveling-off or perhaps a small decrease thereafter (Pike et al., 2019; Víkingsson et al., 2015), thus showing a pattern similar to that from the aerial survey series. Estimates from these surveys have ranged from 1,816 (CV=0.18) in 1987 (Gunnlaugsson & Sigurjónsson, 1990) to a high of 18,105 (95% CI: 7,226 – 45,360) in 2007 (Pike et al., 2020), making our survey estimates a relatively small component of the total feeding stock size. Pike et al. (2019) provide a more complete description of trends in humpback whale distribution and abundance from the NASS and other surveys in adjacent areas.

An analysis of catch statistics and sighting records from Icelandic whaling suggests that the number of humpback whales was reduced to very low levels by the turn of the 20th century but has been increasing since the 1970's (Sigurjónsson & Gunnlaugsson, 1990). The recent increase in numbers is therefore likely due to population recovery.

Seasonal distribution

Surveys conducted from 2003-2005 suggest that humpback whale density is higher in the summer months than in the spring or the fall (Figure 13). Humpback whales are known to be present nearly year-round in Icelandic waters (Magnúsdóttir, Rasmussen, Lammers, & Svavarsson, 2014; Víkingsson, 2004) and are often seen in association with the capelin fishery during the winter months (Gunnlaugsson & Víkingsson, 2014). Densities of humpback whales similar to those observed in the summer months were seen to the north of Iceland in October 2015 (Pike et al., 2019).

White-beaked dolphins

Abundance estimates

Post-stratification reduced estimated abundance by 21% in 2007 (Table 2, Supplementary File 5), primarily because of the reduced size of block 5 caused by the excision of its eastern and western extremes (Figure 5). In this case, the post-stratified estimate is probably more accurate, as sightings have been concentrated in the surveyed central part of block 5 in previous surveys. Extending the high densities observed in this area to the eastern and western extremities of the block would therefore likely result in positive bias. In contrast, post-stratification reduced 2009 abundance by only 1% (Table 2, Supplementary File 8), suggesting that realized coverage was adequate to estimate abundance in that year. While post-stratification reduced estimated abundance for the 2016 survey by only 2% (Table 2, Supplementary File 10), this is certainly an underestimate as the entirety of block 5 remained un-surveyed. Block 5 accounted for 21% of total abundance in 2007 and 54% in 2009, suggesting that the 2016 estimate for the survey area could be negatively biased by a similar proportion.

Observing from a fast-moving plane gives the impression that dolphins spend all their time frolicking at the surface, but of course this is not the case: some proportion of the animals are underwater and invisible to observers as the airplane passes. Unfortunately, there is little available information on the diving behavior of this species in Icelandic waters or elsewhere. One short-term (ca. 14 hr) tagging experiment conducted off western Iceland indicated that this animal spent 18% of its time in the 0-2 m depth interval, where it would likely be visible to aerial observers (Rasmussen, Akamatsu, Teilmann, Víkingsson, & Miller, 2013). While this suggests that availability bias for this species may be substantial, this is based on the behavior of 1 recently disturbed animal over a relatively short period of time.

Trends in abundance

After an initial decline from 1986-1987, uncorrected line transect density has shown a general increase from 1987 to 2016 in the entire survey area (Figure 13). Uncorrected estimates ranged from 12,000 to 19,000 for the survey area from the 1986, 1995 and 2001 surveys, with no significant difference between the estimates (Pike et al., 2009). Most of the increase comes from increases in the northern blocks 4 and 5. These accounted for 48% to 52% of total abundance from

1986-2001, 90% in 2009 and 84% in 2016 when block 5 was not covered. Estimates of abundance corrected for perception bias for surveys after and including 2001 also suggest increasing numbers, particularly in the northern blocks 4 and 5 (Figure 12, Table 5). In contrast, abundance has decreased in southern blocks 1 and particularly 8, where dolphins were absent in 2016. Taken together this suggests increasing abundance over the period, although the increase is not significant for the entire survey area ($P>0.05$), with possibly some re-distribution to the northern part of the survey area.

