

DISTRIBUTION AND ABUNDANCE OF KILLER WHALES IN THE CENTRAL NORTH ATLANTIC, 1987-2015

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ABSTRACT

The North Atlantic Sightings Surveys (NASS), covering a large but variable portion of the Central and Eastern North Atlantic, were conducted in 1987, 1989, 1995, 2001, 2007 and 2015. Sightings of killer whales (*Orcinus orca*), a non-target species, were relatively rare in the Central Atlantic (Icelandic and Faroese) portions of the survey area. In cases where sighting numbers were insufficient, we pooled sightings over several surveys to derive a distance detection function and used this to estimate abundance using standard Distance Sampling methodology. Uncorrected estimates were produced for all surveys, and estimates corrected for perception bias were produced for the 2001 and 2015 surveys. Killer whales were sighted in all areas but were most common in the eastern part of the survey area. Uncorrected abundance in the NASS core area ranged from a low of 4,736 (95% CI: 1,842–12,176) in 1995 to a maximum of 15,142 (95% CI: 6,003–38,190) in 2001. The low precision of the estimates makes the detection of temporal trends unlikely. In 2007 an extension survey revealed relatively high numbers of killer whales to the east of the survey area, in conformity with Norwegian survey estimates in this area. The NASS and other surveys conducted over the period indicate that killer whales number in the low tens of thousands in the Central and Eastern North Atlantic.

Keywords: killer whale, abundance, distribution, North Atlantic, cetacean survey

INTRODUCTION

The North Atlantic Sightings Surveys (NASS) are a series of large scale ship-based and aerial cetacean line transect surveys conducted 6 times over the last 30 years, in 1987, 1989, 1995, 2001, 2007 and 2015 (Pike, 2009; Pike et al., 2020a; Pike, Gunnlaugsson, Sigurjónsson & Víkingsson, 2020b; Pike, Gunnlaugsson, Mikkelsen, Halldórsson & Víkingsson, 2019a; Pike et al., 2019b). The surveys, organized under the supervision of the Scientific Committees of the North Atlantic Marine Mammal Commission (NAMMCO) and the International Whaling Commission (IWC), have had the primary objective of obtaining information on the distribution and abundance of cetaceans to be used in the management of direct (i.e. whaling) and indirect (e.g. by-catch, ship strikes) anthropogenic takes of these animals. In addition, the nearly 3-decade time span of the surveys provides a unique opportunity to monitor temporal changes in the distribution and abundance of these long-lived species. Large offshore areas have been covered by ship, while the coastal areas of Iceland and Greenland have been surveyed using aircraft. Target species of the surveys have been the common minke whale (*Balaenoptera acutorostrata*) in the Norwegian survey area, the common minke whale, fin whale (*Balaenoptera physalus*) and long-finned pilot whale (*Globicephala melas*) in the Icelandic and Faroese areas, and the common minke whale, fin whale and humpback whale (*Megaptera novaeangliae*) in Greenlandic areas. Estimates for these and several other species have been accepted by the Scientific Committees of NAMMCO and the IWC and published (NAMMCO, 2020; IWC, 2020).

Species that occur in low density in the survey area pose a particular challenge for line transect surveys. Encounter rate (the rate at which sightings are detected along a transect), is almost always the largest variance component of any survey estimate (Buckland et al., 2001). As a transect equates to a sample in distance sampling, increasing the number of transects and the amount of total survey effort is effective in increasing the precision of abundance estimates (Buckland et al., 2001). However, this is usually limited by financial and practical considerations: ships and aircraft are expensive to use, and the survey area must be covered in a reasonable amount of time to reduce the possibility of movement between strata during the survey. The design of and effort allocation to a survey are generally guided by prior knowledge of the distribution and abundance of the target species. Abundance estimates for non-target species, particularly ones that are infrequently encountered, will therefore tend to be of lower precision.

Killer whales (*Orcinus orca*) (Figure 1) are of this type: a relatively rare and non-target species in the survey area. Even so, the NASS provide information on the distribution and abundance of this species in the central and eastern North Atlantic, which can be obtained in no other way. In 2017, NAMMCO requested an updated review of the status of this top-level predator in the North Atlantic (NAMMCO, 2017). Jourdain et al. (2019) provided this review, which identified the need for updated estimates of abundance and better information on stock relationships and movement patterns.

Although killer whale populations are generally considered to be recovering from previous whaling and other direct takes, they do face continued threats from climate change, fisheries interactions, pollution and continued direct hunting in Greenland.



Figure 1. Killer whales off the Vestmannaeyjar, Iceland. Photo credit: Fernando Ugarte.

In this paper, we develop abundance estimates for killer whales from the Icelandic and Faroese ship survey components of the NASS surveys from 1987 to 2015. An estimate from the initial (1987) NASS has been published (Gunnlaugsson & Sigurjónsson, 1990); however this was not calculated with what would now be considered standard line transect methodology in that Effective Strip Half-Width (*esw*) was estimated as twice the median perpendicular sighting distance, rather than modelled from the perpendicular distance distribution. Estimates from surveys up to 2001 were provided by Foote et al. (2007), however they provided no information on detection function modelling or other analytical details, and the estimates were not published. We therefore provide new estimates for these surveys and the additional ones carried out in 2007 and 2015, and place these in the context of our wider knowledge of killer whale distribution and abundance in the North Atlantic.

MATERIALS AND METHODS

The survey design and field methods used in the NASS shipboard surveys in the Central North Atlantic have been described elsewhere: 1987: (Sigurjónsson, Gunnlaugsson & Payne, 1989); 1989: (Sigurjónsson, Gunnlaugsson, Ensor,

Newcomer & Víkingsson, 1991); 1995: (Sigurjónsson, Gunnlaugsson, Víkingsson & Gudmundsson, 1996); 2001: (Víkingsson et al., 2009); 2007: (Pike et al., 2020a); 2015: (Pike et al., 2019a); and are summarized briefly below.

