Rate of increase and current abundance of humpback whales in West Greenland

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ABSTRACT

Aerial line transect surveys of the density of humpback whales (*Megaptera novaeangliae*) conducted off West Greenland eight times between 1984 and 2007 were used to estimate the rate of increase on the summer feeding ground. Only surveys in 1993, 2005 and 2007 had enough sightings to construct independent density estimates, whereas the surveys in 1984–85 and 1987–89 had to be merged and treated as two surveys. The annual rate of increase was 9.4% yr^{-1} (SE = 0.01) between 1984 and 2007. This rate of increase is higher than the increase estimated at the breeding grounds in the West Indies, but is of the same magnitude as the observed rate of increase at other feeding grounds in the North Atlantic. A matrix model based on observed life history parameters revealed that the theoretical growth rate of a humpback whale population ranged between 1 and 11%. This confirms that the observed growth in West Greenland is within the plausible values. The survey in 2007 was used to make a fully corrected abundance estimate including corrections for whales that were submerged during the passage of the survey plane. The line transect estimate for 2007 was 1,020 (CV = 0.35). When the estimate was corrected for perception bias with mark-recapture distance sampling (MRDS) methods, the abundance increased to 1,505 (0.49). A correction for availability bias was developed based on time-depth-recorder information on the time spent at the surface (0–4m). However, used directly this correction leads to a positively-biased abundance estimate and instead a correction was developed for the non-instantaneous visual sighting process in an aircraft. The resulting estimate for 2007 was 3,272 (CV = 0.50) for the MRDS analysis. An alternative strip census estimate deploying a strip width of 300m resulted in 995 (0.33) whales. Correction for perception bias resulted in 991 (0.35) whales and corrected for the same availability bias as for the MRDS method resulted in a fully corrected estimate of 2,154 (0.36) humpback whales in West Greenland in 2007.

KEYWORDS: HUMPBACK WHALE; ABUNDANCE ESTIMATE; SURVEY-AERIAL; SATELLITE TAGGING; WEST GREENLAND; MARK-RECAPTURE; DISTANCE SAMPLING

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) undertake long migrations between high latitude, productive feeding grounds during summer and warmer oligotrophic mating/breeding grounds at low latitudes during winter (Kellogg, 1929; Norris, 1967). The main breeding grounds in the North Atlantic are located in the West Indies and the feeding grounds are primarily located in northern Norway, around Iceland, in West Greenland, in eastern Canada, and in the Gulf of Maine (Stevick *et al.*, 2003).

The large catches of North Atlantic humpback whales during the commercial whaling époque nearly exterminated the population and as an effect commercial whaling of humpback whales has been banned since 1955 (Smith and Reeves, 2002). To document the recovery of such long-lived, slowly reproducing migratory species long time series of abundance estimates covering the distributional range of the population is needed. Such time series of abundance have been collected in most of the core areas and there seem to be a general increase in the population. In the West Indies the instantaneous rate of increase between 1979 and 1993 has been estimated at 3.1% (Stevick *et al.*, 2003).

Increases in abundance of humpback whales have also been detected at several of these feeding grounds. For example, annual increases of 11% from 1970 to 1988 (Sigurjónsson and Gunnlaugsson, 1990) and 12% during 1986 and 2001 (Pike *et al.*, 2009) around Iceland, 5.5% in the Gulf of Maine (Barlow and Clapham, 1997) and 9.4% in the Western North Atlantic (Katona and Beard, 1990) have been observed or estimated. Until now, no estimates of changes in abundance have been developed for the West Greenland feeding ground.

Aerial surveys for common minke (*Balaenoptera acutorostrata*) and fin whales (*Balaenoptera physalus*) have been conducted at regular intervals in West Greenland since 1984. Estimates of abundance of humpback whales from these surveys have only been presented for 2005 (Heide-Jørgensen *et al.*, 2008) mostly due to the low number of sightings in the previous years.

In this study the aerial survey data from 1984 to 1993 were re-examined and used to construct a time series of the relative abundance of humpback whales using eight surveys from 1984, 1985, 1987, 1988, 1989, 1993, 2005, and 2007. These estimates are then used together with recent abundance estimates to estimate the rate of increase of humpback whales on the West Greenland feeding ground since 1984. The observed rate of increase is compared to a theoretical model of the plausible range of growth based on

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Table 1

Effort and sightings distributed by year and strata that are comparable between years for the aerial surveys of West Greenland. Only effort and sightings in Beaufort sea state <5 is included.

Year/strata	Effort (km)	Area (km²)	Transects	Effort/area	Sightings	Mean pod size (SE)	Sighting rate
1984							
1: 71°20–70°N	491	24,516	5	0.0200			
2: 70°–68°30'N	435	17,872	3	0.0243			
3A: 68°30–67'N inshore	224	14,913	3	0.0150			
3B: 68°30–67'N offshore	735	19,305	7	0.0381			
4A: 67°–66'N inshore	442	9,446	5	0.0468			
4B: 67°–66°N offshore	398	8,311	6	0.0479			
5A: 66°–65°N inshore	174	6,431	3	0.0271			
5B: 66°–65°N offshore	644	10,900	7	0.0591			
6: 65–64°N	2,145	17,107	15	0.1254	3		
7: 64–63°N	699	11,122	7	0.0628	1		
8: 63°–62°N	410	11,748	4	0.0349	1		
Sum	6,797	151,671	65	0.0448	5	2.14 (0.27)	0.00074
1985							
1: 71°20–70°N	791	24,516	7	0.0323			
2: 70°–68°30'N	321	17,872	2	0.0180			
3A: 68°30–67'N inshore	337	14,913	4	0.0226			
3B: 68°30–67'N offshore	424	19,305	4	0.0220			
4A: 67°–66'N inshore	444	9,446	5	0.0470	1		
4B: 67°–66°N offshore	462	8,311	7	0.0556			
5A: 66°–65°N inshore	829	6,431	9	0.1289	2		
5B: 66°–65°N offshore	1,156	10,900	12	0.1061	1		
6: 65–64°N	1,007	17,107	7	0.0589	3		
7: 64–63°N	298	11,122	3	0.0268			
8: 63°–62°N	772	11,748	6	0.0657			
Sum	6,841	151,671	66	0.0451	7	2.14 (0.27)	0.00102
1987							
1A: 71°30'–69°15'N	1,915	14,779	13	0.1296			
1B: Disko Bay and Vaigat	729	5,358	11	0.1361			
2: 69°15'–67°N	1,153	39,883	7	0.0289			
3: 67°–64°15'N	1,417	42,400	8	0.0334	4		
4: 64°15'–60°40'N	1,673	25,165	9	0.0665	1		
5: 60°40'–58°45'°N	1,118	16,518	8	0.0677	2		
Sum	8,005	144,103	56	0.0556	7	1.9 (0.14)	0.00087
1988							
1A: 71°30'–69°45'N	703	24,560	10	0.0286			
1B: Disko Bay and Vaigat	404	13,876	12	0.0291			
2A: 69°45'–68°N	820	29,228	5	0.0281			
2B: 68°–66°30'N	1,077	19,488	10	0.0553			
3: 66°30'–64°15'N	1,399	41,660	9	0.0336	7		
4: 64°15'–60°45'N	648	50,742	6	0.0128	2		
5: 60°45'N–58°45'N	605	34,283	8	0.0176			
Sum	5,656	213,837	60	0.0265	9	1.1 (0.14)	0.00159
1989							
2A: 69°45'–68°00'N	428	29,228	4	0.0146			
2B: 68°–66°30'N	836	19,488	5	0.0429			
3: 66°30'–64°15'N	706	41,660	11	0.0169	1		
4: 64°15'–60°45'N	1,218	50,742	19	0.0240	2		
5: 60°45'–58°45'N	72	34,283	2	0.0021			
Sum	3,260	175,401	41	0.0186	3	2.7 (0.7)	0.00092
1993							
1A: 71°30'–69°45'N	138	25,130	5	0.0055			
1B: Disko Bay and Vaigat	392	13,110	8	0.0299			
2A–C: 69°45'–68°00'N	1,635	15,160		0.1078			
2B–C: 68°–66°30'N	94	15,700	5	0.0060			
3 offshore: 66°30'–64°15'N	185	26,680	2	0.0069	1		
3 coast: 66°30'–64°15'N	828	23,100	10	0.0358	6		
4 offshore: 64°15'–60°45'N	348	24,320	4	0.0143			
4 coast: 64°15'–60°45'N	2,341	27,410	29	0.0854	9		
5 offshore: 60°45'–58°45'N	436	18,450	6	0.0236	1		
5 coast: 60°45'–58°45'N	881	14,920	11	0.0590	3		
Sum	7,140	178,850	75	0.0399	20	3.2 (0.60)	0.00280
2005							
CF: 59°–58°N	293	11,523	4	0.0254			
CW: 67°30'–64°N	1,958	74,798	30	0.0262	4		
Disko Bay	556	12,312	12	0.0452	1		
SG: 61°–59°N	1,106	19,491	19	0.0567	4		
SH: 68°30'–67°30'N	577	15,669	7	0.0368			
SW: 64°–61°N	1,968	29,781	31	0.0661	13		
Sum	6,458	163,574	103	0.0395	22	8.3 (0.38)	0.00340

Cont.