Little information is available on the stock structure of white-beaked dolphins in the North Atlantic. Densities appear to be highest in 4 main areas: 1) Western North Atlantic (Canadian and northern US waters); 2) Icelandic waters; 3) northern Norway; and 4) around the British Isles and the North Sea. These areas have been identified as putative management units for the species (Evans & Teilmann, 2009). However, our survey area is not likely to contain a discrete stock unit. NASS ship surveys have shown a continuous distribution of white-beaked dolphins far offshore to the north and west of Iceland (Pike et al., 2020; Pike et al., 2019). It is therefore likely that the observed changes in abundance in Icelandic coastal waters result from changes in distribution rather than actual changes in population size.

White-beaked dolphins are piscivorous, consuming a wide variety of fish species over a broad size range (Evans & Smeenk, 2008). Around Iceland, gadoid fish, including haddock (*Melanogrammus aeglefinus*), cod (*Gadus morhua*) and saithe (*Pollachius virens*), as well as pelagic species such as capelin and herring are important components of the diet (Vikingsson & Ólafsdóttir, 2004). The apparent increase in abundance of white-beaked dolphins off northern Iceland may be related to the general northward shift in the distribution of many fish species in the area, probably due to rising sea temperatures (Valdimarsson, Astthórsson, & Pálsson, 2012).

Seasonal distribution

Relative abundance appears to be highest in mid-summer in blocks 1 and 4 (Figure 13) but the differences are largely non-significant. In contrast, density was highest in April in block 8. White-beaked dolphins are present year-round in Icelandic waters (Sigurjónsson & Vikingsson, 1997) and the extent of their seasonal migrations, if any, are not known.

Harbour porpoises

Abundance estimates

Harbour porpoises are small, cryptic and difficult to spot from a fast-moving aircraft. Aerial surveys targeting this species require specialized methods (including flying at a lower altitude in more restricted weather conditions and using observers with experience in sighting small cetaceans), which were not implemented in most of these surveys. The exception was the 2007 survey, when an observer who was highly experienced in harbour porpoise surveys was employed and the survey was flown at an altitude of 183 m rather than 223 m as was standard on the other surveys. This survey provided an estimate, fully corrected for both perception and availability biases, of 43,179 (95% CI: 31,755 – 161,899) (Gilles et al., under revision), much higher than the previous estimates of 4,329 (95% CI: 2,724 – 6,599) for 1986 and 5,156 (95% CI: 3,027 – 8,783) for 1995 provided by Pike et al. (2009). However, it was recognized that these latter estimates were severely negatively biased as they

were uncorrected for perception or availability, both of which can be substantial for this species (see below).

For most of the other surveys, sightings were relatively few and the paucity of between-platform duplicate sightings made the estimation of perception bias unreliable. The 2016 survey was exceptional as some of the observers proved adept at detecting harbour porpoises. In addition, the change to a full double platform configuration, as opposed to the partial double platform used on previous surveys, provided more observing power and resulted in more duplicate sightings. For these reasons we provided an estimate from the 2016 survey, but not from the 2009 survey.

Harbour porpoises are ubiquitous in the survey area but are generally found in larger numbers in the inshore strata (Figure 7). Post-stratification of the 2016 survey area, primarily applied to the offshore blocks, reduced estimated abundance by 20% (Table 2, Supplementary File 11). We consider this a minimum estimate as we have no reason to expect lower densities in the un-surveyed parts of the strata, and also because block 5 was not covered at all.

Our correction for perception bias indicates that each platform sees only about one quarter of the porpoises that are visible at the surface close to the transect. This may actually be an overestimate, as only 7 duplicate sightings were available to estimate the bias and $p(0)$ is probably overestimated due to unmodelled heterogeneity (Laake & Borchers, 2004). Laake et al. (1997) found that while $p(0)$ can approach unity for very experienced observers under ideal conditions, it can be much less for inexperienced observers or under poor conditions. Given that our observers were not focused on detecting this species, the rather low detectability realized in this survey is not surprising.

