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Editorial

Welcome to this the fifteenth volume of the *Journal of Cetacean Research and Management*. This volume contains eight papers covering a wide range of conservation and management issues including abundance, site fidelity, whale watching, ocean noise and ecosystem change. Techniques for data gathering used in the papers varies from aerial and vessel-based surveys and shore-based counting, to the use of photo-identification and satellite telemetry. Species and areas studied include bowhead whales in the Beaufort Sea, southern right whales in the southwest Atlantic Ocean off Patagonia, Argentina, gray whales in the North Pacific Ocean (on migration past the coast of California), minke whales in the Antarctic, together with other studies undertaken in the coastal waters of Iceland, British Columbia and New Jersey.

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G.P. DONOVAN
Editor

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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

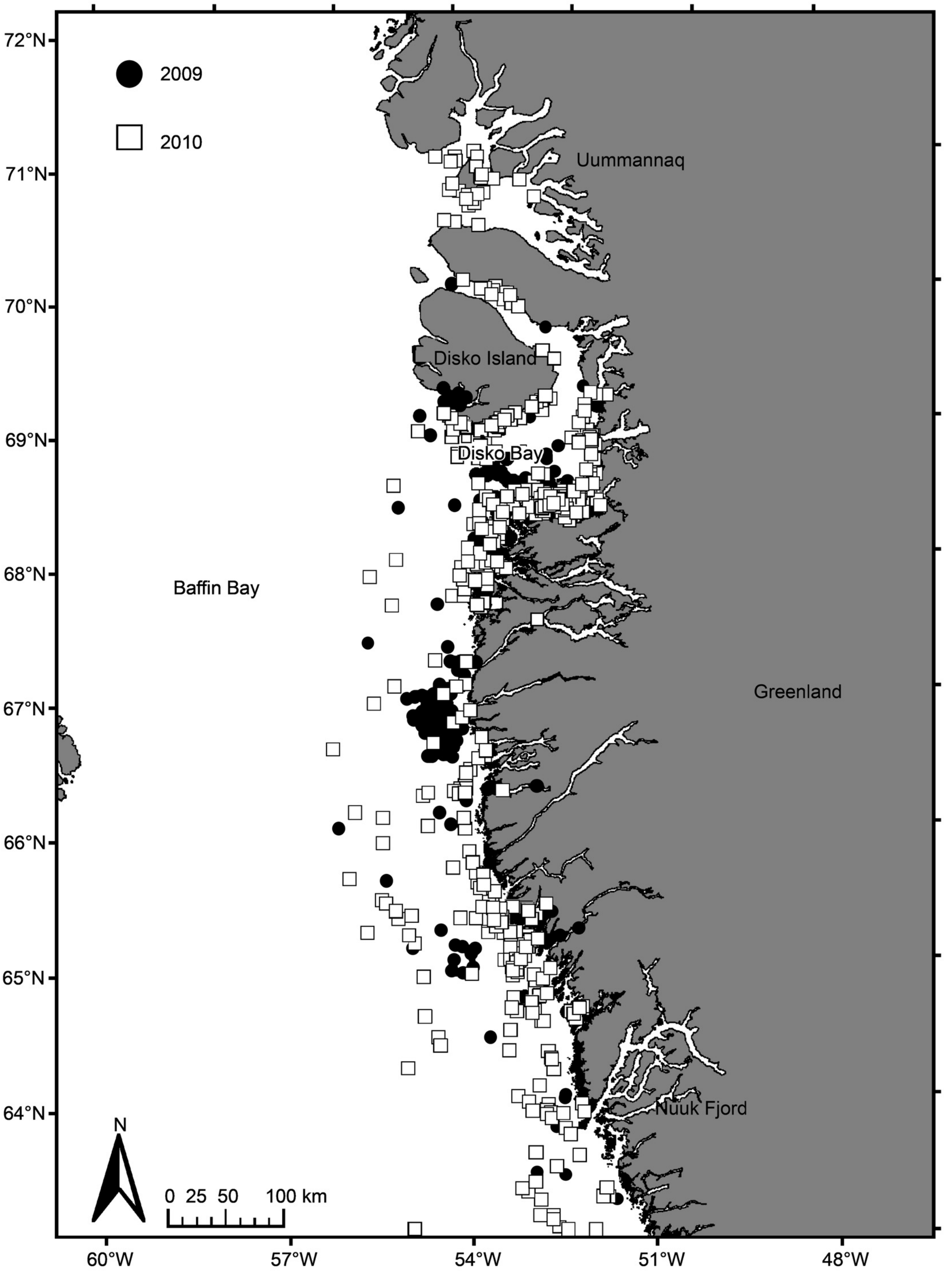

Fig. 1. Daily positions of humpback whales instrumented with SLTDRs in West Greenland in 2009 and 2010.