Table 1 cont.

Year/strata	Effort (km)	Area (km²)	Transects	Effort/area	Sightings	Mean pod size (SE)	Sighting rate
2007							
1: Uummannaq Fjord	191	8,404	3	0.0227			
2: 71°30'–69°45'N	502	22,631	5	0.0222			
3: Disko Bay and Vaigat	532	14,653	9	0.0363			
4: 69°45'–68°N	545	34,272	4	0.0159	1		
5: 68°–66°30'N offshore	862	16,226	9	0.0531	3		
6: 68°–66°30'N inshore	973	14,902	9	0.0653			
7: 66°30'–64°N offshore	551	22,085	6	0.0249	2		
8: 66°30'–64°N inshore	1,345	20,264	12	0.0664	5		
9: 64°–62°N	998	20,334	12	0.0491	4		
10: 62°–60°30'N	932	15,951	10	0.0584	3		
11: 60°30–59°N	1,194	24,085	16	0.0496	2		
14: coastal 67–66°30'N	45	189	6	0.2381	1		
Sum	8,670	213,996	101	0.0405	21	1.5 (0.21)	0.00242

life history observations from North Atlantic and North Pacific humpback whale populations.

MATERIAL AND METHODS

Construction of abundance estimates for 1984 and 1985

Aerial surveys of the West Greenland banks north of 62°N were conducted in June–July 1984 and 1985 (Figs 1a and 1b). East-west going transects separated by two nautical miles were chosen randomly and were flown in a twin-engine high winged *Partenavia Observer P68* at a target altitude and speed of 183m (600ft) and 160km hr^{-1} (100 knots), respectively. Three observers participated and the right front observer also acted as data recorder. Distance to sightings was estimated with *Suunto* inclinometers and was together with information on size of humpback whale groups recorded on tape recorders. The number of sightings from the surveys in 1984 and 1985 were too low to develop reliable detection functions. Instead the detection function from the surveys in 1987–1989 was used with a left truncation at 200m to take into account the effects of the flat windows used in the 1984–85 surveys (cf. Richard *et al.*, 2010).

Construction of abundance estimates for 1987–89 and 1993

Aerial line transect surveys covering the West Greenland banks were completed in July–August 1987–1989 and 1993 (Figs 1c to 1f) and were conducted with a twin engine *Partenavia Observer P68* with two observers in rear seats with bubble windows and one observer in the right front seat with a flat window. Information on size of humpback whale groups and declination angle to sightings measured with *Suunto* inclinometers were recorded.

Due to the low number of sightings, a common detection function was developed for the surveys between 1987 and 1989. These surveys all used the same aircraft, the same target altitude (229m or 750ft), same speed (160km hr^{-1}) and in some cases, the same observers. The surveys were also completed in weather conditions that were similar between years. The survey in 1993 had a sufficient number of sightings to develop an independent detection function.

Construction of abundance estimate for 2005

An aerial survey in 2005 covering most of West Greenland (Fig. 1g) essentially used the same aircraft and techniques as previous surveys and the details of the survey were presented in Heide-Jørgensen *et al.* (2008). The survey provided several sightings of large groups (>10 whales) which caused problems for the line transect estimation. Instead a line transect estimate for all groups <10 whales was derived and added to a strip census estimate of all groups >10 whales (discussed in detail in Heide-Jørgensen *et al.*, 2008).

Construction of abundance estimates for 2007

An aerial line transect survey of humpback whales in West Greenland was conducted between 25 August and 30 September 2007. The survey platform was a *Twin Otter*, with long-range fuel tank and two pairs of independent observers all with bubble windows. Sightings and a log of the cruise track (recorded from the aircrafts GPS) were recorded on a Redhen msDVRs system that also allowed for continuous video recording of the trackline as well as vertical digital photographic recordings. Declination angle to sightings was measured with *Suunto* inclinometers. Target altitude and speed was 213m and 167km hr^{-1}, respectively.

Survey conditions were recorded by the primary observers at the start of the transect lines and whenever a change in sea state, horizontal visibility and glare occurred. The survey was designed to systematically cover the area between the coast of West Greenland and offshore (up to 100km) to the shelf

Table 2

Estimates of relative abundance of humpback whales in West Greenland. Numbers in parenthesis indicate the coefficient of the variation. Photo-id estimates from 1982 from Perkins *et al.* (1984; 1985) and from 1988–92 from Larsen and Hammond (2004). Aerial line-transect estimates from 1984–85 and 1987–93 from this study, from 2005 from Heide-Jørgensen *et al.* (2008) and from 2007 from this study. The ship-based line transect estimate is from Heide-Jørgensen *et al.* (2007). *=partial coverage.

Year	Aerial line transect abundance	Ship-based line transect abundance	Photo-id
1982	–	–	271 (0.13)
1984	99 (0.46)*	–	–
1985	177 (0.44)*	–	–
1987	220 (0.62)	–	–
1988	200 (0.74)	–	–
1989	272 (0.75)	–	357 (0.16)
1990	–	–	355 (0.12)
1991	–	–	376 (0.19)
1992	–	–	566 (0.42)
1993	873 (0.53)	–	348 (0.12)
2005	1,158 (0.35)	1,306 (0.42)	–
2007	1,020 (0.35)	–	–

break (i.e. the 200m depth contour). Transect lines were placed in an east-west direction except for south Greenland where they were placed in a north-south direction. The surveyed area was divided into 12 strata (Fig. 1h).

Conventional line transect abundance estimation for all the surveys

Declination angles to sightings were converted to perpendicular distance of the animal to the trackline from: *distance* (m) = 213*tan(90-*angle*). Using conventional distance sampling (CDS) methods, animal abundance in each stratum was estimated by

$$\hat{N} = \frac{n}{2L\hat{\mu}}\hat{E}[s]A$$

where A is the area of the stratum, L is the total search effort in the stratum, n is the number of unique groups detected in the stratum by either observer and $\hat{\mu}$ was the estimated effective strip width of perpendicular distances to detected groups and $\hat{E}[s]$ was the estimated mean group size estimated using a regression of log group size against estimated detection probability (cf. Buckland *et al.*, 2001).

Mark-recapture distance sampling correction for perception bias for the 2007 survey

The search method deployed during the 2007 survey used an independent observer configuration where the primary and secondary observer teams acted independently of each other. Detections of animals by the primary observer served as a set of binary trials in which a success corresponded to a detection of the same group by the secondary observer in the same side of the aircraft. The converse was also true because the observers were acting independently; detections by secondary observers served as trials for the primary observers. Analysis of the detection histories using logistic regression allowed the probability that an animal on the trackline was detected by an observer to be estimated, and thus, abundance could be estimated without assuming $g(0)$ was one. These methods combine aspects of both mark-recapture (MR) techniques and distance sampling (DS) techniques and so they are known as mark-recapture distance sampling (MRDS) methods (Laake and Borchers, 2004).

Although observers were acting independently, dependence of detection probabilities on unmodelled variables (called unmodelled heterogeneity) can induce correlation in the detection probabilities. Laake and Borchers (2004) and Borchers *et al.* (2006) developed estimators which assumed that detections were independent at zero perpendicular distance only (called point independence estimators) that are well suited for aerial surveys where no responsive movements are expected.

The effects of the correlation in detections can be reduced by modelling the effects of variables which cause the correlation. Variables, additional to perpendicular distance, can be included in the MRDS models using a model selection criteria to select the best model. Detection probability was estimated using the independent observer configuration implemented in Distance 6.0 (Thomas *et al.*, 2009).

Group abundance was estimated in each stratum using:

$$\hat{N}_G = \frac{A}{2wL}\sum_{i=1}^{n}\frac{1}{\hat{p}(\underline{z}_i)}$$

where w is the truncation distance, $\underline{z}_i$ is a vector of explanatory variables for group i (possibly including the group size, s_i) and $\hat{p}(\underline{z}_i)$ is the estimated probability of detecting group i obtained from the fitted MRDS model. Individual animal abundance is estimated by

$$\hat{N} = \frac{A}{2wL}\sum_{i=1}^{n}\frac{s_i}{\hat{p}(\underline{z}_i)}$$

The estimated mean group size in the stratum is given by

$$\hat{E}[s] = \frac{\hat{N}}{\hat{N}_G}$$

Strip census estimation of the survey in 2007

Most of the humpback whale sightings were made within 300m from the trackline and at relatively short distances. The detection function dropped beyond 300m and it was therefore decided to assume a constant probability of detecting a group of humpback whales in a 300m strip on each side of the aircraft. The mark-recapture line transect analysis indicates that no variables other than distance and observer affect detection probability (see later). Thus in addition to the CDS estimates a strip census estimate was also obtained using a simple arithmetic mean of the group size across all strata ($\overline{s}$). To correct for perception bias (p') by the observers Chapman's (1951) modification of the Petersen estimator was used to estimate group abundance within w = 300m of the trackline (the 'covered region') over all strata:

$$\hat{N}_{G.strip} = \frac{(n_1+1)(n_2+1)}{(m_2+1)} - 1$$

Table 3

Humpback whale abundance estimates in 2007 using CDS methodology showing the encounter rate (n/L), effective strip width (*esw*) and estimates for pod size $E[s]$, pod density D_G, pod abundance N_G, animal density D and animal abundance N. Strata without sightings are not shown although the total densities take all strata into account. CV are given in parentheses.

