Surfacing time, availability bias and abundance of humpback whales in West Greenland

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ABSTRACT

Visual aerial surveys of large whales are negatively biased unless correction factors are developed to correct the availability of whales at the surface. One method for developing a correction factor for this bias is by instrumenting whales with recorders that measure the amount of time spent at the surface. Thirty-one SLTDRs (three different models) were deployed on humpback whales (*Megaptera novaeangliae*) in West Greenland in May and July 2009–10. The SLTDRs recorded the proportion of a 6 hour period that the whales spent at or above 2m depth (defined here as surfacing time). This depth is considered to be the maximum depth that humpback whales are reliably detected from the air on visual aerial surveys in West Greenland. Eighteen transmitters provided data on the surfacing time and the drift of the pressure transducer. The average surfacing time for whales over the study period during the two 6 hour periods with daylight was 28.3% (CV = 0.06). Six whales met the data filtering criteria and had low drift in transmitter depth. Their average surface time was 33.5% (CV = 0.10). Previous analyses of visual aerial survey data have shown that the amount of time whales are available to be seen by observers is not an instantaneous process. Therefore, surface time must be corrected for a positive bias of about 10% when developing a correction factor for availability bias. This increases the availability in this study to 36.8% (CV = 0.10). The most recent survey of humpback whales in West Greenland was conducted in 2007 and corrections using this availability factor produce fully corrected abundance estimates of 4,090 (CV = 0.50) for mark-recapture distance sampling analysis and 2,704 (CV = 0.34) for a strip census abundance estimate. These estimates are about 25% larger than previous estimates from the same survey.

KEYWORDS: SATELLITE TAGGING; SURVEY-AERIAL; ABUNDANCE ESTIMATE; HUMPBACK WHALE; NORTHERN HEMISPHERE

INTRODUCTION

Robust abundance estimates are essential for the management of exploited populations of baleen whales. In general abundance estimates have been based on visual encounters from aerial or ship-based survey platforms or through mark-recapture studies with photo or genetic identification of the whales. Aerial and ship-based surveys essentially count the portion of the population available at the surface and through various measures account for the proportion that were not available at the surface to be detected by the observers. This 'availability bias' (Marsh and Sinclair, 1989) can be substantial and has a large impact on the abundance estimates if bias correction is not applied to the at-surface-estimate or if the correction is inaccurate.

One method for estimating the availability of cetaceans detected by visual surveys of the sea surface is by instrumenting whales with dive-data collection telemetry systems (Heide-Jørgensen *et al.*, 2001). These tend to be archival instruments that are attached to whales and are designed to automatically detach after a few days and then release (e.g. Laidre *et al.*, 2002). They are retrieved at sea and data on the diving behaviour are downloaded. Archival recorders tend to log high resolution data over short time periods, although it can be desirable to collect data over longer time spans and in less accessible offshore areas. Other instruments utilise concatenated dive information transmitted through satellite connections (e.g. the Argos Data Collection System). The amount of data that can be collected by the Argos method is limited to brief messages transmitted during the surfacing events of the whales. No full resolution dive cycles can be relayed by this method and instead, only pre-defined summary information can be transmitted. The limited, filtered and pre-analysed data relayed through this system do not allow for a post-deployment instrument calibration. It is therefore critical that the instruments perform reliably and show no signs of drift. One way of monitoring the performance of the transmitters is through examination of the instrument's ability to detect the surface, which is logged with a wet-dry sensor when the instrument is above the surface of the water and exposed to air. This is particularly important for quantifying the at-surface-time used for correcting the availability bias in visual surveys. Any drift in detection of the surface may change the bias correction and lead to erroneous estimates of abundance.

Visual aerial surveys have been found to be the most cost efficient method for abundance estimation of humpback whales (*Megaptera novaeangliae*) in West Greenland (Heide-Jørgensen *et al.*, 2012; Heide-Jørgensen *et al.*, 2006) but they rely heavily on estimation of the fraction of the whales available to be detected at the surface by the observers. In this study, a dataset of surfacing time for humpback whales in Greenland obtained from satellite telemetry (Fig. 1) was examined. The present study assessed the importance of transducer drift for estimating the surfacing time. An estimation was made for the acceptable average surfacing time and then used to correct abundance estimates from an aerial survey of humpback whales conducted in West Greenland in 2007.

MATERIAL AND METHODS

Three types of satellite-linked time-depth-recorders (SLTDRs) were used in this study; all manufactured by

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Wildlife Computers (Redmond, Seattle) and modified for deployment and use on whales by Mikkel Villum Jensen[3].

The cylindrical tag (Mk10A; Fig. 2) was designed to be implanted into the blubber and muscles of the whales. It consisted of a 151mm long (22mm in diameter) stainless steel tube with a 38mm (in diameter) stop plate to prevent the tag from being implanted deeper that 113mm. The upper part of the steel tube had a 6mm screw used for mounting a 205mm long and 8mm wide cylindrical stainless steel anchoring spear ('tulip' anchor) equipped with a sharp triangular pointed tip and foldable barbs (40–50mm) to impede expulsion from the blubber-muscle layer. The rear end of the steel tube had an antenna (160mm length) and a salt water switch that ensured that transmissions were only conducted when the rear part of the tag was out of the water. A pressure transducer was positioned just below the stop plate. The mass of the transmitter with the anchoring spear was 250g and the tag had one AA cell in the front part of the steel tube.