The surveys

Survey design, stratification and field methodology have evolved over the 30 years in which the 6 surveys were conducted. The first (1987) survey was more finely stratified and had more total effort than all subsequent surveys (Table 1). As knowledge of the summer distribution of the target fin, long-finned pilot, and common minke whales improved, stratification and effort intensity were adjusted in later surveys to optimize estimates of these species.

Most surveys began in early to mid-June and ended in late July to early August. The exception was the 1989 survey, which began and ended later in the season and extended farther south to better target the spatio-temporal distribution of long-finned pilot and sei (*Balaenoptera borealis*) whales.

The spatial extent of the surveys varied considerably (Figure 2), with the largest coverage by NASS alone achieved in 1989. The Irminger Sea and Denmark Strait between Iceland and East Greenland were covered by all surveys. Extension to the south varied considerably and was greatest in 1989. Similarly, coverage to the northeast into the Greenland and Norwegian Seas was variable, however much of the area outside of the Icelandic and Faroese zones was covered by simultaneous Norwegian surveys, especially prior to and including 1995 (Leonard & Øien, 2020a, b; Øien, 2009).

The 2007 survey was exceptional in employing "extension" vessels to increase the spatial extent of the survey. These vessels were primarily engaged in fish surveys but operated a single cetacean survey platform when conditions were favourable. A large area to the northeast and a smaller area to the southwest of the primary survey area were covered by these vessels (Figure 2), and they also conducted some survey effort within the primary area (Figure 3). Further details of their operation are provided in Pike et al. (2020a).

Stratification

Stratification for all surveys is shown in Figure 2. Stratum areas were estimated in the Albers Equal Area Conic projection using MapViewer GIS software (version 8, goldensoftware.com).

Table 1. Effort and sightings of killer whales on NASS ship surveys, 1987-2015, in sea states of Beaufort 4 or less. The data for the 2007 extension survey is provided separately. DUR - duration, days; VESS. - number of vessels; K - number of transects; EFF - survey effort; OO - number of killer whale sightings. Number of ? indicates identification uncertainty. Group - group size.

SURVEY	START	END	DUR	AREA	VESS.	STRATA	K	EFF	SIGHTINGS				GROUP	
				(nm ²)				(nm)	OO	OO?	OO??	OO_TOT	AVG	MAX
1987	17/06/87	12/08/87	56	667,349	5	22	189	14,968	21	1		22	8.3	20
1989	10/07/89	15/08/89	36	874,659	5	15	113	8,093	18	3		21	7.9	40
1995	22/06/95	06/08/95	45	709,194	3	14	103	6,182	5			5	6.2	11
2001	20/06/01	30/07/01	40	799,754	4	7	84	8,058	41	4		45	6.9	25
2007	26/06/07	23/07/07	66	605,020	4	9	151	6,406	7		2	9	3.7	8
2007 EXT	31/05/07	05/08/07	66	441,191	3	2	128	4,978	23	3	2	26	7.1	40
2015	11/06/15	09/08/15	59	812,775	3	8	81	6,800	30	1		31	8.4	23

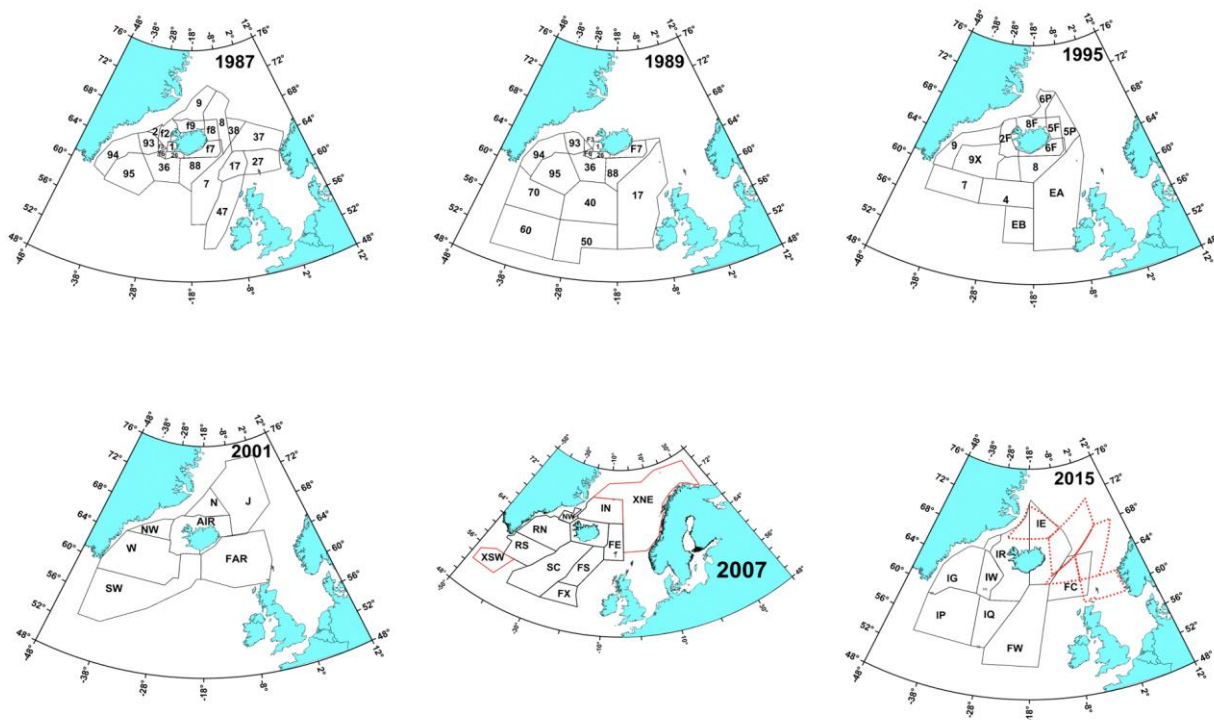


Figure 2. Stratification of NASS. Iceland is in the center of the maps. For 2007, extension strata are shown in red, and for 2015, overlapping strata from a concurrent Norwegian survey are shown in red.