Stratum	n/L (pods/km)	*esw* (km)	$E[s]$	D_G (pods/km^2)	N_G (pods)	D (whales/km^2)	N (whales)
4	0.0018 (0.81)			0.0030 (0.83)	101 (0.83)	0.0041 (0.84)	141 (0.84)
5	0.0035 (0.77)			0.0056 (0.79)	91 (0.79)	0.0078 (0.80)	127 (0.80)
7	0.0036 (0.96)			0.0058 (0.97)	129 (0.97)	0.0081 (0.98)	180 (0.98)
8	0.0037 (0.61)			0.0060 (0.64)	121 (0.64)	0.0083 (0.65)	169 (0.65)
9	0.0050 (0.38)	0.311 (0.19)	1.394 (0.12)	0.0081 (0.43)	164 (0.43)	0.0112 (0.44)	228 (0.44)
10	0.0021 (0.68)			0.0035 (0.71)	55 (0.71)	0.0048 (0.72)	77 (0.72)
11	0.0017 (0.60)			0.0027 (0.63)	65 (0.63)	0.0038 (0.64)	90 (0.64)
14	0.0223 (0.85)			0.0358 (0.87)	7 (0.87)	0.0500 (0.88)	9 (0.88)
Total	0.0022 (0.20)			0.0033 (0.33)	732 (0.33)	0.0046 (0.35)	1,020 (0.35)

Table 4

MRDS point independence model fitted to the data from 2007 survey.

Distance sampling model	Mark recapture model	AIC	ΔAIC
Uniform	Petersen	205.34	0
Half Normal: Distance	Distance	296.03	90.69
Hazard rate: Distance	Distance	296.55	91.21
Half normal: Distance	Distance + Observer	292.97	87.63
Hazard rate: Distance	Distance + Observer	293.49	88.15

where n is the total number of sightings, n_1 and n_2 are the total number of sightings by the primary and secondary observers and m_2 is the number of sightings by both pairs of observers.

The abundance in stratum v (v = 4,5,7,8,9,10,11,14) was estimated as follows:

$$\hat{N}_{G,v} = \frac{n_v A_v}{\hat{p}' 2wL_v}$$

where n_v is the number of groups detected in stratum v, L_v is the total length of transect in stratum v, A_v is the surface area of stratum v and the combined detection probability for both observers (p') across all strata was estimated as follows:

$$\hat{p}' = \frac{n}{\hat{N}_{G.strip}} = \frac{n}{\frac{(n_1+1)(n_2+1)}{(m_2+1)} - 1}$$

The variance of $\hat{p}'$, $\hat{N}_{G,v}$ and $\hat{N}_{G(Chapman)} = \sum_v \hat{N}_{G,v}$ was estimated using a nonparametric bootstrap with transect as the sampling unit. Transects were sampled with replacement, separately in each stratum, until the total number of sightings was at least as large as the original number of sightings in the stratum (n_v).

The mean group size $\bar{s}$ and its coefficient of variation, $cv(\bar{s})$ was estimated across all strata and estimated individual abundance and its CV was obtained by

$$\hat{N}_{(Chapman)} = \hat{N}_{G(Chapman)} \bar{s}$$

and

$$cv(\hat{N}_{(Chapman)}) = \sqrt{cv(\hat{N}_{G(Chapman)})^2 + cv(\bar{s})^2}$$

Correction for availability bias of the survey in 2007

The above estimates of abundance from aerial surveys are negatively biased if some animals were underwater and hence undetectable during the passage of the plane. To correct for this availability bias satellite-linked time-depth recorders were deployed on five humpback whales off Central West Greenland (Fyllas Bank 64°N, 52°W) in June–July 2000 to estimate the probability of an animal being available for detection. The satellite transmitters (SDR-T16) produced by Wildlife Computers (Redmond, Washington) were fitted with a harpoon spear for attachment. The transmitter had a length of 10cm and a diameter of 2.5cm and was sitting on the outside of the whale while an anchoring spear of 14.5cm was partly or fully inside the whale. The tags were programmed to collect and summarize measurements of the time spent at or above 4m depths in four 6hr periods and the data were transmitted through Service Argos. The tags were deployed from the stern of a MK II Zodiac powered by a 40 Hp engine.

Table 5

Number of sightings seen by each observer and the number of duplicates (seen by both) during the 2007 survey. The total column shows the number of sightings seen by observer 1 plus observer 2 minus sightings seen by both.

Pod size	Primary observer	Secondary observer	Seen by both	Total
1	14	11	10	15
2	4	1	1	4
3	1	1	1	1
5	1	1	1	1
Total	20	14	13	21

A person fixed with a harness deployed the transmitter with a 6.8m aluminum pole (diameter 33mm).

As humpback whales are available for more than an instant during aerial surveys and some whales may even be seen ahead of the plane, the probability that an animal is available is not simply the probability that it is available at a randomly-chosen instant in its dive cycle. McLaren (1961) derived an equation, used by others, including Barlow *et al.* (1988) for estimating the average probability that an animal is available (at the surface) at least some of the time within a time interval of length t:

$$\Pr(\text{available}) = (s+t)/(s+d)$$

where s is the average time the whale is at the surface, d is the average time it is below the surface and t is the window of time the whale is within visual range of the observers. However, this equation is inappropriate if t is not very small relative to d, as is clear by noting that when $t>d$ the probability is greater than 1. A more appropriate estimator of the probability that an animal is available within time t was provided by Laake *et al.* (1997):

$$\hat{a} = \frac{E[s]}{E[s]+E[d]} + \frac{E[d](1-e^{-t/E[d]})}{E[s]+E[d]}$$

where E[s] is the average time the whale is at the surface, E[d] is the average time it is below the surface and t is the window of time the whale is within visual range of the observers.

It was assumed that the whales were available for detection when within 4m of the surface and the times spent at above and below this measurement from 7 June through 18 July from the satellite-linked time-depth-recorders were used to estimate this probability.

Abundance (corrected for availability bias) was then estimated as

$$\hat{N}_c = \frac{\hat{N}}{\hat{a}}$$

with estimated CV

$$cv(\hat{N}_c) = \sqrt{cv(\hat{N})^2 + cv(\hat{a})^2}.$$

Construction of time series

A time series of indices of relative abundance of humpback whales was constructed from previous photo ID mark-recapture studies and from aerial and ship-based surveys presented previously (Heide-Jørgensen *et al.*, 2007; Larsen and Hammond, 2004), re-analysed in this study (Heide-

Table 6

Humpback whale abundance estimates in 2007 using MRDS methodology showing the encounter rate (n/L), estimates for pod size $E[s]$, pod density D_G, pod abundance N_G , whale density D and whale abundance N. Strata without sightings are not shown although the total densities take all strata into account. CV's are given in parentheses.

Stratum	n/L (pods/km)	D_G (pods/km²)	N_G (pods)	D (whales/km²)	N (whales)	$E[s]$
4	0.0018 (0.81)	0.0040 (0.90)	136 (0.90)	0.0040 (0.90)	136 (0.90)	1.00 (00.0)
5	0.0035 (0.77)	0.0075 (0.86)	122 (0.86)	0.0125 (0.96)	203 (0.96)	1.67 (0.21)
7	0.0036 (0.96)	0.0078 (1.03)	173 (1.03)	0.0157 (1.03)	346 (1.03)	2.00 (00.0)
8	0.0037 (0.61)	0.0080 (0.72)	163 (0.72)	0.0080 (0.73)	163 (0.73)	1.00 (00.0)
9	0.0050 (0.38)	0.0108 (0.54)	220 (0.54)	0.0238 (0.60)	484 (0.60)	2.20 (0.34)
10	0.0021 (0.68)	0.0046 (0.78)	74 (0.78)	0.0046 (0.78)	74 (0.78)	1.00 (0.24)
11	0.0017 (0.60)	0.0036 (0.71)	87 (0.71)	0.0036 (0.71)	87 (0.71)	1.00 (00.0)
14	0.0223 (0.85)	0.0482 (0.93)	9 (0.93)	0.0489 (0.94)	9 (0.94)	1.00 (00.0)
Total	0.0022 (0.20)	0.0045 (0.47)	985 (0.47)	0.0068 (0.49)	1,505 (0.49)	1.53 (0.14)

Jørgensen *et al.*, 2008; Larsen, 1995; Larsen *et al.*, 1989) or presented for the first time here. The trend in abundance or instantaneous rate of increase ($N_t = N_o e^{rt}$) was estimated by weighted (weight = $1/cv(N_t)^2$) regression through the log transformed estimates of relative abundance (N_t) with jack-knifed standard error.