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

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

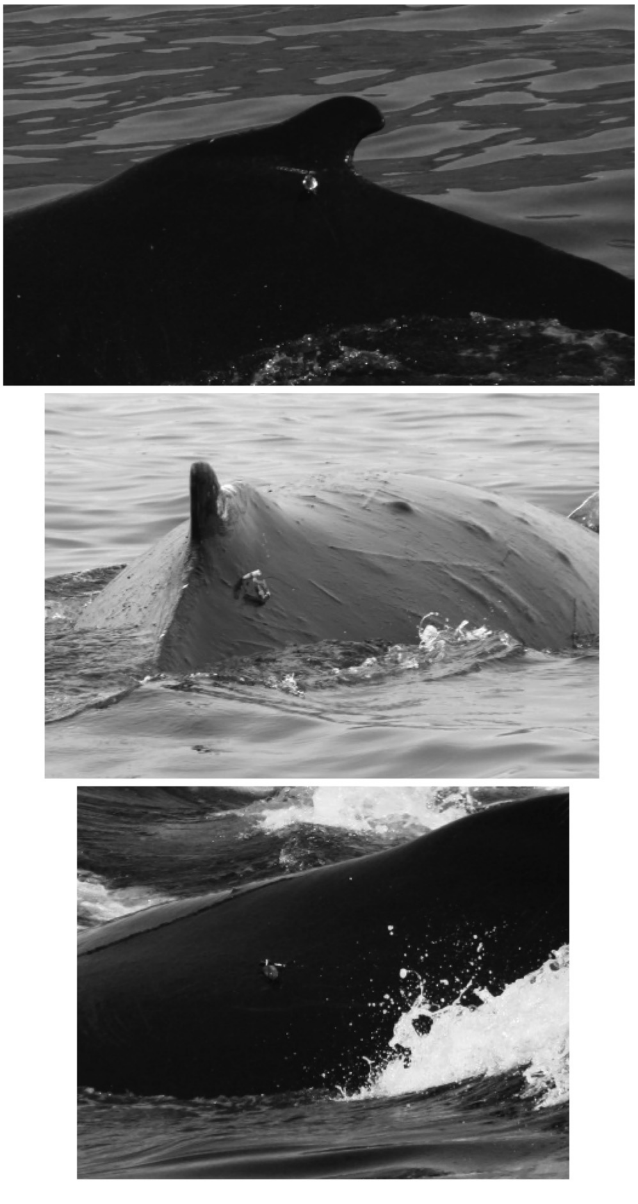

Fig. 2. Humpback whales instrumented with a Mk10A transmitter (top), Splash transmitter (middle), and a mini Mk10 (bottom).