The externally-positioned tag (Splash-200; Fig. 2) used a spear similar to the one described above, however the transmitter was mounted on a steel plate attached to the rear end of the spear and sat externally on the whale. The total length of the anchoring spear was 235mm (210mm with barbs of 8mm diameter). These were implanted into the blubber and

[3]*http://www.mikkelvillum.com.*

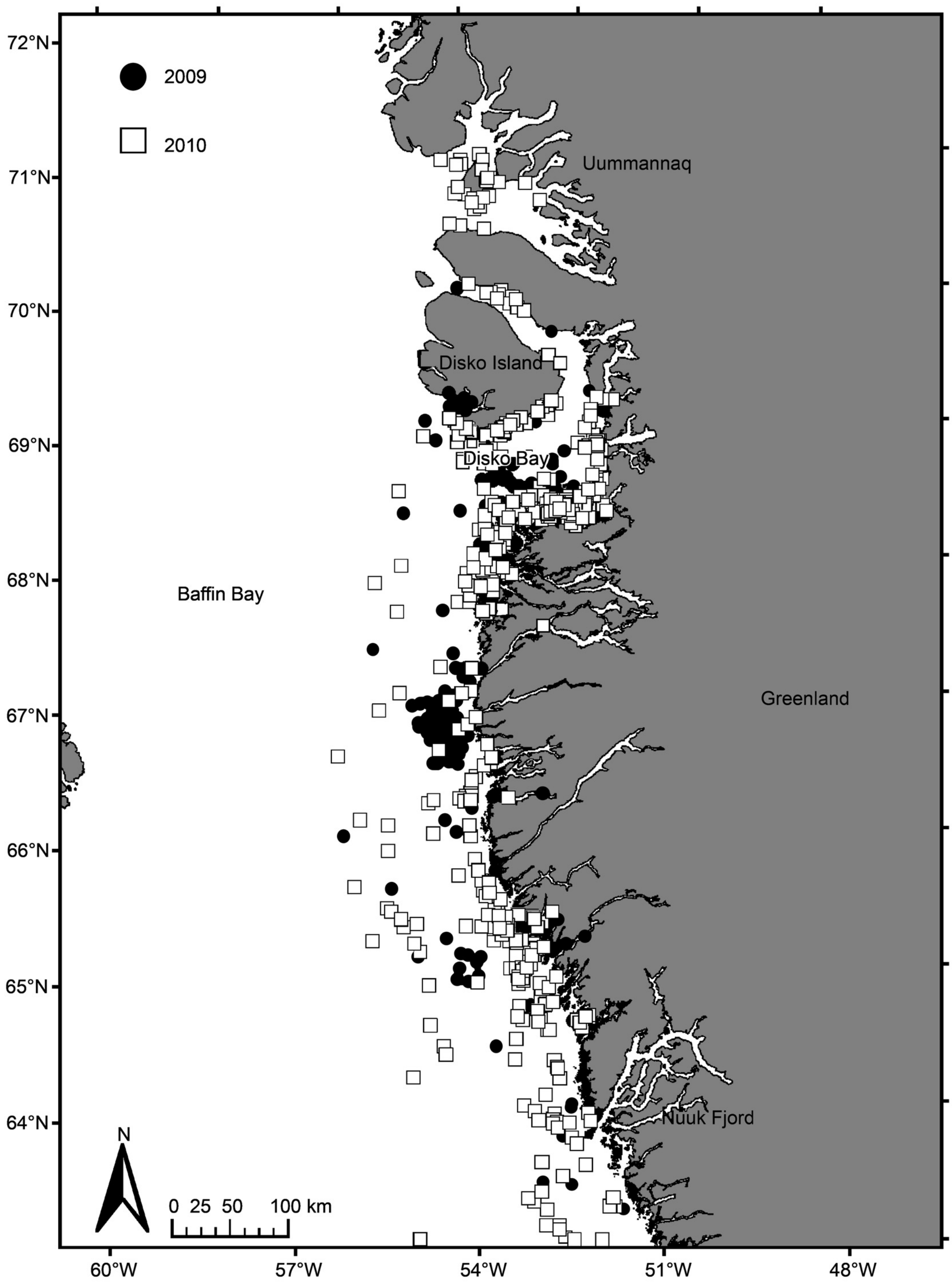

Fig. 1. Daily positions of humpback whales instrumented with SLTDRs in West Greenland in 2009 and 2010.

muscle layer and 25mm remained outside the skin with the attachment to the steel plate. The steel plate with the transmitter (85 × 50 × 25mm) could swivel freely around the spear, thereby keeping the tag in a position with the least drag. The salt water switch and the pressure transducer were mounted on top of the transmitter next to the antenna and the tag (300g) had two AA cells as a power supply.