Population dynamics model

An age based Leslie-matrix model was created (Caswell, 2001; Leslie, 1945; 1948) using life-history data obtained from literature (Barlow and Clapham, 1997; Clapham, 1992; Gabrielle *et al.*, 2001; Mizroch *et al.*, 2004). This model was used to calculate the growth rate at a stable age structure as the dominant positive eigenvalue of the matrix. The matrix only projects female individuals, and due to this, the fertility used is half of that reported in the literature, since there is no evidence of a strongly biased sex ratio at birth.

Table 7

Proportion of time spent at surface (0–4m) for four humpback whales instrumented on Fyllas Bank in June 2006.

Whale	Date	6 hr period	Percentage time at 0–4m
21809	8/6/2000	03–09	47.92
20158	7/6/2000	03–09	19.80
20158	8/6/2000	03–09	25.59
			31.10
21801	10/6/2000	09–15	37.17
21801	20/06/2000	09–15	42.51
21802	10/6/2000	09–15	34.35
21802	17/6/2000	09–15	68.42
21802	18/6/2000	09–15	71.75
21802	22/6/2000	09–15	32.04
			47.71
21801	10/6/2000	15–21	33.52
21801	14/6/2000	15–21	26.57
21801	15/6/2000	15–21	40.67
21801	16/7/2000	15–21	34.94
20160	9/6/2000	15–21	26.53
21802	14/6/2000	15–21	37.73
21802	17/6/2000	15–21	57.77
21802	19/6/2000	15–21	39.58
			37.16
21801	9/6/2000	21–03	31.79
21801	11/6/2000	21–03	26.35
21801	14/7/2000	21–03	44.44
21801	18/7/2000	21–03	42.62
20158	5/6/2000	21–03	48.89
20158	7/6/2000	21–03	30.72
21802	16/6/2000	21–03	57.64
21802	23/6/2000	21–03	35.30
			39.72
Average	All days all whales	09–21	41.68
SD			14.24
n			14.00
SE			3.81
CV			0.09

RESULTS

Construction of estimates of relative abundance

In all years, the aerial surveys covered the coastal areas of West Greenland from 60°N (in 1984 and 1985 from 62°N) to 70°N with the maximum effort between 62° and 66°N (Figs 1a–h). The total survey effort however ranged between 3,260 and 8,670km (Table 1). The average ratio between survey effort and stratum area was 0.04 (SD = 0.01). However this fluctuated in the first five years between 0.02 and 0.06, but remained constant around 0.04 after 1989. The seven abundance estimates were not significantly correlated with the survey effort ($p = 0.42$). There was an increasing trend in sighting rate in the aerial surveys with $r = 0.06$ (CV = 0.28, $r^2 = 0.69$) for the period 1984 to 2007.

The combined detection function for humpback whales for the surveys in 1987–89 was fitted with a half-normal function with a left truncation at 200m to construct a detection function for the surveys in 1984–85 that used flat windows. The sample size was 10 and the effective search width was 587m (CV = 0.37) (Fig. 2a). The distribution of perpendicular distances to the 15 humpback whale sightings were combined for the surveys in 1987–1989 and a half-normal model was selected to fit the sightings distance data (Fig. 2b). The effective search width was estimated at 708m (CV = 0.20). The survey in 1993 had 18 sightings that were fitted to the half-normal model to derive an effective search width of 503m (CV = 0.43, Fig. 2c). A simple mean of the group sizes was used for each of the years.

In 2005, 22 sightings within the truncation distance of 3km were used for deriving a half-normal detection function model with an effective search width of 664m (CV = 0.12, Fig. 2d), similar to that found in previous years (see Heide-Jørgensen *et al.*, 2008). A regression of log group size against estimated detection probability was used to estimate mean group size across all strata.

In 2007, the distribution of perpendicular distances of sightings shows some sightings close to the trackline indicating the absence of a blind spot for observers beneath the plane (Fig. 2e). However, in the distributions for both observers there was a peak in sightings between 200–250m after which detection declined substantially. In 2007 all

Table 8

Humpback whale estimates in 2007 using strip census methodology and estimated detection probability $\hat{p}'$ = 0.98 (cv = 0.03) with esw = 300m showing the encounter rate (n/L) and simple estimate of pod size $\bar{s}$, pod density D_G, pod abundance N_G, animal density D, and N animal abundance. Strata without sightings are not shown. CV's are given in parentheses.

Stratum	n/L (pods/km)	$\bar{s}$	D_G (pods/km^2)	N_G (pods)	D (animals/km^2)	N (animals)
4	0.002 (0.81)		0.003(0.81)	105 (0.81)	0.004 (0.82)	149 (0.83)
5	0.004 (0.77)		0.006 (0.77)	94 (0.77)	0.008 (0.78)	134 (0.78)
7	0.004 (0.96)		0.006 (0.96)	134 (0.96)	0.009 (0.97)	190 (0.97)
8	0.003 (0.75)		0.005 (0.75)	100 (0.75)	0.007 (0.77)	143 (0.77)
9	0.004 (0.47)	1.42 (0.16)	0.007 (0.47)	136 (0.47)	0.010 (0.49)	193 (0.49)
10	0.002 (0.68)		0.004 (0.68)	57 (0.68)	0.005 (0.70)	81 (0.70)
11	0.002 (0.60)		0.003 (0.60)	67 (0.60)	0.004 (0.62)	96 (0.62)
14	0.002 (0.85)		0.037 (0.85)	7 (0.85)	0.053 (0.86)	10 (0.86)
Total	0.002 (0.22)		0.003 (0.29)	700 (0.29)	0.005 (0.33)	995 (0.33)

sightings were within 500m from the trackline which is very different from the distribution in 2005 where most sightings were beyond 500m. The difference is due to a combination of a different type of survey planes and observer instruction in 2007 to concentrate on covering the trackline. Both hazard rate and half normal functional forms were considered for the 2007 distribution of sightings, but based on AIC the half-normal model was chosen. The effective search width was 311m (CV = 0.19). The survey region in the 2007 survey included an area of 213,996km^2 with 8,670km tracklines covered in Beaufort sea states less than 5 (Fig. 1h and Table 1). The group sizes varied between 1 and 5 whales and all the 21 humpback whale sightings were seen in strata 4 to 11 with the exception of one sighting in stratum 14.

Trends in abundance

The uncorrected estimates from the aerial surveys are smaller than the estimates from the photo identification study except for 1993 where the survey abundance estimate was about twice the estimate from the photo ID study (Fig. 3). It is however not straightforward to compare the estimates as the aerial surveys covered a much larger area and they are not corrected for the time the whales were not available at the surface to be seen by the observers. The aerial survey estimate from 2005 (1,158 95% CI 595–2,255) is similar to a ship-based line transect survey in 2005 (Fig. 3).

The time series of aerial line transect surveys provides an index of the changes in relative abundance (i.e. uncorrected for perception and availability bias) of humpback whales in West Greenland from 1984 through 2007 (Table 2). If it is assumed that the bias remains constant, the rate of increase of humpback whales on the feeding ground in West Greenland can be estimated. The abundance estimates from 1984–1985 and 1987–1989 used the same detection function and were therefore averaged for the purpose of estimating the rate of increase. The overall exponential rate of increase from 1984 to 2007 was 0.09 or 9.4% per year (SE = 0.01, p = 0.010).

Current abundance

The CDS estimate of 1,020 (CV = 0.35) humpback whales for 2007 does not include animals that were submerged or missed by the observers (Table 3). Both the conventional DS model and the MRDS models were fitted to the data without truncation. The final MRDS model included a term for observer in the MR model (Table 4). This indicated that the secondary observers had a much smaller probability of detection on the trackline than the primary observers (Table 5); 0.66 (CV = 0.43) for the primary observers compared to 0.22 (CV = 0.76) for the secondary observers (Fig. 4). The estimate for both observers combined was 0.73 (CV = 0.34). The abundance of humpback whales was 1,505 animals (CV = 0.49; 95% CI 581–3896) when using MRDS methods to correct for perception bias (Table 6).

Data on surface time obtained from the satellite-linked time-depth-recorders indicate that humpback whales in West Greenland spend on average 42% (CV = 0.09) of their time during daylight periods (09–21hr) at depths <4m (Table 7). In the relatively productive waters of West Greenland, 4m is probably the maximum depth to which humpback whales can be reliably detected on the trackline from an aircraft passing at 213m altitude. Humpback whales are known to have long dive cycles with average dive times lasting several minutes and with average time spent at the surface (<4m) mostly lasting >40 seconds (Winn and Reichley, 1985). Both the dive time and the at-surface-time are considerably longer than the average time the whales are visible from an aircraft. In this survey the time between first sighting of the whales and the time when the whales passed abeam was on average 3.21s (CV = 0.38). If the probability of detecting a whale at the surface given the observation time of 3.21s and the ratio between dive and surface times is compared to an instantaneous correction of whales at the surface then the most severe positive bias can be expected for short durations of surfacings and dives (Fig. 5). For surface times >30s the positive bias from using an instantaneous correction of availability ranges between 7 and 15% for observation times between 2 and 7s, or 10% for an average 3.21s observation period. This positive bias can be eliminated by increasing the availability correction factor to 0.46. Applying this correction to the MRDS estimate gives a fully corrected abundance estimate of 3,272 (CV = 0.50, 95% CI 1,300–8,233) humpback whales in West Greenland in 2007.