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-

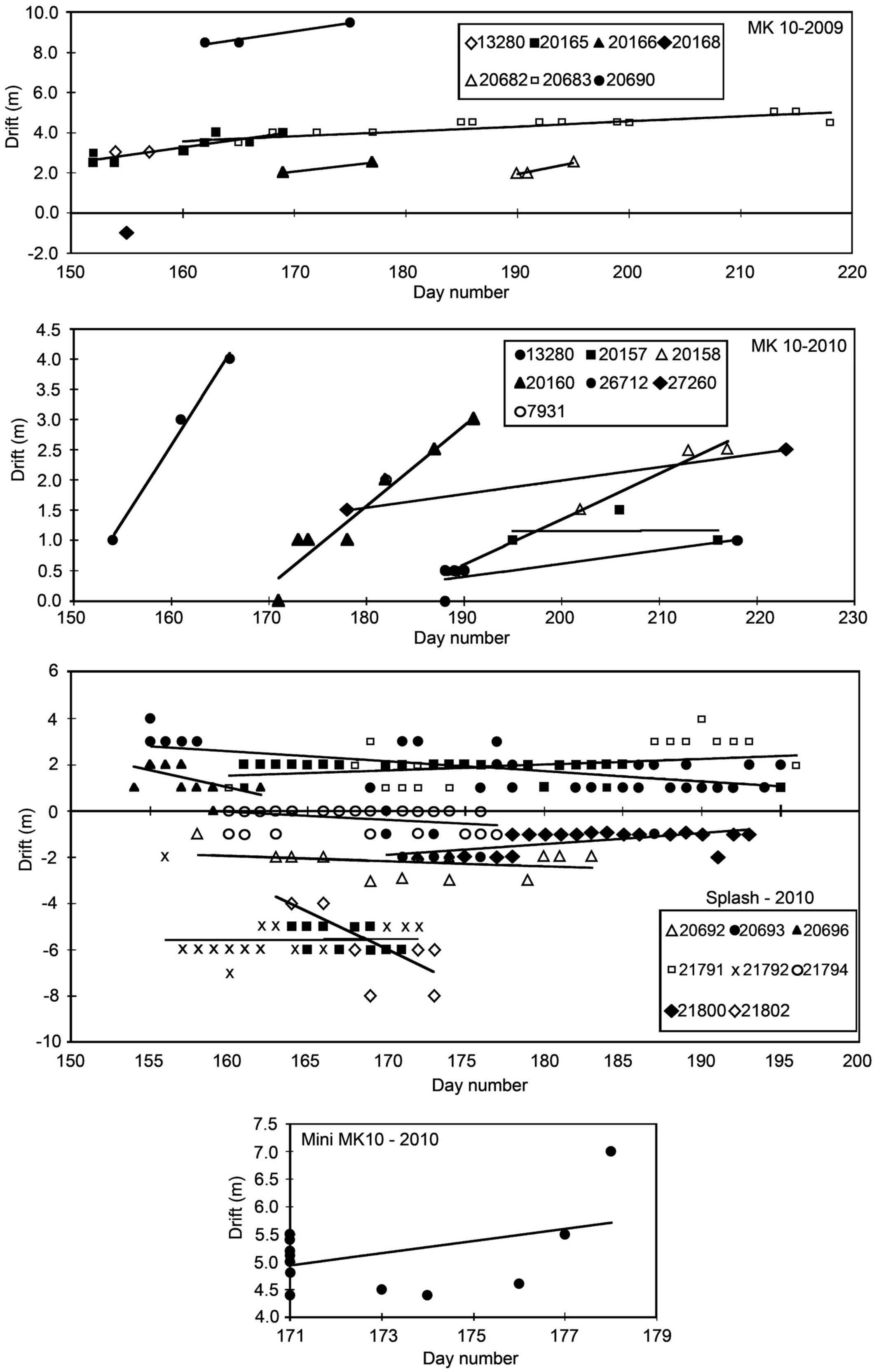

Fig. 3. Drift of pressure transducer for Mk10 and Splash transmitters used on humpback whales in West Greenland in 2009 and 2010.