Norwegian ship surveys conducted from 2013–2018 overlapped with the eastern part of the Icelandic/Faroese survey area in 2015 (Leonard & Øien, 2020a). In order to derive an estimate of abundance that was additive with that of Leonard & Øien (2020a), we post-stratified blocks FC and IE (Figure 2) to remove the area of overlap. Abundance was then re-estimated using the revised surface area, realised effort and sightings in the post-stratified blocks with the same detection function used in the original estimates.

Transect design

An equal-spaced zig-zag transect design was used in most strata up until 1995 (Figure 3). Beginning in 2001, parts of the survey area to the west of Iceland and on the Icelandic shelf were covered by a vessel that was simultaneously conducting a fish survey. In these strata, an equal-spaced parallel line design, with some additional effort from vessel transits, was used.

Field procedures

The evolution of field procedures used in the NASS is detailed in Pike et al. (2019b). The 1987, 1989 and 1995 (except in the Faroese strata) surveys used a single platform configuration with observers on the bridge roof and in the crow's nest. These surveys were conducted in passing mode with delayed closing on some sightings if species identification and/or group size were uncertain. After 1995, and in 1995 on the Faroese vessel, most effort was conducted using a double platform mode. The 1995 (Faroese only), 2001 and 2007 surveys used a Buckland-Turnock (B-T) mode (Buckland & Turnock, 1992), which incorporates asymmetrical platforms with 1-way independence: a "tracker" platform that searches far ahead of the vessel using binoculars and tracks sightings, and a primary platform which searches closer to the vessel. In this mode, the tracker

platform monitors the primary platform and is aware of their sightings, and duplicate sightings are usually identified in the field by a designated observer. The primary platform is visually and aurally isolated from the tracker platform and is not aware of their sightings. Further details are provided in Pike et al. (2020a). In 2015, an independent observer (IO) mode, incorporating symmetrical fully-independent platforms, was used. Duplicates were usually identified post-survey (see below).

Field procedures used on extension vessels in 2007 were identical to those used on the primary platforms on the dedicated NASS vessels.

Species identification certainty

Surveys up to and including 2001 classified species identification as either certain or uncertain. The 2007 and 2015 surveys used 3 classifications for certainty in species identification: high, moderate and low. All species certainty levels were included in analyses, with certainty tested for inclusion as a detection function covariate (see below).

Duplicate identification

In surveys conducted in B-T mode, duplicates were usually identified in the field by a dedicated observer on the Tracker platform (Pike et al., 2020a). In the 2015 survey, duplicates were identified post hoc by: 1) similarity of sighting location taking into account the time interval between the sightings; and 2) similarity of species identification, group size, cue type and whale heading. Whale sightings were generally classified as non-duplicates if they differed by 10° or more in angle to track when seen within a short interval by the platforms, or the distance between sighting spots was estimated to be over a mile when different dive cycles were observed over several minutes.

Data selection

In surveys up to 2007, Beaufort Sea state (BSS) was recorded at sea by the survey leader. In 2015, true wind speed was recorded from the bridge. This was converted to BSS for consistency with earlier surveys. Only effort and sightings of BSS less than or equal to 4 were retained for this analysis.

In cases of duplicate sightings between the tracker and primary platforms, distance measurements from the tracker platform were considered more reliable and therefore preferred, specifically the last distance measurement before detection by the primary. For the 2015 survey, what were considered to be the most reliable measurements based on observer comments were used.

In 2015, in strata covered by the combined cetacean/fisheries research vessel, some cetacean survey effort was maintained while ferrying between transects, resulting in some transects that paralleled the coast of Iceland or Greenland. As these transects were aligned with suspected gradients in killer whale density, their inclusion could result in positively biased estimates (Pike et al., 2019a). Therefore, sightings from these “compromised” transects were not included in the estimation of encounter rate but were used in modelling the detection function (see below).

Abundance estimation

Single and combined platform analyses

The 1987, 1989 and 1995 analyses used single platforms only. For the later surveys that used double platforms, analyses were performed using combined distinct (i.e. duplicate sightings recorded once) sightings from both platforms, as well as a perception-bias corrected estimate described below.

Density and abundance were estimated using stratified line transect methods (Buckland et al., 2001) using the DISTANCE

6.2 (Thomas et al., 2010) software package. The perpendicular distance data were right-truncated to exclude up to 10% of sightings to reduce the leverage of distant sightings and in some cases, to eliminate the need for adjustment terms.

While there is no minimum number of detections necessary to derive a detection function model, other than the number of detections must exceed the number of model parameters, we considered 30 sightings as a minimum for a robust model. If the number of detections was less than 30, we derived a detection function using pooled sightings from 2 or more survey years and included survey year as a possible covariate (see below). For surveys conducted from 1987 to 1995, which had fewer than 30 killer whale sightings, we tested a detection function estimated from all 3 surveys as they were conducted using similar field methods and vessels (see above). If the number of detections was less than 30 but exceeded 20, we attempted to derive an un-pooled detection function as described below, for comparison with the pooled results. The model (pooled or un-pooled) that delivered the greatest precision was chosen.