The third tag was a mini Mk10A (Fig. 2) with two M3 batteries (35 × 53mm, 100g). It was mounted on a rubber plate attached to a short (100mm × 6mm) stainless steel spear and one set of small (30mm) barbs.

The cylindrical Mk10A tags were deployed either with the Air Rocket Transmitter System (Heide-Jørgensen *et al.*, 2001) or an 8m fiberglass pole (Heide-Jørgensen *et al.*, 2006). The external Splash was deployed with a fibreglass pole. The mini Mk10A was delivered using a small airgun (Dan Inject).

Positions of the whales were determined from transmitter uplinks received by Argos satellites and a daily average position was calculated for each whale. The tags also provided data on the accumulated proportion of time spent at two depth intervals (time-at-depth) recorded during four 6 hour periods starting at 00:00 GMT or 22:00 local time. The depth readings were collected from the pressure transducer at 1 second intervals and at a resolution of 0.5m and the readings were sorted into 12 time-at-depth bins, of which only the first two (0m and 0–2m) were used for this study. The data were sequentially relayed (previous 24 hour transmitted while new 24 hour data were collected) through the Argos Data Collection and Location System and decoded using Argos Message Decoder (DAP Ver. 3.0, build 058, Wildlife Computers). Time-at-depth data for two depth bins 0m and 0–2m were extracted for May–July. Drift of the pressure transducer (obtained from status messages included in every 50 transmission) was assessed for the study period.

Data from the first day of deployment were omitted to reduce the risk of behaviour being influenced by the tagging. Time-at-depth observations with surfacing times recorded as 0 or 100% were considered erroneous and discarded, likely due to malfunctioning of the pressure transducer. The rate of change in drift of the pressure and time-at-depth data was examined using a linear model ($y = \beta \times \text{Daynr} + k$) of the recordings against day number (from 1 January) where β was a measure of the rate of change. The influence of drift on the surfacing time was also assessed by linear regression where a single daily drift reading was assumed to represent the entire day. Statistical significance was detected at 5% level.

It was assumed that whales were available for visual detection when they were ≤2m from the water's surface (see Discussion). Thus the proportion of time spent at or above this depth (= surfacing time) was used to estimate the availability correction factor from the satellite-linked time-depth-recorders. Abundance (corrected for availability bias) was then estimated as:

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

with estimated CV

$$\text{CV}\left(\hat{N}_c\right) = \sqrt{\text{CV}\left(\hat{N}\right)^2 + \text{CV}\left(\hat{a}\right)^2}$$

RESULTS

Thirty one tags were deployed on humpback whales in West Greenland: 12 tags in 2009 and 19 tags in 2010 (Table 1). Of these, 22 humpback whales had the implantable Mk10A, eight whales were tagged with Splash tags, and one whale was tagged with the mini Mk10A tag during May–July 2009–10 (Fig. 2). Eight of the Mk10As failed to provide data on time spent at the surface. An additional five tags did not provide data on drift of the pressure transducer although they did provide records of time spent at the surface. Data from the remaining 18 tags were examined for the range and speed of the drift on the pressure transducer and for temporal changes in surfacing time. All whales were located in the shelf area off the West Greenland coast (Fig. 1), which is the same area covered by aerial and ship-based surveys for estimating the abundance of humpback whales in West Greenland.

Most transmitters had a positive transducer drift (i.e. increasing the depth assumed to be 0m) but a few also had negative drift that detected the surface above 0m. The average drift of the 18 tags was about 40cm per day and most