Our 2016 estimate of 22,806 (95% CI: 9,166 – 56,746) is 53% of that from 2007 (Gilles et al., under revision), but the latter estimate is fully corrected for availability bias while ours is not. This can be substantial for harbour porpoises partially because they can be seen only a relatively short distance from the plane and therefore the observer has a very short time in which to detect a sighting. We lack data on the dive cycle of harbour porpoises in Icelandic waters to correct for this bias, however, such data are available from Danish waters. Teilmann et al. (2007) found that tagged harbour porpoises spent 58% of their time in the 0-2 m depth interval during the day in July. Assuming that harbour porpoises can be seen to this depth by observers (submerged porpoises were frequently sighted), and given the short time in view for this species, this would translate to an availability bias of roughly 60%, and would increase our estimate to approximately the same magnitude of that estimated for 2007.

Trends in abundance

Pike et al. (2009) found that relative abundance, in this case encounter rate, of harbour porpoises in aerial surveys around Iceland conducted between 1986 and 2001 had decreased at an annual rate of 7% (95% CI: 3% – 11%). However, the authors were sceptical of this conclusion because of uncorrected biases and differences in observer efficiency between surveys. Despite the results presented here, we lack sufficient data to come to any firm conclusions about trends in harbour porpoise abundance in Icelandic coastal waters, although the estimates

from 2007 and 2016 appear to be of similar magnitude when biases are considered (see above).

Harbour porpoises are not directly harvested in Iceland, however they are caught as by-catch in gillnet fisheries. Although studies are in progress, to date no estimate of the total by-catch level has been adopted (NAMMCO, 2018).

Other species

Several other species were sighted in the surveys but generally the number of sightings in any one survey was not sufficient to estimate abundance (Figure 8). Some of these, such as blue, fin, sperm and northern bottlenose whales, occur in larger numbers farther offshore and estimates are available from concurrent NASS ship surveys (Pike et al., 2019).

Evaluation of the survey series

The NASS series, of which many of the aerial surveys were a part, has been successful in elucidating major changes in the distribution and abundance of several cetacean species (Pike et al., 2019; Víkingsson et al., 2015). The aerial survey series has detected changes in the abundance of common minke and humpback whales and white-beaked dolphins in the survey area, suggesting that survey power is sufficient for this purpose. The series has also produced estimates that have been used in the harvest management of common minke whales (e.g. NAMMCO, 2017) and evaluation of the impact of incidental catch on harbour porpoises (NAMMCO, 2018). The survey series has been extremely conservative in that the survey design and methodology remained virtually unchanged until 2015, when the transect design in the inner strata was changed, and 2016, when a different plane, platform setup and angle recording system was used. This has greatly simplified inter-survey comparisons as there are few issues with the compatibility of stratification, survey effort allocation, or methodology between surveys.

We consider the change in transect design to equal-spaced parallel lines in the irregularly shaped inner strata in 2015 (Figure 1) to be advantageous as it results in equal coverage probability in these strata and was not noticeably more time consuming or difficult to fly. Similarly, the shift to a full double platform configuration in 2016 has resulted in better data with which to correct observer biases than the previous configuration. The adoption of the geometer in 2015 (Hansen et al., in prep) has simplified angle measurement for observers and made data transcription less time consuming.

Particularly the 2015 survey, but also the 1987 and 2016 surveys, achieved relatively low coverage, mainly because stable and persistent weather patterns precluded surveying in some parts of the survey area. If the survey is to be repeated, it may be necessary to extend the available time by up to 2 weeks to ensure that it can be completed.

In conclusion, this survey series has provided valuable information on the distribution and abundance of cetaceans in Icelandic waters. The 30-year time span of the series increases its value by providing insight into temporal trends that could not be obtained in any other way. The cost is moderate compared to vessel surveys, and future developments in drone and video technology may make aerial surveys even more cost effective.

ADHERENCE TO ANIMAL WELFARE PROTOCOLS

The research presented in this article has been done in accordance with the institutional and national animal welfare laws and protocols applicable in the jurisdictions in which the work was conducted.

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