The Hazard Rate and Half Normal models for the detection function $f(x)$ were initially considered and the final model was chosen by minimisation of AIC (Buckland et al., 2001). Covariates were incorporated into the detection function through the scale parameter in the key function and were retained only if the resultant Akaike Information Criterion (AIC) value was lower than that for the model without the covariate. The following covariates were considered: vessel identity; species identification certainty (1987–2001: high, low; 2007–2015: high, moderate, low), BSS; cloud coverage (scale 1=0%–24%, 2=25%–69%, 3=70%–89%, 4=>90%), visibility (nm); and platform making the sighting (2001–2015: primary, secondary/tracker or duplicate). Covariates were only considered if there were more than 5 observations per covariate level. If survey years were pooled for estimation of the detection function, survey identity was also considered as a

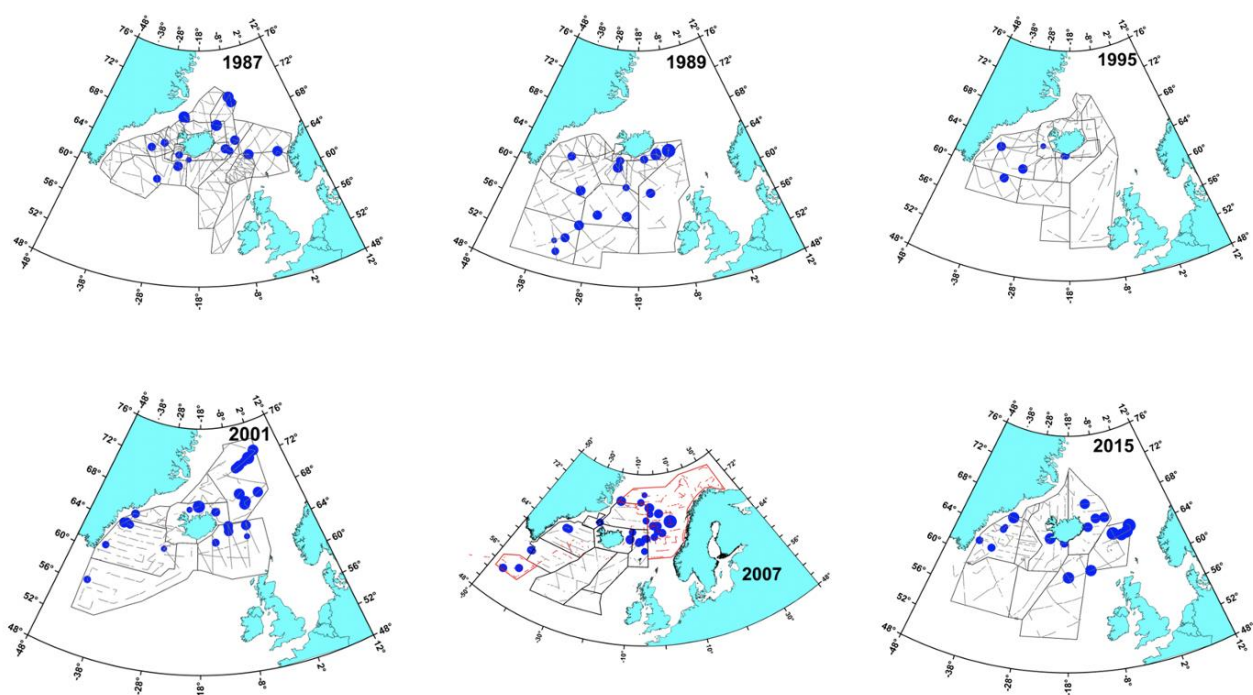


Figure 3. Realized survey effort (BSS<5) and sightings of killer whales. Symbol size varies with group size from 1 to 40.

covariate. Similarly, for the 2007 survey, a covariate was included to discriminate sightings from the Dedicated and Extension vessels. In cases where covariates were retained, the detection function was estimated at the stratum level and could therefore vary in scale by stratum depending on covariate levels; otherwise the detection function was estimated at the survey level. Encounter rate and expected cluster size ($E(s)$) were estimated at the stratum level. Stratum and total variance were estimated using the method of Innes et al. (2002).

Regression of the natural log of cluster size ($\ln(s)$) against estimated detection probability was used to determine if there was size bias in group detectability. If this regression was significant at the $P < 0.15$ level, the detection of groups was considered to be size biased and the estimate of mean cluster size was adjusted using this regression; otherwise, the simple mean of cluster size was used.

Perception bias corrected estimates

In some cases, usually due to poor weather or equipment issues, survey vessels reverted to a single platform mode during which both platforms were staffed and in communication. This was particularly true in 2007 when a substantial proportion of effort (15% at $BSS < 5$) was conducted in single platform mode, with both platforms combined and no tracking conducted. Only effort and sightings realised in double platform mode could be included in this analysis.

Density and abundance (corrected for perception bias) were estimated using stratified mark-recapture distance sampling (MRDS) techniques (Laake & Borchers, 2004) using the DISTANCE 6.2 software package (Thomas et al., 2010). In the 2001 and 2007 surveys, observers on the tracker platform were aware of sightings made by observers on the primary platform, so the platforms were not independent. Therefore the “trial configuration” (Burt et al., 2014; Laake & Borchers, 2004), in which the secondary (tracker) platform serves to generate trials to estimate the proportion of sightings on the trackline that are seen by the primary platform ($p(0)$), was used. Note that the $p(0)$ derived here cannot be applied to the combined platform estimates described above as they include sightings from the tracker platform; estimation therefore requires a separate detection function for the primary platform only, which was derived as described above for the combined platform estimates. In the 2015 survey, the platforms were completely independent from one another and did not communicate. Therefore the “independent observer” (IO) mode (Burt et al., 2014; Laake & Borchers, 2004), in which the platforms are considered to be equivalent and either platform can “mark” a sighting for the other, was used. In this case, the detection function described above for the combined platforms was retained.

We initially attempted 2 types of analyses: using the assumption of “full independence” (FI) wherein sightings from the platforms are considered independent at all perpendicular distances, and under the assumption of “point independence” (PI), wherein the probability of detection by the tracker and primary platforms is assumed to be independent only on the trackline (Laake & Borchers, 2004). The model type was selected by minimization of AIC. The assumption of point independence requires the estimation of 2 detection functions: one for primary platform (B-T mode surveys, 2001 and 2007) or combined platform (IO mode, 2015) detections, and a separate

conditional detection function for detections of one platform conditional on the other. Analyses under the assumption of full independence require only the latter detection function. The conditional detection function was implemented as a logistic regression model with the same covariates (except for platform identity) available as for the primary platform detection function. Again, the final model was chosen by minimization of AIC, after the distance detection function for the primary or combined platforms had been finalized.