The Chapman estimate of perception bias was 0.98 (CV = 0.03) and correcting for this bias results in an abundance of 995 (0.33) humpback whales in 2007 from the strip census analysis (Table 8). In comparison the CDS estimate was 1,020 (0.35) and the MRDS estimate was 1,528 (0.51). Further correction of the strip census analysis with $\hat{a}$ 46% (CV = 0.09) gives an estimate of 2,154 (CV = 0.36, 95% CI 1,087–4,270) humpback whales corrected for whales that were submerged during the passage of the plane or a slightly lower but more precise estimate than the MRDS estimate.

Table 9
Life history data used to calculate plausible growth rates for North Atlantic humpback whales.

	Lower CI	Average	Upper CI	Geographical region	Reference
Fertility (females)	0.20	0.21	0.22	North Atlantic	Barlow and Clapham (1997)
Age at sexual maturity	6.4	5.9	5.4	North Atlantic	Clapham (1992)
Calf survival	0.797	0.805	0.813	North Pacific	Gabriele *et al.* (2001); Zerbini *et al.* (2010)
Juvenile survival	0.797	0.895	0.995		Estimated
Adult survival	0.954	0.984	0.995	North Pacific	Mizroch *et al.* (2004)
Growth rate	0.9964	1.0578	1.1070		Calculated

Population dynamics

Age at first parturition is reported in decimal numbers in the literature and was included in the age based matrix by adding partial fertility at age 5 (Upper 95% CI and average models in Table 9) or 6 (Lower CI model, based on the 95% CI for the individual life history traits used) corresponding to the deviation from the closest higher integer, i.e. 60% fertility at age 5 (Upper) and 6 (Lower) for the CI models and 10% fertility at age 5 for the average model. Calf survival was multiplied by the fertility to obtain the chance of birth and survival to age 1. Due to uncertain data in the literature, juvenile survival (up to an age of first parturition of 5 or 6, depending on model) was set as the average of calf and adult survival in the average model, as the same value as calf survival in the Lower CI model and as the same value as adult survival in the Upper CI model. These widely ranging numbers were used to avoid under- or over-estimation of the extreme lambdas. The effect of juvenile survival was tested within the average model where juvenile survival was stepwise changed from calf survival values to the adult survival values (0.8 to 0.96) which consequently affected the growth rate linearly from 3% to 8% with all other parameters kept constant. Survival estimates and fertility affected the theoretical growth rates in a linear fashion whereas earlier age of first parturition increased the growth exponentially (Fig. 6). Estimates of the longevity of the whales had relatively little effect on the theoretical growth rate.

DISCUSSION

Humpback whales have generally been protected in the North Atlantic since 1955 although a low level of exploitation (total catch 1955–85; 24) continued in West Greenland until 1985 (IWC, 2003). After 1985, they were completely protected although a few whales were taken as bycatch in fishery operations (total 1986–2001; 7, IWC, 2003). Considering this low level of exploitation and the fact that the number of humpback whales have clearly increased on their breeding ground (i.e. the West Indies) and feeding grounds in other areas of the North Atlantic, it is not surprising that the abundance on the West Greenland feeding ground has also increased. The detected increase is considerably larger than the increase of 3.1% per year observed in the West Indies (Stevick *et al.*, 2003). However, it is of the same magnitude as some of the estimates of increase from other North Atlantic feeding grounds (Katona and Beard, 1990; Pike *et al.*, 2009; Sigurjónsson and Gunnlaugsson, 1990).

The analysis of the dynamics of a hypothetical humpback whale population in the North Atlantic shows that the observed growth in West Greenland is within the upper range of plausible growth rates based on an age structured model with life history parameters from observed populations of humpback whales. Both the age at first parturition and subadult survival had a profound effect on the dynamics of the population and population specific determination of these life history parameters is required to narrow the range of plausible growth rates. The values used in the model were from the Gulf of Maine (Clapham, 1992), an area considered to be part of the range of the western North Atlantic humpback whale breeding population that also is found in West Greenland.

The use of upper and lower CI models should not be interpreted as the 95% CI of population growth, since it is based on the assumption that all life history traits are at their own individual 95% CI border values. This leads to an over- and under-estimation for the possible 95% CI for the whole population growth since the probability of all life history traits to be at their maximum/minimum values at the same time is low. The matrix model does not discern between calf survival for first time mothers and experienced mothers, something that can have significant impact on other mammal species (for example rabbits (Rödel *et al.*, 2009) and cheetahs (Durant *et al.*, 2004)). A recent study on Hawaiian humpback whales also show that larger females attract more male suitors (Pack *et al.*, 2009), which could have a significant impact on young female fertility rates.

The estimates of humpback whale abundance derived from the photo-identification study in West Greenland in 1989–1993 (Larsen and Hammond, 2004) may provide a correct magnitude of the occurrence of humpback whales in the areas where the photo-identification work was concentrated at that time. However, the photo-identification work covered a smaller area of West Greenland than the aerial surveys and it is reasonable to expect that an increasing humpback whale population will also expand its distribution. Satellite tracking studies in 2001 and 2002 demonstrated that some humpback whales do not spend time within the area used for the photo-identification study (Heide-Jørgensen and Laidre, 2007; GINR, unpubl. data). In recent surveys humpback whales were found more widely in West Greenland than in previous surveys and there are now frequently records of observations far north in West Greenland (e.g. in Uummannaq 71°N; GINR, unpubl. data).

If detection probability varies with distance within the first 300m (and the CDS and MRDS analyses strongly suggest it does), then the strip transect estimate is negatively biased because it neglects heterogeneity due to distance. If some animals at distance zero are missed (and the MRDS analysis suggests that this is the case), then the CDS estimate is negatively biased. If the detection function does in reality initially increase with distance from the transect line, the

MRDS estimator of abundance might be positively biased, because while the MR component of the model allows this, the CDS component does not (i.e. the CDS detection function is monotonically decreasing) – see Fig. 4. While it is difficult to say whether or not the MRDS estimate of abundance is positively biased, it is probable that both the strip transect and CDS estimates are negatively biased.

The best estimate of the abundance of humpback whales in 2007 was 3,299 whales, with a relatively large coefficient of variation (0.57). Even the lower bound of this estimate (1,170 whales) is substantially higher than any previous estimates. The estimate is based on a visual aerial line transect survey that covered a larger part of West Greenland than in previous surveys. However coverage was still partial with poor coverage west of Disko Bay and humpback whales were often observed at the westernmost point of the transects indicating that the West Greenland feeding ground may extend over deeper water (>200m) west of the shelf area into areas not covered in any of the surveys.

The observed rate of increase and the estimates of current abundance of humpback whales on the summering ground in West Greenland change the status of this stock and allows for the resumption of a low level of harvesting which was abandoned in 1985.

ACKNOWLEDGEMENTS

We thank the observers Finn Christensen, Arne Geisler, Anita Gilles and Werner Piper for their involvement and persistence during the 2007 survey. The North Atlantic Marine Mammal Commission is acknowledged for organizing the 2007 TNASS survey, which the survey presented here was part of. The Greenland Institute of Natural Resources provided funding for the survey and the Vetlessen Foundation supplied additional funding for purchasing the recording equipment.

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Date received: January 2010
Date accepted: October 2010

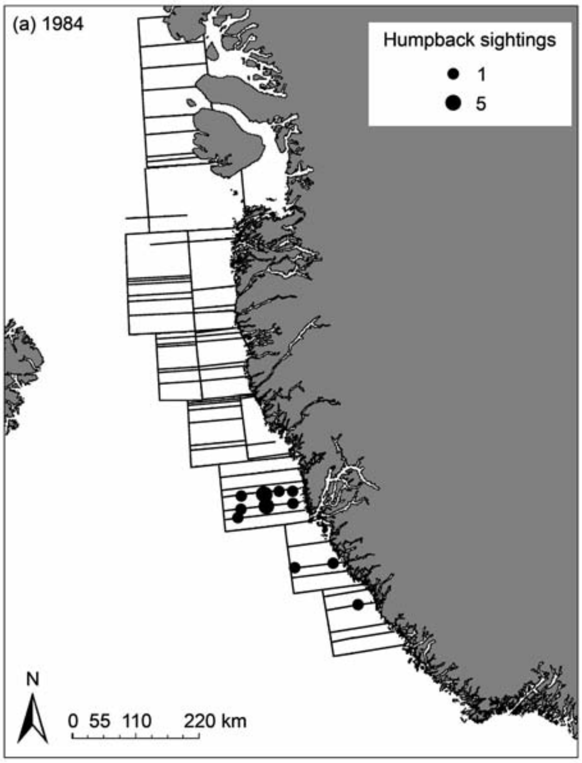

Fig. 1a. Strata, survey lines and sightings (incl. off effort sightings) of humpback whales in 1984.