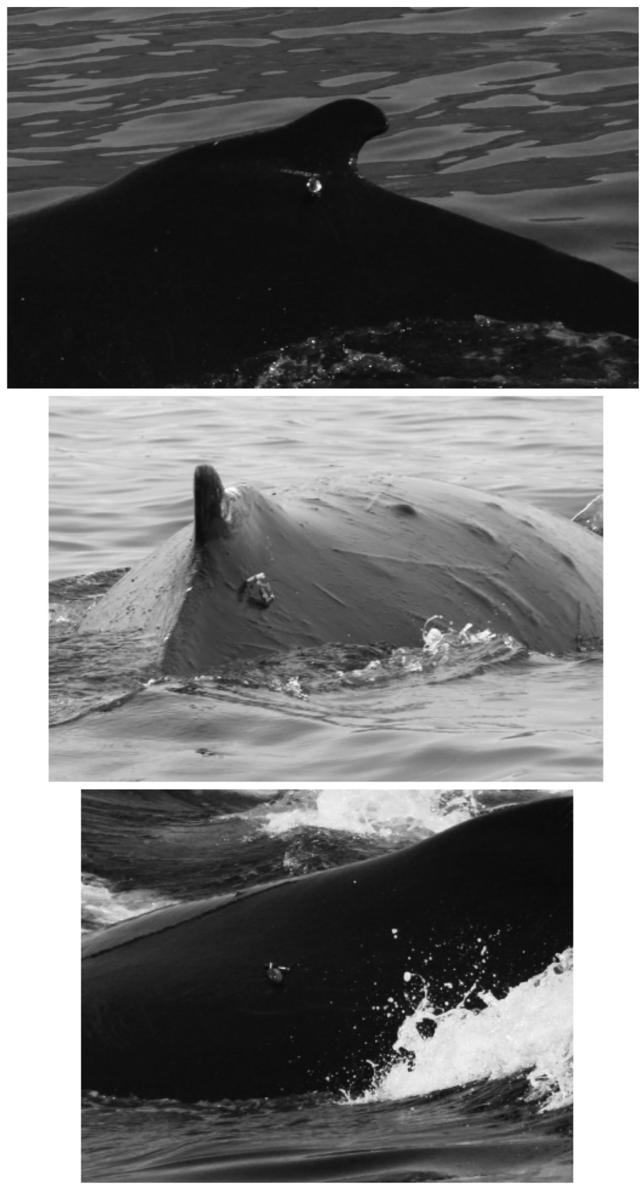

Fig. 2. Humpback whales instrumented with a Mk10A transmitter (top), Splash transmitter (middle), and a mini Mk10 (bottom).

Table 1

Humpback whales tagged with satellite linked time-depth-recorders in West Greenland 2009–10 where data on drift of pressure transducer and surfacing time (ST) were obtained during daylight hours (10–22 hours), across 24 hours, and during days with limited drift (0–1m) of the pressure transducer.

PTT ID	Tag type/ tag ware	Date	Position (°N °W)	Place-ment	Sex	Length (m)	Deploy-ment method	*n*	ST change/ day (%)	Drift change per day (β, m)	Range drift (m)	Signif-icance of trend of ST on drift (*p*)	ST (22–22 hrs) (%)	ST (24 hrs) (%)	Day no. with drift within 0–1m	ST with drift within 0–1m (%)
13280	Mk10/ 1.24d	27/05/09	68°38.433 53°07.414	RBH	♂	13	Pole	67	–1.9	0	3–3	N/A	28.78	31.61	–	–
20160	Mk10/ 1.24d	31/05/09	68°44.984 52°51.940	LBL	♀	13	Pole					Unreliable data				
20164	Mk10/ 1.24d	03/06/09	68°45.778 52°37.507	LMH	♂	14	ARTS	130	–0.3	N/A	N/A	N/A	19.67	21.57	–	–
20165	Mk10/ 1.24d	01/06/09	68°38.281 53°12.942	RFH	N/A	14	Pole					Unreliable data				
20166	Mk10/ 1.24d	01/06/09	68°44.788 52°54.172	RMH	♂	14	ARTS	107	–0.6	0.1	2–2.5	0.391	18.66	18.02	–	–
20168	Mk10/ 1.24d	03/06/09	68°44.995 52°37.857	LMH	♀	11	Pole	3	1	N/A	N/A	N/A	26.30	24.20	–	–
20682	Mk10/ 1.24d	07/06/09	68°43.057 52°18.683	RMH	♂	–	ARTS	104	–0.2	0.1	2–2.5	0.390	19.88	28.07	–	–
20683	Mk10/ 1.24d	06/06/09	68°43.586 52°51.730	LMH	♂	8	ARTS					Unreliable data				
20684	Mk10/ 1.24d	03/06/09	68°46.144 52°29.688	RMM	♂	–	ARTS	47	–1.4	N/A	N/A	N/A	18.55	19.92	–	–
20690	Mk10/ 1.24d	07/06/09	68°43.454 52°35.735	RMH	N/A	11	ARTS					Unreliable data				
20692	Mk10/ 1.24d	07/06/09	68°43.044 52°21.630	RMH	N/A	13	ARTS					Unreliable data				
20693	Mk10/ 1.24d	11/06/09	68°43.255 52°07.776	LMH	N/A	11	ARTS					Unreliable data				
7931	Mk10/ 1.24k	01/07/10	65°25.656 52°43.784	LMH	N/A	N/A	Pole	18	2.9	N/A	N/A	N/A	22.53	21.67	–	–