RESULTS

Sightings and distribution

Killer whales were spotted rarely in the survey area compared to some other species, with total numbers of sightings ranging from a high of 45 in 2001 to a low of 5 in 1995 (Table 1, Figure 3). Of the 35 sightings in 2007, 26 were sighted by the extension vessels, mainly to the east of the main survey area. In all surveys, killer whales were sighted throughout the survey area, but most commonly to the east and northeast of Iceland.

Killer whales were identified with relatively high certainty compared to most other species, with high certainty identifications comprising 92% of the total from the NASS dedicated vessels (Table 1).

Killer whales occurred in small groups in the area, with pairs being most frequently sighted and groups of 10 or fewer comprising 85% of total sightings. Larger groups of up to 40 animals were also reported on rare occasions (Table 1).

Abundance estimates

Specifications of the models used in estimating abundance are provided in Table 2 and are described by survey below. Detection functions are shown in Figure 4. Abundance estimates are summarised by survey in Table 3 and presented in greater detail in Supplementary Files 1–7.

1987

With only 22 detections available (Table 1), we estimated abundance in 2 ways: using a detection function pooling detections from 1987–1995; and using detections from 1987 only. Both the pooled and un-pooled functions incorporated a 2 level (0–2, 3+) factor covariate for BSS (Table 2). Higher BSS reduced the scale of the detection functions (Figure 4). The pooled function delivered slightly better precision and we accept that estimate of 8,899 (CV=0.46, 95% CI: 3,621–21,870) (Table 3). Density was highest in the northeast part of the survey area in blocks 8, 9 and F8 and these 3 strata accounted for 72% of the total estimate (Supplementary File 1).

1989

With 21 detections, we again estimated abundance using both the pooled (1987–1995) detection function described above and an un-pooled detection function for 1989 only. The latter function included no covariates. The pooled function resulted in a more precise estimate and we therefore accept that estimate of 10,316 (CV=0.37, 95% CI: 4,960–21,456). Density was highest to the southeast and south of Iceland, particularly in strata F7, 36 and 88 which accounted for 52% of total abundance (Supplementary File 2).

Table 2. Model specifications. MODE - platform configuration; SP - single platform; CP - combined platforms; HN - half normal; HZ - hazard rate; BSS - Beaufort Sea state; VESS - vessel identity; CLUS - cluster size.

SURVEY	MODE	POOL	TRUNCATION (m)	DS MODEL		MR MODEL	
				KEY	Covariates/Adj	TYPE	Covariates
1987	SP	87	2500	HN	BSS (0-2, 3+)		
1987	SP	87-95	2500	HN	BSS (0-2, 3+)		
1989	SP	87-95	2500	HN	BSS (0-2, 3+)		
1989	SP	89	2500	HN			
1995	SP	87-95	2500	HN	BSS (0-2, 3+)		
2001	CP	2001	2900	HN	BSS (0-1, 2+)		
2001	SP	2001	3000	HZ		Trial PI	CLUS
2007	CP	2007	1000	HN	BSS (0-1, 2+)		
2015	CP	2015	2600	HN	VESS (AB, H)	IO PI	NONE

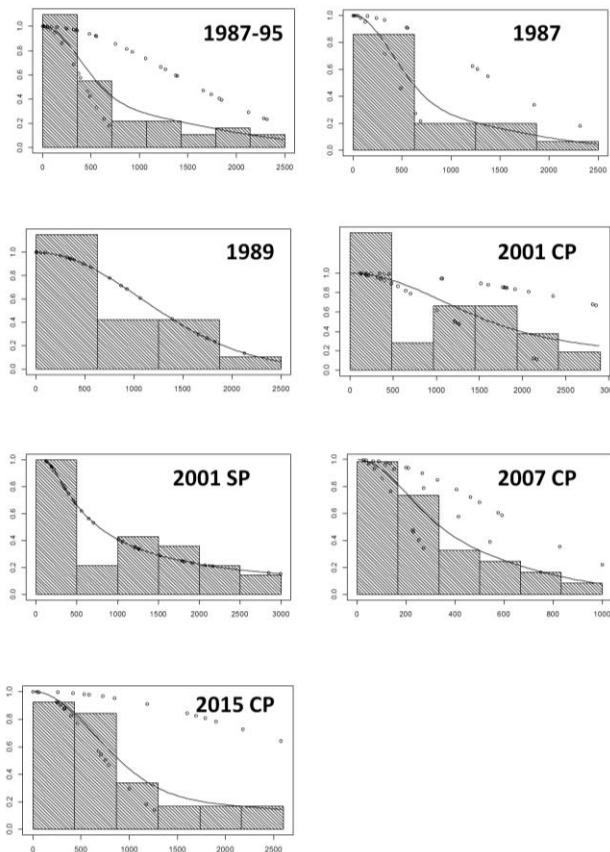


Figure 4. Detection functions, showing probability of detection (Y-axis) with perpendicular distance from trackline (m) (X-axis). Points are predicted values of observations based on distance and covariate levels (see Table 2). CP - combined platforms; SP - single platform.

1995

As only 5 killer whale sightings were detected in 1995, we estimated abundance using only the pooled (1987–1995) detection function, resulting in an estimated abundance of 4,736 (CV=0.48, 95% CI: 1,842–12,176) (Supplementary File 3).

2001

More killer whale sightings (45) were recorded in 2001 than in any other NASS (Table 1). For the combined platform estimate (i.e. using distinct sightings from both platforms), a half-normal key function with a 2-level (0–1, 2+) covariate for BSS produced best fit for the detection function, resulting in an uncorrected estimate of 15,142 (CV=0.47, 95% CI: 6,003–38,190) (Table 3, Supplementary File 4). Density was highest in the coastal Icelandic block and in block J to the northeast of Iceland, with these 2 strata accounting for 88% of total abundance.