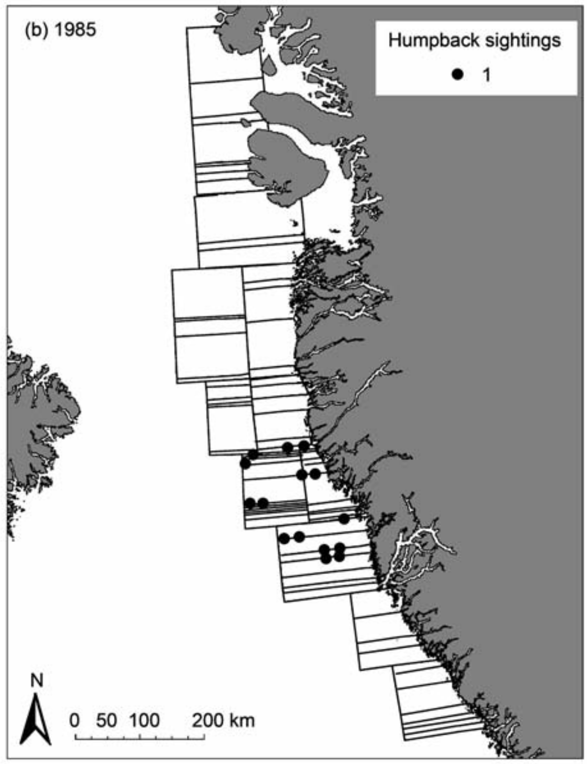

Fig. 1b. Strata, survey lines and sightings (incl. off effort sightings) of humpback whales in 1985.

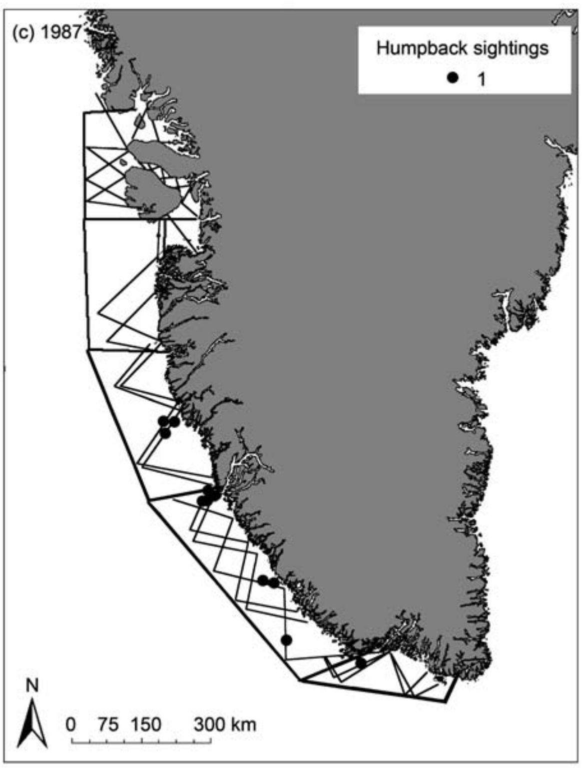

Fig. 1c. Strata, survey lines and sightings (incl. off effort sightings) of humpback whales in 1987.

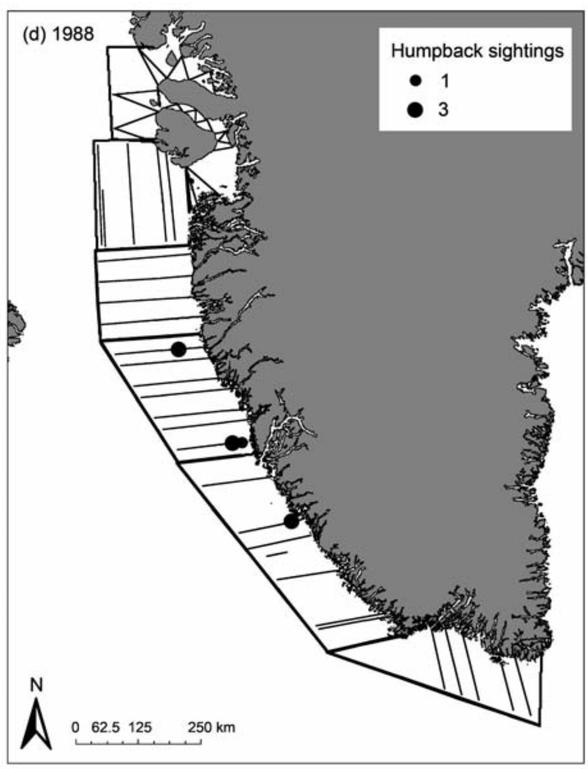

Fig. 1d. Strata, survey lines and sightings (incl. off effort sightings) of humpback whales in 1988.

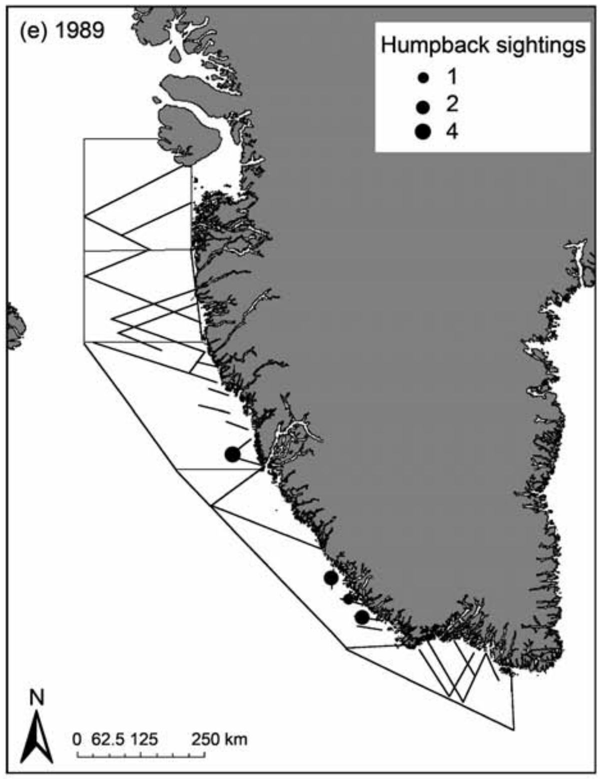

Fig. 1e. Strata, survey lines and sightings (incl. off effort sightings) of humpback whales in 1989.

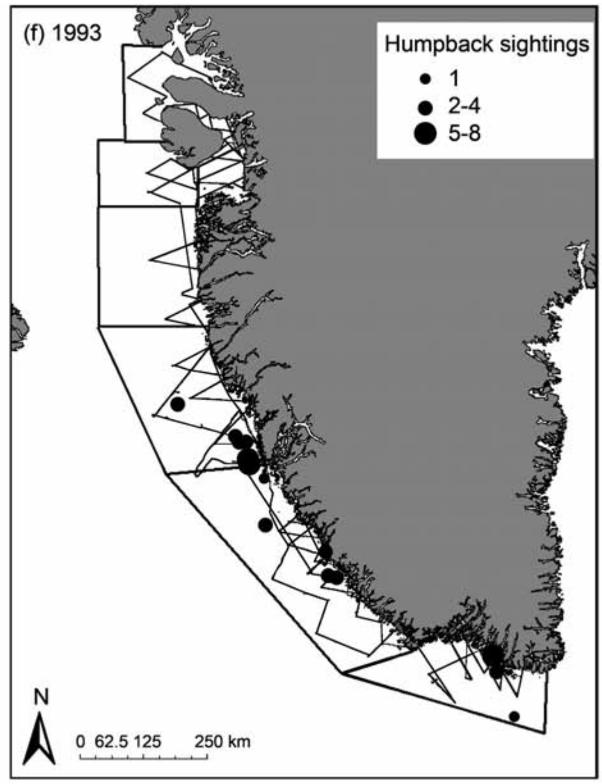

Fig. 1f. Strata, survey lines and sightings (incl. off effort sightings) of humpback whales in 1993.

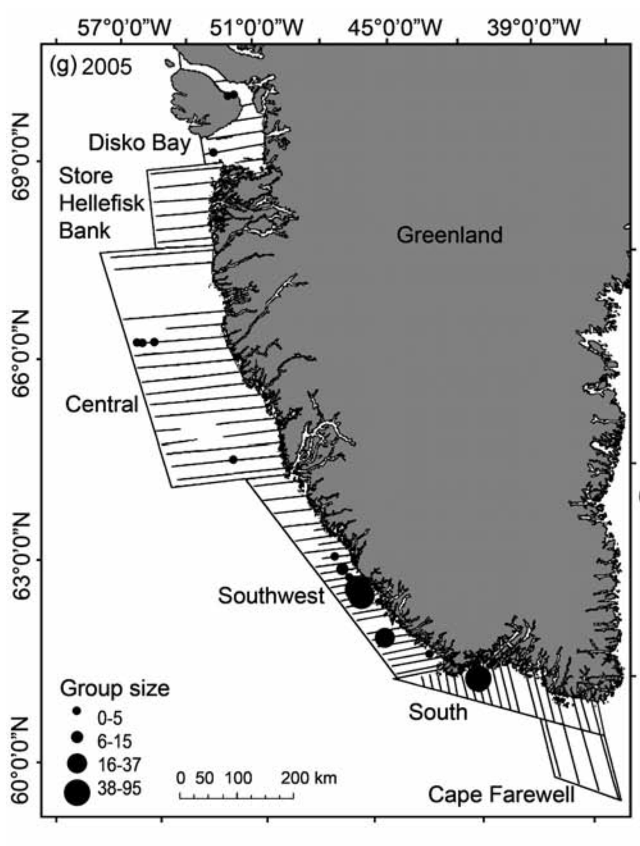

Fig. 1g. Strata, survey lines and sightings (incl. off effort sightings) of humpback whales in 2005.