13280	Mk10/ 1.24k	02/06/10	68°43.019 52°16°714	RMH	♂	N/A	Pole	102	–0.1	0.3	1–4	0.732	22.96	22.22	–	–
20157	Mk10/ 1.24k	02/07/10	65°25.177 52°47.461	RMH	N/A	N/A	Pole	102	–0.5	0	1–1.5	0.562	26.85	28.61	–	–
20158	Mk10/ 1.24k	07/07/10	68°44.003 52°46.667	RMH	N/A	N/A	Pole	80	0.3	0.1	0.5–2.5	0.258	34.24	31.91	189–204	32.92
20160	Mk10/ 1.24k	20/06/10	69°14.256 53°24.395	LMH	♀	N/A	Pole	120	0.3	0.1	0–3	0.129	51.58	52.46	171–178	45.40
20167	Mk10/ 1.24k	01/07/10	65°26.054 52°43.787	RMM	N/A	N/A	Pole					Unreliable data				
26712	Mk10/ 1.24k	07/07/10	68°43.259 52°19.194	LMH	N/A	N/A	Pole	44	0.1	0	0–1	0.401	31.65	28.76	188–218	31.60
27260	Mk10/ 1.24k	19/06/10	69°11.660 53°47.129	LMH	♂	N/A	Pole	106	0.4	0	1.5–2	0.029	45.33	40.18	–	–
50681	Mk10/ 1.24k	18/06/10	69°27.263 54°13.699	LMH	♂	N/A	Pole	39	0.4	N/A	N/A	N/A	25.18	26.93	–	–
50684	Mk10/ 1.24k	02/07/10	65°32.137 52°59.260	LMH	N/A	N/A	Pole					Unreliable data				
20692	Splash/ 1.001	02/06/10	68°40.165 52°08.802	RMM	♀	N/A	Pole	61	–0.1	0	–2– –2	0.543	18.23	16.79	–	–
20693	Splash/ 1.001	03/06/10	68°33.060 53°11.815	RMH	♀	N/A	Pole	148	0.6	0	3–3	0.001	25.86	22.24	–	–
20696*	Splash/ 1.001	02/06/10	68°39.825 52°09.659	RMM	♂	N/A	Pole	32	0	–0.2	2–1	0.617	28.14	26.72	157–162	29.85
21791	Splash/ 1.001	09/06/10	69°15.933 53°25.628	LMH	♂	N/A	Pole	137	0.2	0	2–2	0.094	22.40	23.58	–	–
21792	Splash/ 1.001	04/06/10	68°43°501 52°21°657	RMM	♂	N/A	Pole	66	–0.6	0	–2– –6	0.611	31.32	27.21	–	–
21794	Splash/ 1.001	07/06/10	69°14.141 53°48.691	RMH	♂	N/A	Pole	76	–0.7	0	0	0.328	41.12	40.43	160–177	38.68
21800	Splash/ 1.001	18/06/10	69°26.979 54°15.524	LMH	♂	N/A	Pole	94	0.2	0.5	–2 0	0.578	21.87	22.09	178–193	22.25
21802	Splash/ 1.001	11/06/10	69°10.170 51°28.388	LMH	♂	N/A	Pole	41	–0.6	–0.3	–3– –7	0.047	37.68	36.52	–	–
46135	MiniMk10/ 1.24k	20/06/10	69°14.177 53°24.431	LMH	♂	N/A	Pole	38	–0.4	0.1	5–5.5	0.170	40.89	39.79	–	–
												Average:	**28.68**	**28.33**	**–**	**33.45**
												CV:	**0.06**	**0.06**	**–**	**0.10**