Within the truncation distance of 3,000 m for sightings from just the primary platform, observers on that platform detected 13 of 18 detections made by the tracker platform, including all detections made within a perpendicular distance of 750 m from the trackline. A half-normal model with no covariates resulted in an uncorrected estimate of abundance of 20,300 (CV=0.63, 95% CI: 6,312–65,286) (Supplementary File 5) for the primary platform alone. A PI model with a covariate for group size in the conditional detection function resulted in a mean $p(0)$ of 0.99 (CV=0.01) and a corrected estimate of 20,345 (CV=0.63, 95% CI: 6,317–65,523).

2007

There was an insufficient number of sightings (9, Table 1) from the NASS dedicated vessels alone to form a detection function, so sightings from the extension vessels (26) were included. For the combined platforms, a half-normal key function with a 2 level (0–2, 2+) covariate for BSS produced best fit, resulting in an uncorrected abundance estimate for the NASS and Extension strata combined of 57,460 (CV=0.50, 95% CI: 22,385–147,494) (Table 3). The NASS strata accounted for 19% of this total. Density was highest in the extension strata with the X-NE block alone accounting for 71% of total abundance (Supplementary File 6). Within the NASS strata, density was highest in the IC block around coastal Iceland and the FE block around the Faroes, or generally the area to the east of Iceland (Figure 3).

Of the 4 killer whale sightings made by the Tracker platform on the NASS dedicated vessels while B-T mode, 1 sighting was

duplicated by the primary platform. We consider these data insufficient to estimate perception bias. Within dedicated NASS strata in which Dedicated and Extension vessels overlapped, encounter rate was 3.6 (CV=0.70, 95% CI: 0.82–10.1) times higher on the Extension survey vessels than it was on the Dedicated vessels.

2015

A total of 31 killer whales were sighted. A half-normal key function with a 2-level covariate for vessel identity (2 Icelandic vessels combined, Faroese vessel) provided best fit for the detection function. Uncorrected abundance was estimated as 14,611 (CV=0.55, 95% CI: 4,055–52,773) (Table 3). Density was highest in the Faroese block FC and block IE east of Iceland, which together accounted for 84% of total estimated abundance (Supplementary File 7).

Of the 31 detections by both platforms, 5 were duplicates. A PI model with no covariates provided best fit for the conditional detection function, estimating $p(0)$ as 0.48 (CV=0.30) and resulting in a perception bias corrected estimate of 30,540 (CV=0.63, 95% CI: 8,316–112,120) (Supplementary File 7).

Post-stratification to exclude the area of overlap with Norwegian surveys reduced the surface areas of block FC by 36% and IE by 66%. Most killer whale sightings were in the eastern parts of these blocks and were therefore excluded from the abundance estimate, resulting in a 77% decrease of total uncorrected and corrected abundance estimates to 3,370 (CV=0.54, 95% CI: 1,197–9,490) and 7,044 (CV=0.62, 95% CI: 2,240–22,155) respectively (Supplementary File 7). Summing our corrected estimate with that from the Norwegian survey of 15,056 (CV=0.29, 95% CI: 8,423–26,914) (Leonard & Øien, 2020a) results in a total estimate for the Central and Eastern North Atlantic of 22,100 (CV=0.28, 95% CI: 15,282–32,023).

DISCUSSION AND CONCLUSIONS

The low number of sightings, combined with a clustered distribution, together give our estimates a relatively low level of precision, with survey CV's ranging from 0.37 to 0.55 for the uncorrected estimates in the NASS survey area (Table 3). Nevertheless, the estimates do constrain the numbers of killer whales in the area, likely to the low tens of thousands.

Potential biases

Perception bias

While the 2001, 2007 and 2015 surveys used double platforms that should allow the estimation of perception bias through mark-recapture distance sampling, in practice this was only possible for the 2001 and 2015 surveys. Of 4 killer whale sightings made by the tracker platform in 2007, only 1 was re-sighted by the primary platform, making a robust estimation of perception bias impossible.

In 2007, encounter rate was higher (although not significantly so) on the Extension vessels than on the NASS Dedicated vessels in strata in which both types were sampled, which suggests that perception bias may have been less severe on the Extension vessels. This is surprising since the opposite was true for all species other than the common minke whale in the survey (Pike et al., 2020a). We can suggest no explanation for this apparent discrepancy.

Perception bias also varied greatly between the 2 surveys for which it is available, being almost non-existent in 2001 but substantial at 0.48 (CV=0.30) in 2015. The difference is made even more substantial by the fact that the $p(0)$ for 2001 applies to the primary platform only, while that for 2015 applies to the combined platforms. We can provide no certain explanation for the discrepancy.

Table 3. Survey estimates for killer whales. Blue highlighted estimates are considered best. Estimates by Foote et al. (2007) are shown for comparison. SP - single platform; CP - combined platforms; C - corrected for perception bias; POOL - surveys pooled in detection function; N - NASS dedicated (2007); E - NASS extension (2007).