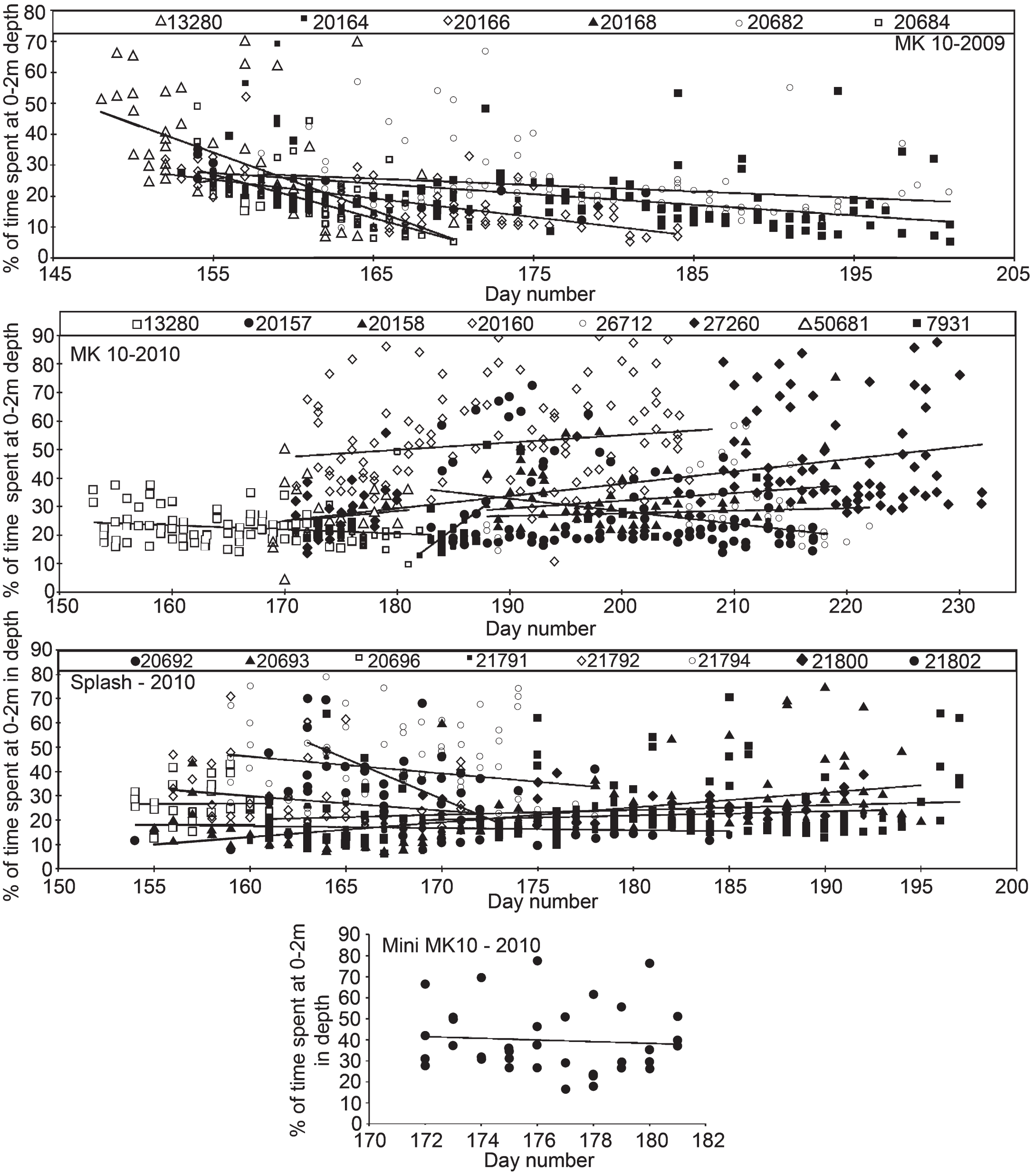

Fig. 4. Trends in surfacing times for humpback whales instrumented with Mk10 transmitters in 2009, Splash transmitter 2010, Mk10 transmitters 2010, Mini Mk10 transmitter in 2010.

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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Updated marine mammal distribution and abundance estimates in British Columbia

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ABSTRACT

Information relating to the distribution and abundance of species is critical for effective conservation and management. For many species, including cetacean species of conservation concern, abundance estimates are lacking, out of date and/or highly uncertain. Systematic, line-transect marine mammal surveys were conducted in British Columbia's (BC) coastal waters over multiple years and seasons (summer 2004, 2005, 2008, and spring/autumn 2007). In total, 10,057km of transects were surveyed in an 83,547km^2 study area. Abundance estimates were calculated using two different methods: Conventional Distance Sampling (CDS) and Density Surface Modelling (DSM). CDS generates a single density estimate for each stratum, whereas DSM explicitly models spatial variation and offers potential for greater precision by incorporating environmental predictors. Although DSM yields a more relevant product for the purposes of marine spatial planning, CDS has proven to be useful in cases where there are fewer observations available for seasonal and inter-annual comparison, particularly for the scarcely observed elephant seal. The summer abundance estimates (with lower and upper 95% confidence intervals; all DSM method unless otherwise stated), assuming certain trackline detection (underestimates true population size) were: harbour porpoise (*Phocoena phocoena*) 8,091 (4,885–13,401); Dall's porpoise (*Phocoenoides dalli*) 5,303 (4,638–6,064); Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) 22,160 (16,522–29,721); humpback whale (*Megaptera novaeangliae*) 1,092 (993–1,200); fin whale (*Balaenoptera physalus*) 329 (274–395); killer whale (all ecotypes; *Orcinus orca*), 371 (222–621); common minke whale (*B. acutorostrata*) 522 (295–927); harbour seal (total; *Phoca vitulina*) 24,916 (19,666–31,569); Steller sea lion (total; *Eumetopias jubatus*) 4,037 (1,100–14,815); and northern elephant seal (CDS method; *Mirounga angustirostris*) 65 (35–121). Abundance estimates are provided on a stratum-specific basis with additional estimates provided for Steller sea lions and harbour seals that were 'hauled out' and 'in water'. This analysis updates previous estimates by including additional years of effort, providing greater spatial precision with the DSM method over CDS, novel reporting for spring and autumn seasons (rather than summer alone), and providing new abundance estimates for Steller sea lion and northern elephant seal. In addition to providing a baseline of marine mammal abundance and distribution, against which future changes can be compared, this information offers the opportunity to assess the risks posed to marine mammals by existing and emerging threats, such as fisheries bycatch, ship strikes, and increased oil spill and ocean noise issues associated with increases of container ship and oil tanker traffic in British Columbia's continental shelf waters.