*Later tagged with #27260 on 19 June 2010.

transducers did not correctly identify the surface when they provided the first data on surfacing times (Fig. 3).

Changes in the surfacing time (0–2m depth) over the study period were most prominent for the Mk10 tags used in 2009 using tag software ('tagware') generation 1.24d (Fig. 4). Data on drift were not available for all the surfacing time values. With the MK10 tags deployed in 2009 and 2010, only 7% and 12%, respectively of the surfacing time estimates had associated drift values because data on drift were only included in every 50th transmission. However, drift readings were available for 72% of the surfacing times for the Splash tags and 53% of the surfacing estimates for the single mini-

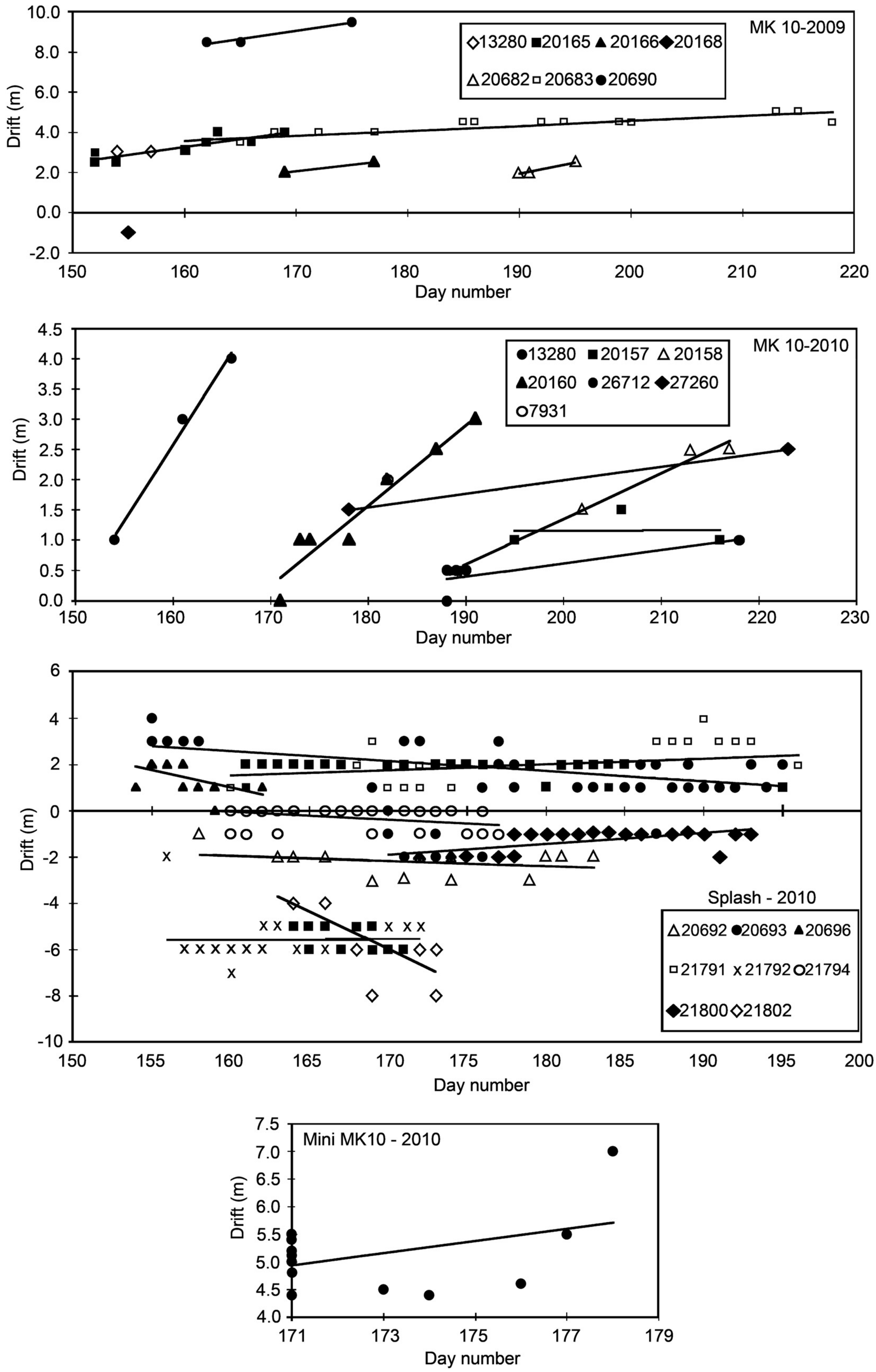

Fig. 3. Drift of pressure transducer for Mk10 and Splash transmitters used on humpback whales in West Greenland in 2009 and 2010.