SURVEY	TYPE	POOL	N	CV	LCL	UCL	Foote et al., 2007			
							N	CV	LCL	UCL
1987	SP	87–95	8,899	0.46	3,621	21,870	8,260	0.45	3,516	19,408
1987	SP		8,689	0.47	3,478	21,709				
1989	SP	87–95	10,316	0.37	4,960	21,456	26,774	0.63	8,341	85,943
1989	SP		13,194	0.44	5,776	30,137				
1995	SP	87–95	4,736	0.48	1,842	12,176	4,413	1.21	575	33,990
2001	CP		15,142	0.47	6,003	38,190	15,014	0.42	6,637	33,964
2001	C		20,345	0.63	6,317	65,523				
2007-N	CP	N+EXT	10,853	0.49	4,051	29,077				
2007-E	CP	N+EXT	46,607	0.60	15,457	140,532				
2007-TOT	CP	N+EXT	57,460	0.50	22,385	147,494				
2015	CP		14,611	0.55	4,045	52,773				
2015	C		30,540	0.63	8,319	112,120				

Perception bias for killer whales in Norwegian ship surveys, which use an IO mode similar to that used in the Icelandic and Faroese surveys in 2015, ranged from 0.82 to 0.93 over 3 survey periods (Leonard & Øien, 2020a, b), which suggests that our $p(0)$ for 2015 is anomalously low for ship surveys of this species. Norwegian surveys are focussed on common minke whales, a species of similar size to killer whales, while the primary target species of the Icelandic surveys is the fin whale. This may make the Icelandic and Faroese surveys less effective in detecting smaller species.

Availability bias

Whales that are submerged during the passage of the vessel cannot be detected by observers, leading to "availability bias". This bias is most severe for long-diving whales such as sperm (*Physeter macrocephalus*) and beaked whales (*Ziphiidae*), for which dive times can exceed 1 hr. Killer whales typically have mean dive durations of 2 to 3 minutes (Baird et al., 2005) and dives rarely exceed 10 minutes in length (Miller et al., 2010). Maximum detection distances in these surveys were 1–2 km, a distance covered by the survey vessels in 200–400 seconds. This suggests that availability bias is unlikely to be severe for this species and we made no attempt to correct for this.

Responsive movement

Some cetaceans react to approaching vessels by fleeing (aversion) or approaching (attraction) them. If this responsive movement occurs before the initial detection by observers, it will result in biased abundance estimation because of influence on the detection function and *esw* (Buckland & Turnock, 1992; Canadas et al., 2004; Palka & Hammond, 2001). Attractive movement, particularly common with some dolphin species (Canadas et al., 2004), can result in positively biased estimates.

Methods available to detect and address this bias generally include the use of asymmetric observer platforms, such as the B-T method used in 2001 and 2007, in which a Tracker platform sights whales well ahead of the vessel using visual aids, and tracks them until they are detected by the primary platform or pass abeam. Unfortunately, killer whales were not a priority for tracking efforts in these surveys, so no data on the response of killer whales to the survey vessels was obtained. In addition, a potential measurement bias on the primary platform in 2007 (see below) made comparison of measurements by the 2 platforms to duplicate sightings problematic (Pike et al., 2020a). Surveys conducted in European waters using B-T mode encountered killer whales rarely and provide no information on reactions to survey vessels (Hammond et al., 2017, 2013). Lacking specific data on the behaviour of killer whales in response to passing vessels in this area, we cannot predict whether this bias is problematic for these surveys.

Pooling

As 3 of the surveys (1987, 1989, 1995) did not have a sufficient number of detections to estimate a robust detection function, we took the approach of using a detection function that combined sightings from these 3 surveys, while testing a scale covariate for survey identity to account for variation between surveys. We also developed individual detection functions for 1987 and 1989 for comparison. We accepted estimates using the pooled model, which did not include the survey identity covariate, as they were of greater precision.

Similarly, an insufficient number of sightings forced us to pool sightings from the Extension and Dedicated NASS vessels in the 2007 survey. Again, the accepted model did not include a covariate related to survey type.

This approach is not ideal in that we can expect survey-level differences in detection functions due to environmental conditions, observers, platform heights and other factors (Buckland et al., 2001). While the addition of a covariate for survey identity can account for survey-level differences in the scale of the detection function, it is possible that the functional form of the detection function might also vary between surveys. However, this disadvantage is diminished relative to the risk of producing highly biased estimates due to random variation resulting from very small sample sizes. We therefore consider this approach conservative and the best that can be realized with these limited data. Pike, Víkingsson, Gunnlaugsson and Øien (2009) used inter-survey pooling in the detection function to estimate the abundance of rarely-sighted blue whales (*Balaenoptera musculus*) in NASS ship surveys, while Pike et al. (2020b) employed it to estimate the relative abundance of several species from partial aerial surveys around Iceland.

Measurement bias

Pike et al. (2020a) found evidence suggesting negative bias for distance measurements from the primary platform in the 2007 NASS. Such a bias would lead to positively biased abundance estimates, with the magnitude of the bias estimated as 12% to 28%.

Comparison to previous estimates

The estimates given here are similar to those reported by Foote et al. (2007) for 1987, 1995 and 2001, with <10% difference (Table 3). However, their estimate for 1989 is 160% higher than ours, and also has a higher CV. Foote et al. (2007) do not provide any detail about data selection, truncation distance, or model choice so we cannot explain this discrepancy.

Gunnlaugsson and Sigurjónsson (1990) provided an estimate of 6,618 (CV=0.32) for the 1987 NASS, which is 26% lower than ours. However, they assumed an *esw* equivalent to twice the median sighting distance of 556 m (i.e. 1,111 m), which is 26% higher than our mean *esw* for 1987 of 884 m (Supplementary File 1) and thus largely accounts for the difference between the magnitudes of the estimates.

Distribution

While distribution varied between surveys, density was generally highest to the east and northeast of Iceland, especially in the western Norwegian Sea in years when that area was covered. This was particularly apparent in the 1987, 2001 and 2007 Extension surveys (Figure 3). This is in accordance with the results of Norwegian surveys described below and with the historical distribution of commercial catches by Norway (Foote et al., 2007; Øien, 1988). The 1995 survey was anomalous in producing few sightings and none to the east or northeast of Iceland.