KEYWORDS: SURVEY-VESSEL; ABUNDANCE ESTIMATE; DISTRIBUTION; CONSERVATION; BRITISH COLUMBIA; PACIFIC OCEAN; HUMPBACK WHALE; KILLER WHALE; COMMON MINKE WHALE; FIN WHALE; PACIFIC WHITE-SIDED DOLPHIN; STELLER SEA LION; ELEPHANT SEAL; HARBOUR SEAL; HARBOUR PORPOISE; DALL'S PORPOISE; NORTHERN HEMISPHERE

INTRODUCTION

Information relating to the distribution and abundance of species is critical for effective conservation and management approaches. Currently only a handful of marine mammal species in British Columbia's (BC) coastal waters are adequately monitored to gain information about their distribution, abundance, and/or population trends (e.g., resident killer whales, *Orcinus orca,* humpback whales, *Megaptera novaeangliae*, and sea otters, *Enhydra lutris*). For the remainder of species, including some that are listed under Canada's Species At Risk Act (SARA), there is a lack of quantitative abundance estimates. This problem is not unique to Canada; a recent global assessment showed that 75% of the world ocean has never been surveyed for cetaceans, and only 6% has been surveyed frequently enough to detect trends (Kaschner *et al.*, 2012).

In 2007, preliminary distribution and abundance estimates for eight marine mammal species were generated from the first systematic line-transect survey in BC's coastal (essentially continental shelf) waters during summer 2004 and 2005 (Williams and Thomas, 2007). As might be expected for the first survey of its kind, low sample sizes for many species resulted in abundance estimates with large confidence intervals. Large confidence intervals offer low power to detect trends, and available estimates apply only to summer waters. As the only estimates for some species in the region, they have been used in a management context. For example, the abundance estimates for harbour porpoise were used as conservation targets for Canada's Management Plan for the species in the Pacific Region (Fisheries and Oceans Canada, 2009). The estimates were used to calculate sustainable limits for small cetacean bycatch in fisheries (Williams *et al.*, 2008) and ship strikes of fin, humpback and killer whales (Williams and O'Hara, 2010), but these limits may have been overly precautionary because of the uncertainty around the abundance estimates, or insufficiently precautionary by not providing information on seasons other than summer.

With additional systematic surveys completed in 2006-08, the objective was to generate updated estimates. Here,

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updated abundance estimates for eight marine mammal species are given along with new estimates for elephant seals (*Mirounga angustirostris*) and Steller sea lions (*Eumetopias jubatus*). Estimates are directly compared with previous abundance estimates derived using a Conventional Distance Sampling (CDS) approach (Williams and Thomas, 2007) to gauge the effect of increased sample size on precision. New abundance estimates have been created for all 10 species using Density Surface Models (DSM), which uses statistical models to explain spatial heterogeneity in animal distribution using environmental covariates and therefore offers potential to improve precision (Hedley *et al.*, 1999; Marques and Buckland, 2003; Miller *et al.*, 2013). This DSM approach was essential to meeting the final objective of providing updated information on the distribution of marine mammals in BC's coastal waters for use in spatial planning and spatially explicit risk assessments.

Systematic, line-transect marine mammal surveys were conducted throughout the continental shelf waters of British Columbia during summer 2004, 2005, 2006, and 2008, and spring and autumn 2007. With the exception of 2004, surveys were concentrated in the Queen Charlotte Basin and mainland inlets of the North and Central Coasts. The summer 2004 survey encompassed a far larger area of BC's continental shelf waters, stretching from the BC-Alaska border south to the BC-Washington border.