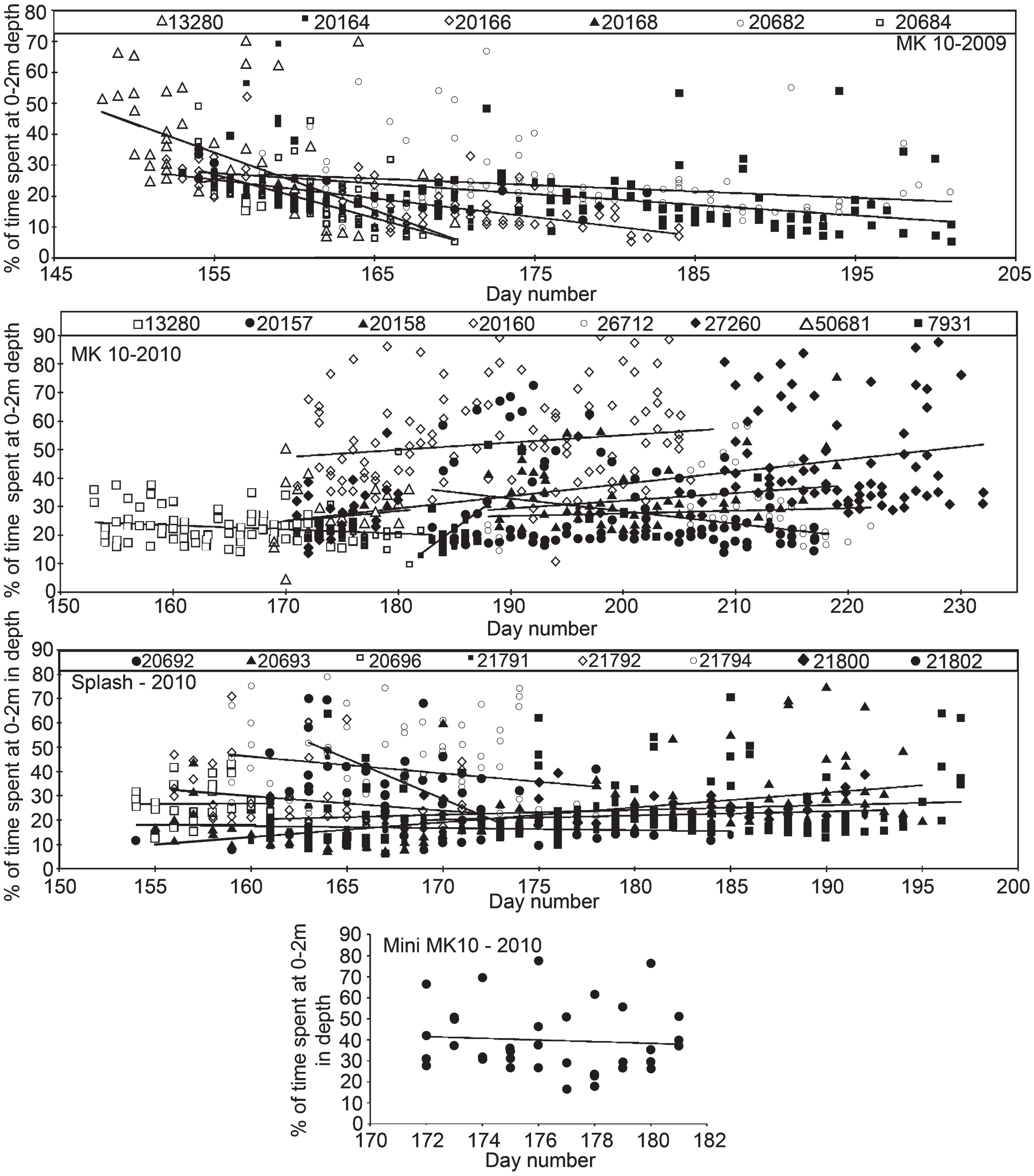

Fig. 4. Trends in surfacing times for humpback whales instrumented with Mk10 transmitters in 2009, Splash transmitter 2010, Mk10 transmitters 2010, Mini Mk10 transmitter in 2010.

MK10A tag. Correlation between drift and surfacing time was assessed with linear regressions and only three instruments showed a significant effect of drift on the surfacing time. If the zero depth readings were gradually biased towards greater depth than 0m, surfacing time should show a similar decrease; however, it was not possible to extrapolate surfacing times to zero drift values as most pressure transducers indicated drift from the very first depth readings.

It is likely that the tags with tag-ware 1.24d did not correctly adjust the depth transducer for the surface readings from the conductivity switch. Therefore tags with tag-ware 1.24d were excluded from estimates of surface time. Later generations of tag-ware did not indicate drift of the pressure transducer and it was assumed that effects of drift in the pressure transducer, if any, would have a marginal influence on the average surfacing time when data from many instruments were examined. The analysis was therefore restricted to instruments and time periods when the transducer drift indicated values in the range of 0 to ±1m, approximating the resolution of the depth readings. This further reduced the sample size to six whales with 89 days of data. There was no statistical difference between the time-at-depth for the four periods (each six hours long) where surfacing time data were collected. However, only data from two of the six hour periods (10:00–16:00 and 16:00–22:00), coincided with the period when visual aerial surveys would have been operating; only these were included in the development of the correction factor.

The average surfacing time for the six animals was 33.5% (CV = 0.10) of the time spent ≥2m depth. If data from all 23 whales with surfacing data during daylight hours were examined, the average surfacing time declined to 28.3% (CV = 0.06), which was not significantly different from the restricted dataset. The average surfacing time for the 13 tags without significant correlation between drift and surfacing time was 28.8% (CV = 0.09) with a range between 18.2 and 51.6% which emphasises that correction for the initial drift is necessary.

Detection of whales at the surface from a passing plane cannot be considered an instantaneous process because the whales are in view for a small but certain amount time. Heide-Jørgensen *et al.* (2012) estimated the positive bias in the instantaneous availability correction factor for time-in-view data from the humpback whale survey in 2007 and for surfacing times >30 seconds. Following their approach correction for a positive bias of 10% to the surface time increases the availability correction factor estimated here (33.5–36.8%; CV = 0.10).

At-surface abundance estimates of humpback whales in West Greenland were available from a survey in 2007 (Heide-Jørgensen *et al.*, 2012); two of the estimates were corrected for perception bias (strip census and mark-recapture-distance-sampling) and one conventional distance sampling estimate was not. When the availability correction factor developed above was applied to these estimates the strip census and conventional distance sampling estimates were in good agreement whereas the mark-recapture-distance-sampling estimate was about 50% larger (Table 2). The strip-census estimate including both correction for perception and availability bias results in the most precise estimate with an abundance of 2,704 humpback whales in West Greenland in 2007 (95% CI 1,402–5,215).

DISCUSSION

Richard *et al.* (1994) and Heide-Jørgensen (2004) conducted experiments submersing models of narwhals (*Monodon monoceros*) in clear water to estimate the depth at which they reliably can be detected from the air. They found that a detection depth of 2m could be used for visual surveys of narwhals. No similar studies have been conducted for humpback whales, but since the white flippers of North Atlantic humpback whales are relatively easy to detect below the surface, and given humpback whales occur in more turbid water than narwhals, 2m is considered acceptable by the authors. None of the sightings in the 2007 survey had sightings of humpback whales that were submerged below the surface. The whales were either approaching the surface or diving when detected, thus they were all breaking the surface.