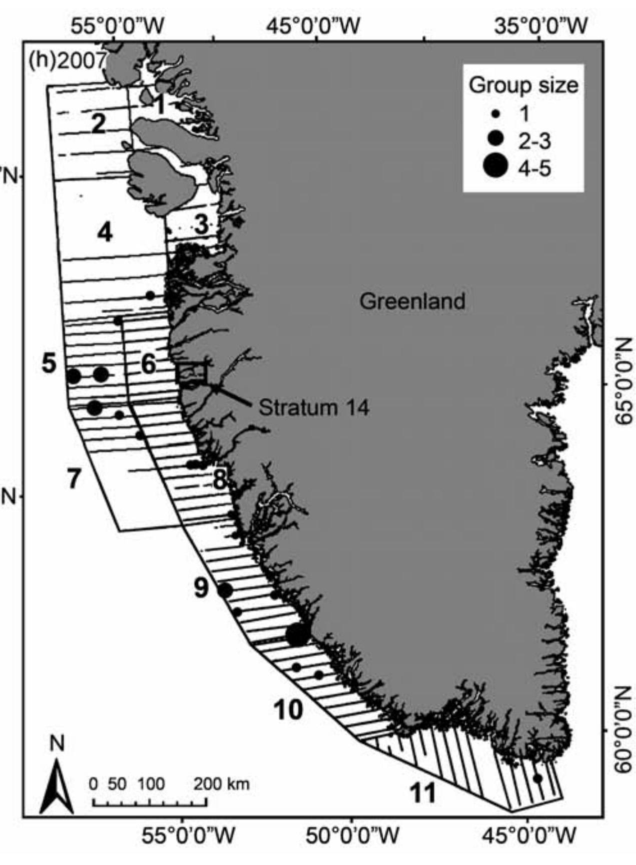

Fig. 1h. Strata, survey lines and sightings (incl. off effort sightings) of humpback whales in 2007. Note that stratum 14 is inside coastal fjords.

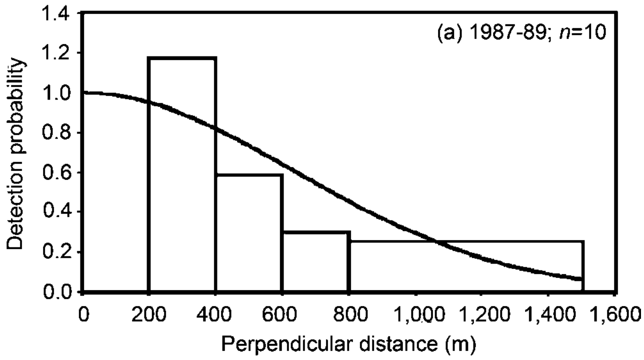

Fig. 2a. Distribution of humpback whale sightings at various distances from the trackline during the surveys in 1987–89 with a left truncation at 200m to allow the detection function to be applied to the surveys in 1984 and 1985 that used flat windows instead of the bubble windows that were used in subsequent surveys. Data has been fitted to the half-normal model and the fitted curve shows the expected number of sightings. The sightings were truncated at 1,500m and the effective search width was 587m (CV = 0.37).

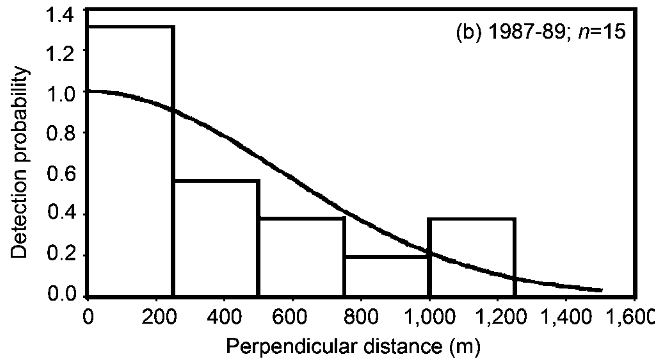

Fig. 2b. Distribution of humpback whale sightings at various distances from the trackline during the surveys in 1987–89. Data has been fitted to the half-normal model and the fitted curve shows the expected number of sightings. The sightings were truncated at 1,500m and the effective search width was 708m (CV = 0.20).

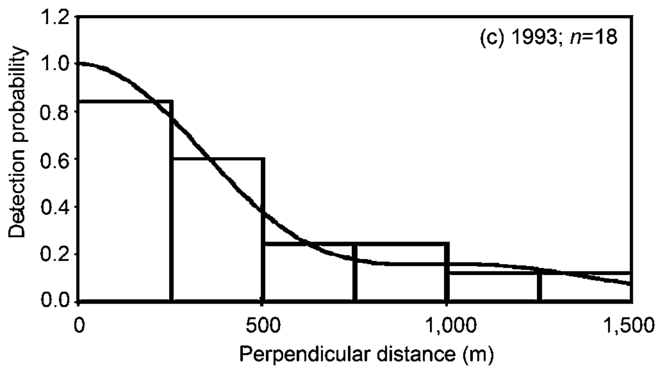

Fig. 2c. Distribution of humpback whale sightings at various distances from the trackline during the survey in 1993. Data has been fitted to the half-normal model and the fitted curve shows the expected number of sightings. The sightings were truncated at 1500 m and the effective search width was 503m (CV = 0.43).

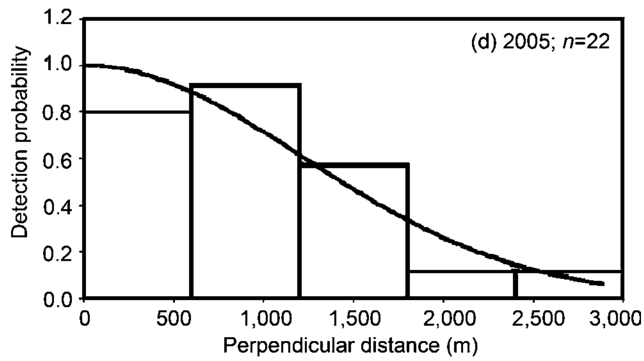

Fig. 2d. Distribution of humpback whale sightings at various distances from the trackline during the survey in 2005. Data has been fitted to the hazard rate function and the fitted curve shows the expected number of sightings. The effective search width was 1,506m (CV = 0.17) (see also Heide-Jørgensen *et al.*, 2008).

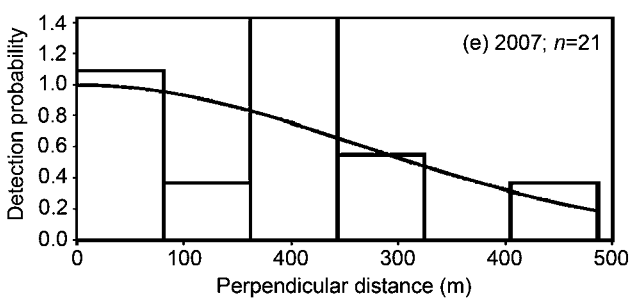

Fig. 2e. Distribution of humpback whale sightings at various distances from the trackline during the survey in 2007. Data has been fitted to the hazard rate function and the fitted curve shows the expected number of sightings. The effective search width was 311m (CV = 0.19).

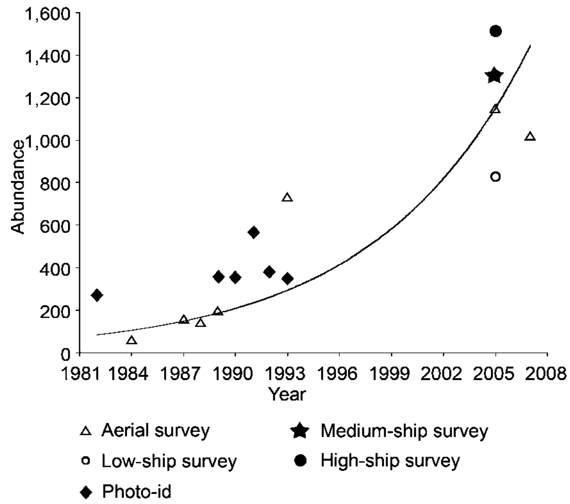

Fig. 3. Trends in relative abundance of humpback whales in West Greenland 1982–2007. The exponential growth model is fitted to the estimates from the aerial surveys. Details of the three abundance options from the ship-based survey in 2005 are given in Heide-Jørgensen *et al.* (2007).