Density surface modelling (Hedley & Buckland, 2004) offers a means of relating animal density to static and dynamic (i.e. changing temporally) environmental variables, such as water depth, bottom slope, primary production, and prey distribution, which are known or measured concurrently with the survey. Density is modelled as a function of these external variables,

which can result in greater precision than design-based estimates while also providing information about the ecology of the animals (Paxton et al., 2009). In addition, a density surface model can be extrapolated to areas outside of the area covered by the actual survey, although this must be done with extreme caution. The distribution of killer whales is likely related to the distribution of their prey (Jourdain et al., 2019), however, this relationship is likely to be dynamic and prey distribution is not often assessed concurrently with cetacean surveys. Killer whale density may be related to other environmental variables for which we do have data, and work is currently ongoing to produce such models for the NASS series.

Trends in abundance

Trends in the abundance of several species have been detected over the 30-year time span of the NASS (Pike et al., 2020b; Pike et al., 2019b; Víkingsson et al., 2009). However, the low precision in the estimates of killer whale abundance precludes any meaningful analysis of trends.

Abundance in neighbouring areas

Killer whales are known to occur throughout the North Atlantic, commonly from about 35° N to as far north as the seasonal Arctic ice edge, but detailed information on distribution and abundance patterns throughout the year is lacking for most regions (Jourdain et al., 2019).

Killer whale abundance has been estimated from Norwegian shipboard surveys conducted between 2002–2018. Three estimates are available, each assigned to the span of years over which the area was surveyed: 2002–2007: 18,821 (95% CI: 11,525–30,735); 2008–2013: 9,563 (95% CI: 4,713–19,403) (Leonard & Øien, 2020b); 2014–2018: 15,056 (95% CI: 8,423–26,914) (Leonard & Øien, 2020a). Most sightings were recorded in the central and western Norwegian Sea, an area that partially overlaps with the surveys described here (Figure 2). Post-stratifying to eliminate this overlap resulted in a total estimate for the Central and Eastern North Atlantic of 22,100 (CV=0.28, 95% CI: 15,282–32,023). The precision of this estimate is overestimated as it does not include additional variance due to distributional shifts resulting from the survey being carried out over multiple years (2014–2018) in the Norwegian sector (Leonard & Øien, 2020a).

The Extension component of the 2007 NASS confirms the central Norwegian Sea as being an important area of killer whale distribution in the North Atlantic. Most sightings were made to the east and northeast of the main survey area, which is covered by the Norwegian surveys mentioned above (Leonard & Øien, 2020a, b). While our point estimate of 40,814 (CV=0.66, 95% CI: 12,432–133,991) for the XNE block is higher than the Norwegian estimates for about the same area, the low precision of our estimate makes the difference non-significant.

Further to the southeast in British, Irish and western European waters, the SCANS (Hammond et al., 2017) and offshore CODA (Hammond et al., 2013) had very low numbers of killer whale detections, despite considerable survey effort in these areas, suggesting low numbers in this region during the summer.

The low numbers of killer whale sightings recorded on aerial surveys around coastal Iceland between 1986 and 2016 (Pike et al., 2020b) precluded estimation of abundance. However, all of the NASS ship surveys reported here included all or part of the

aerial survey area, although they did not cover near-shore areas.

To the west of our survey area, killer whales were rarely sighted in aerial surveys conducted off East and West Greenland in 2015 (Hansen et al., 2019). Similarly, an insufficient number of sightings were made in aerial surveys conducted off Labrador, Newfoundland and the Gulf of St Lawrence in 2016 to estimate abundance (Lawson & Gosselin, 2018). Killer whales certainly occur in these regions and indeed are hunted in West and East Greenland (Jourdain et al., 2019), but densities are too low to estimate using current levels of survey effort.

Seasonal distribution

There is little information on the distribution of killer whales outside of the summer (June–August) season in the survey area. It is well known that components of the population track the seasonal movements of herring (*Clupea harengus*) in Icelandic waters (Sigurjónsson, 1984; Sigurjónsson et al., 1988) and killer whales may also associate with mackerel (*Scomber scombrus*) or other fish species in the survey area (Jourdain et al., 2019; Samarra et al., 2017).

Some survey effort has been conducted to the northwest of the NASS survey area in October in conjunction with capelin (*Mallotus villosus*) surveys, however no killer whale sightings were detected (Pike et al., 2019a).

Aerial surveys have been conducted in Icelandic coastal waters in April/May 2004 and 2005 and in September 2003 and 2004 (Pike et al., 2020b). Killer whales were sighted more frequently in spring 2004 than in the summer or early fall surveys, suggesting that they may be more common in the area at that time of year, perhaps in association with overwintering herring populations. However, numbers were nevertheless very low and abundance could not be estimated.

As noted above, killer whales are relatively abundant in the central Norwegian and southern Barents Seas during the summer (Leonard & Øien, 2020a, b). They are also found along the Norwegian coast at all times of the year, where they are known to feed actively on herring schools (Similä, 1997; Similä, Holst & Christensen, 1996). Recent work has shown that they likely feed predominantly on herring in offshore areas as well (Vogel, 2020).

Conclusion

Killer whale populations in the North Atlantic are thought to be recovering from past commercial whaling in Norway, subsistence hunting in Greenland, live captures for aquaria and some culling efforts in Iceland in the 1950's (Jourdain et al., 2019). While the NASS ship surveys do not provide evidence of population trends, they do indicate that killer whales number in the low tens of thousands in the central and eastern North Atlantic.

The low precision of our estimates results from a low number of sightings and extreme variation in encounter rate within strata. While increasing survey effort and perhaps modifying stratification could alleviate this issue, it is likely that the amount of effort required would be practically prohibitive. Efforts are already underway to estimate numbers and movement patterns using photographic and genetic mark-recapture methods (Jourdain et al., 2019), and these may offer

a more practical means of monitoring these relatively rare top predators in the North Atlantic.

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.

ACKNOWLEDGEMENTS

The authors would like to thank the captains, crews, and observers on all the vessels used in the surveys for their dedication and hard work. We thank 2 anonymous reviewers for their very helpful comments on the manuscript. Funding for the NASS was provided by the Icelandic and Faroese governments. Funding for this analysis was provided by NAMMCO.

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