Although more than 20 marine mammal species are found in BC's coastal waters, only 10 marine mammal species yielded a sufficient number of sightings for analysis: harbour porpoise (*Phocoena phocoena*); Dall's porpoise (*Phocoenoides dalli*); Pacific white-sided dolphin (*Lagenorhynchus obliquidens*); killer whale (resident, transient and offshore ecotypes); humpback whale (*Megaptera novaeangliae*); common minke whale (*Balaenoptera acutorostrata*); fin whale (*B. physalus*); harbour seal (*Phoca vitulina*); Steller sea lion; and elephant seal. Several of these species are of significant conservation concern at provincial, national and international levels (Table 1).

Sighting and density estimation of pinnipeds were further separated into 'haul-out' or 'in-water' categories, as both detectability on the trackline and the detection function are expected to differ widely.

Species information

Harbour porpoise

Harbour porpoises are listed as 'Least Concern' by the International Union for Conservation of Nature (IUCN) but as a species of 'Special Concern' within Canada's Pacific region (COSEWIC, 2003). Found predominantly in shallow waters less than 200m in the Northern Hemisphere, four subspecies have been genetically identified globally (Rice, 1998). Despite continuous distribution alongshore from Point Conception around the Pacific rim to the northern islands of Japan and as far north as Barrow, Alaska, many small populations appear genetically distinct, suggesting the need to consider small subpopulation management units (Chivers *et al.*, 2002). To date, no such stock structure analyses have been conducted in BC.

Dall's porpoise

Dall's porpoises are globally abundant with an estimated population of more than 1.2 million individuals. The species is listed as of 'Least Concern' by the IUCN (Hammond *et al.*, 2008) and 'Not At Risk' within Canada, but has not been assessed by Canada since 1989, when no abundance estimates were available. Dall's porpoise are distributed throughout the North Pacific Ocean, generally in deeper coastal waters, but no information is available on stock structure.

Pacific white-sided dolphin

Pacific white-sided dolphins are listed by the IUCN as a species of 'Least Concern' and 'Not At Risk' in Canadian waters, but the species has not been assessed by Canada since 1990, when no abundance estimates were available. They are distributed along the temperate coastal shelf waters and in some inland BC waterways of the North Pacific from approximately 35°N to 47°N (Heise, 1997; Stacey and Baird, 1991).

Humpback whale

Humpback whales were listed by the IUCN in 2008 as a species of 'Least Concern' and in Canada, were listed as of 'Special Concern' (COSEWIC, 2011) in 2014 by SARA. Studies indicate that the North Pacific population is

Table 1

Conservation status of marine mammals in British Columbia waters, including year assessed and designations for subpopulations and breeding status, where available. Note: COSEWIC lacked a 'Data Deficient' category in the 1980s and early 1990s, so older assessments in the 'Not At Risk' category should be interpreted with caution.

Common name	Provincial: British Columbia	National: COSEWIC	Global: IUCN
Harbour porpoise	Special Concern, 2006	Special Concern, 2003	Least Concern, 2008
Dall's porpoise	Apparently Secure/Secure, 2006	Not At Risk, 1989	Least Concern, 2008
Pacific white-sided dolphin	Apparently Secure/Secure, 2006	Not At Risk, 1990	Least Concern, 2008
Humpback whale	Special Concern, 2006	Special Concern, 2011	Least Concern, 2008
Fin whale	Imperilled (non-breeding), 2006	Threatened, 2005	Endangered, 2008
Killer whale	Special Concern, 2006		Data Deficient, 2008
Offshore	Imperilled, 2011	Threatened, 2008	
Transient	Imperilled, 2011	Threatened, 2008	
Southern resident	Critically Imperilled, 2011	Endangered, 2008	
Northern resident	Imperilled, 2011	Threatened, 2008	
Common minke whale	Apparently Secure (non-breeding), 2006	Not At Risk, 2006	Least Concern, 2008
Harbour seal	Secure, 2006	Not At Risk, 1999	Least Concern, 2008
Steller sea lion	Imperilled/Special Concern (breeding), 2006 Special Concern (non-breeding), 2006	Special Concern, 2003	Near Threatened, 2012
Northern elephant seal	Not Applicable, 2006	Not At Risk, 1986	Least Concern, 2008

recovering (e.g., Calambokidis *et al.*, 2008; Dahlheim *et al.*, 2009), following the substantial reduction of the population by commercial whaling (Baird, 2003). Within BC, adult survival is high (0.979, 95% CI: 0.914, 0.995), and a significant increase in abundance was observed between 2004 and 2011 in Ashe *et al.* (2013), although population growth and increased search effort were confounded in that study.