The calibration of the depth transducer is an important component in assessing availability bias. This is something that is mandatory in oceanographic studies but rarely seen in marine mammal studies. The present analysis stresses the importance of assessing drift in the pressure transducer when fine scale resolution of the surface layer is needed. Ideally the pressure transducer should calibrate the location of the surface from the conductivity switch when it breaks the water surface; however this is not always the case. The software version used for the tags deployed in 2009 (tag-ware 1.24d) did not use the conductivity switch information for correctly altering the surface readings, and pressure transducers drifted rapidly out of the critical range for assessing surfacing time of whales. The drift was unidirectional towards increasing depth (except for 1 tag with only three data points) which led to a negatively biased surfacing time. There is no simple way to correct for transducer drift because drift reports are not connected to surfacing time. Even if this was the case, there is no straightforward way to correct the surface time as the drift may be changing during the period with surfacing estimates. The problem was solved with tag-ware 1.24k but the drift message from the tags still reported some level of fluctuating drift. Even though no clear direction in the surfacing time could be detected in tag-ware 1.24k, we chose only to include whales for periods where the drift was within the depth resolution of the tags.

Heide-Jørgensen *et al.* (2012) reported on the surfacing time of humpback whales in West Greenland in 2000 using Telonics SDR-T16 SLTDRs. In that study there was no consideration of pressure transducer drift. Due to the resolution of the depth readings the surface was defined as 0–4m rather than 0–2m (used in this study) and the proportion of time spent at the surface (0–4m depth) was higher than estimated in the present study. Although the Heide-Jørgensen *et al.* (2012) values are not significantly different from this study, the later instrumentation technique and the more rigorous examination of the drift of the pressure transducer render the current surfacing estimates more reliable.

The simplest availability correction factor $\hat{a}$ is the estimated proportion of time an animal is available for detection, which is an estimator of the probability that an animal is available at any randomly chosen instant. This is therefore an appropriate correction factor when the survey is instantaneous, as for example in photographic surveys (Heide-Jørgensen, 2004). However, for aerial surveys, where the survey platform is moving at high speed, there is still a period where the animals are within view of the observers. Borchers *et al.* (2013) developed hidden Markov models to account for the detection process in situations where the diving whales are available for detection for a certain period (i.e. time-in-view) and the animals are either submerged or at the surface in a certain sequence. Detailed data on the diving events (duration of dives and surfacings below and above the detection limit) of humpback whales in West Greenland are not available.

Table 2

Aerial survey data on humpback whale abundance in West Greenland in 2007 (Heide-Jørgensen *et al.*, 2012). The data were not corrected for whales that were submerged during the passage of the airplane (availability bias). Availability bias was estimated to be 36.8% (CV = 10).

Method	Estimate	Estimate corrected for availability bias	95% confidence limits
Conventional distance sampling without correction for perception bias	1,020 (0.35)	2,772 (0.36)	1,388–5,534
Mark-recapture distance sampling corrected for perception bias	1,505 (0.49)	4,090 (0.50)	1,620–10,324
Strip census estimation corrected for perception bias	995 (0.33)	2,704 (0.34)	1,402–5,215

Although the bias correction may differ for a stochastic series of diving events, the deterministic availability bias correction factor is still applicable to the surveys off West Greenland.

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REFERENCES

Borchers, D.L., Zucchini, W., Heide-Jørgensen, M.P., Cañadas, A. and Langrock, R. 2013. Using hidden Markov models to deal with availability bias on line transect surveys. *Biometrics* 69(3): 703–13.

Heide-Jørgensen, M.P. 2004. Aerial digital photographic surveys of narwhals, *Monodon monocerus,* in Northwest Greenland. *Mar. Mammal Sci.* 20(2): 246–61.

Heide-Jørgensen, M.P., Kleivane, L., Øien, N., Laidre, K.L. and Jensen, M.V. 2001. A new technique for deploying satellite transmitters on baleen whales: Tracking a blue whale (*Balaenoptera musculus*) in the North Atlantic. *Mar. Mammal Sci.* 17(4): 949–54.

Heide-Jørgensen, M.P., Laidre, K., Hansen, R.G., Burt, M.L., Simon, M., Borchers, D.L., Hanssen, J., Harding, K., Rasmussen, M.H., Dietz, R. and Teilmann, J. 2012. Rate of increase and current abundance of humpback whales in West Greenland. *J. Cetacean Res. Manage* 12(1): 1–14.

Heide-Jørgensen, M.P., Laidre, K.L., Jensen, M.V., Dueck, L. and Postma, L.D. 2006. Dissolving stock discreteness with satellite tracking: bowhead whales in Baffin Bay. *Mar. Mammal Sci.* 22(1): 34–45.

Laidre, K.L., Heide-Jørgensen, M.P. and Dietz, R. 2002. Diving behaviour of narwhals (*Monodon monoceros)* at two localities in the Canadian High Arctic. *Can. J. Zool.* 80: 624–35.

Marsh, H. and Sinclair, D.F. 1989. Correcting for visibility bias in strip transect aerial surveys for aquatic fauna. *J. Wildl. Manage.* 53(4): 1017–24.

Richard, P., Weaver, P., Dueck, L. and Barber, D. 1994. Distribution and numbers of Canadian High Arctic narwhals (*Monodon monoceros*) in August 1984. *Meddelelser om Grønland, Bioscience* (*Geoscience, Man and Society*) 39: 41–50.