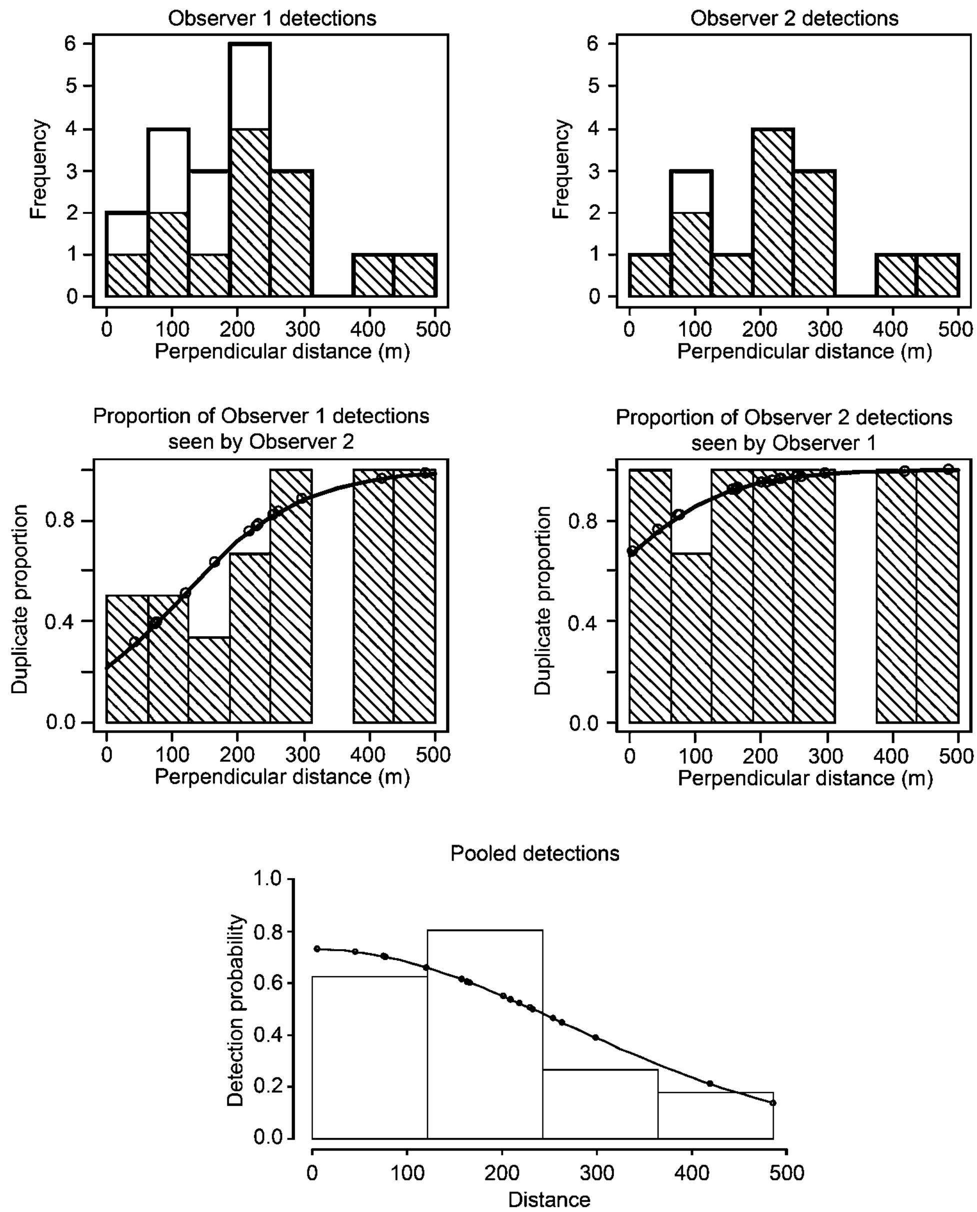

Fig. 4. Detection function plots for the MRDS analyses. Duplicate detections are indicated in the shaded areas; as a number in the top plots and as a proportion in the middle plots. The points are the probability of detection for each sighting given its perpendicular distance. The lines are the fitted models (in the pooled detection plot, the line is a smooth function fitted to the points).

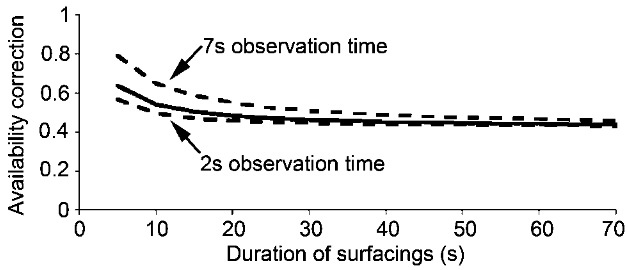

Fig. 5. Estimation of the positive bias in instantaneous availability correction factors compared to correction based on the probability of detecting a whale given surface-dive patterns with 42% of time at surface and average observation times of 2, 3.1 and 7 seconds.

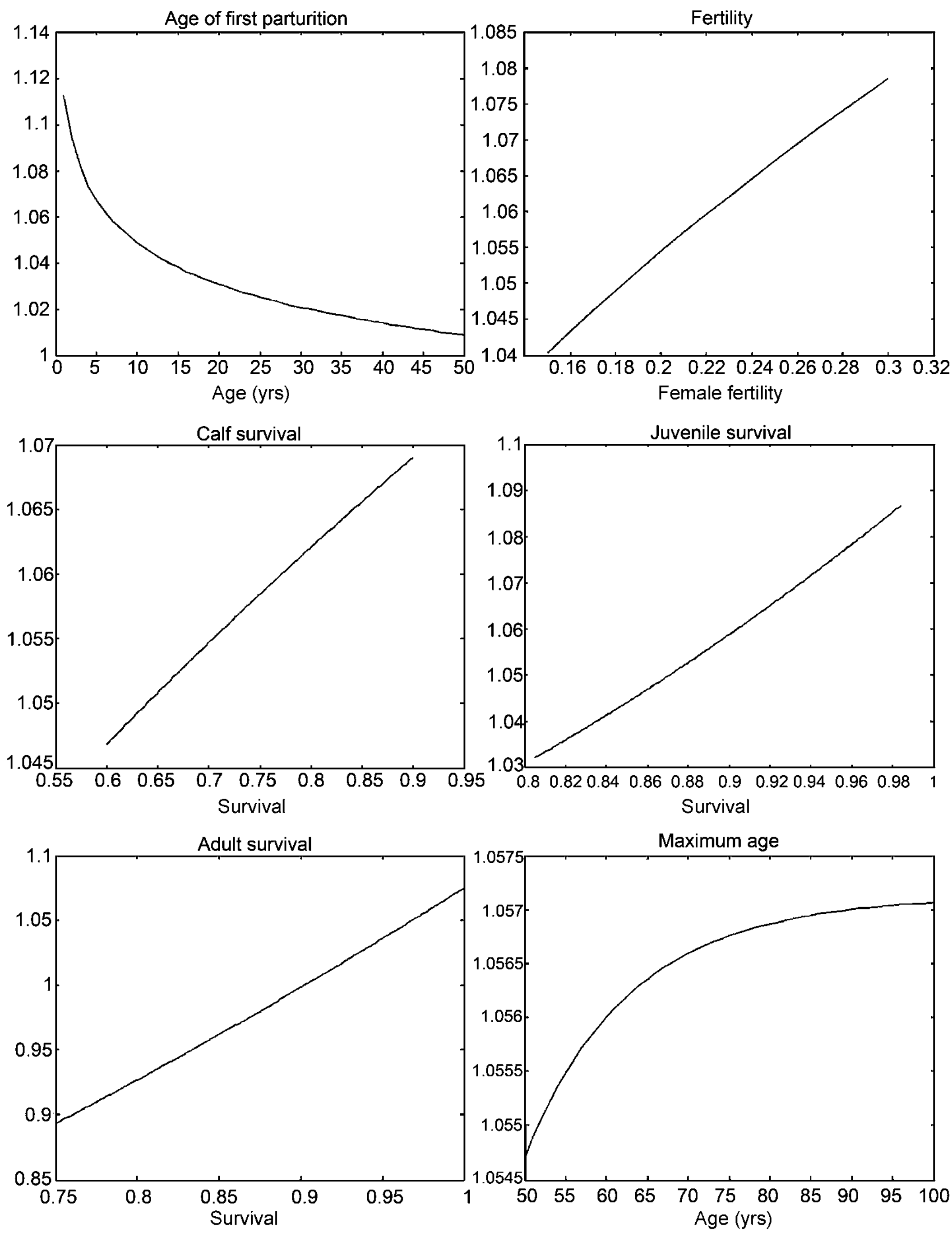

Fig. 6. Changes in lambda (y-axis) due to changes in different life history traits (x-axis). Base values used for the life history traits are not changed: Age of first parturition = 6, Fertility = 0.21, Calf survival = 0.805, Juvenile survival = 0.894, Adult survival = 0.984, Max age = 100 years. Based on Barlow and Clapham (1997), Clapham (1992), Gabriele et al. (2001) and Mizroch *et al.* (2004).