Fin whale
Fin whales are listed as 'Endangered' by the IUCN, 'Threatened' in Canada's Pacific region (COSEWIC, 2005) and 'Imperilled' in BC. Fin whales are found across the world's oceans, largely in offshore waters and less so in warm tropical regions (Reilly *et al.*, 2008a). Historical records reveal that fin whales were once one of the most abundant and heavily exploited marine mammals in the inshore waters of BC (Gregr *et al.*, 2000). Since the 1975 North Pacific estimate of roughly 17,000 animals, down from an estimated 44,000 that preceded intensive commercial whaling, survey data have been too insufficient to generate regional abundance estimates (Reilly *et al.*, 2008a). However, in the waters of western Alaska and the central Aleutian Islands, Zerbini *et al.* (2006) found a 4.8% annual rate of increase by comparing survey information from 1987 with 2001–03 surveys.

Killer whale
Found throughout the world's oceans, killer whales are listed by the IUCN as 'Data Deficient' (Taylor *et al.*, 2008). In BC, three ecotypes of killer whale have been identified (with 2006 population estimates based on photo-identification): (1) 261 Northern Residents (Ellis *et al.*, 2011) and 85 Southern Residents; (2) 243 West Coast Transient; and (3) Offshore (>288; COSEWIC, 2008). All of these populations are classified as 'Threatened' within Canadian waters, with the exception of the Southern Residents, which are listed as 'Endangered' (COSEWIC, 2008). In general, these populations feed on different prey, are reproductively isolated, and are genetically distinct (Ford *et al.*, 2009). Individuals are usually identified by dorsal fin morphology and relationships between individuals are often known, particularly with killer whales. The residents feed on fish (especially Chinook salmon), whereas transients prey on marine mammals. The more recently discovered and far less understood offshore ecotype feed on sharks (Ford *et al.*, 2011) and fish (Ford *et al.*, 2009).

Common minke whale
Common minke whales are found throughout the world's oceans and are listed by the IUCN as a species of 'Least Concern'. Population sizes for parts of the Northern Hemisphere are estimated at over 100,000 animals (Reilly *et al.*, 2008b). In Canada they are considered 'Not At Risk', but this assumes a potential rescue effect from whales in adjacent US or international waters. Without information on stock structure, it is conceivable that BC's common minke whales constitute a naturally small population.

Harbour seal
Harbour seals inhabit the temperate and polar coastal areas of the Northern Hemisphere with a global population estimated between 350,000 to 500,000 individuals (Thompson and Härkönen, 2008). The species is listed by the IUCN as 'Least Concern' and considered 'Not At Risk' in Canada. Following population reduction by commercial harvesting and subsequent predator control programmes, the British Columbia population of harbour seals appears to have recovered; the abundance of harbour seals in BC waters (including west coasts of Vancouver Island and Haida Gwaii, which are beyond our study area) is estimated at 105,000 animals (1966–2008; Olesiuk, 2010).

Steller sea lion
Steller sea lions inhabit the coastal waters of the North Pacific and are listed as 'Near Threatened' by the IUCN and as a species of 'Special Concern' in Canada. Recognised as 'Imperilled' and/or of 'Special Concern' in BC, the provincial breeding population is estimated to be 20,000–28,000 animals in 2006 (Fisheries and Oceans Canada, 2008), out of a total estimated Eastern Pacific population of between 46,000 and 58,000 animals (Fisheries and Oceans Canada, 2011). Although the population is increasing in BC, Steller sea lions breed at only four known locations in BC which makes them vulnerable to disturbances at these locations (e.g., oil spills), and unexplained population declines have occurred (e.g., 2002; Fisheries and Oceans Canada, 2011).

Northern elephant seal
Considered by the IUCN as a species of 'Least Concern', listed as 'Not at Risk' in Canada and as 'Not Applicable' within British Columbia, elephant seals have recovered from near extinction from historic hunting. Elephant seals are found throughout the northeastern Pacific and their population is estimated at around 171,000 (2005; Campagna, 2008). Their at-sea distribution and habitat preferences are very poorly described in BC.

METHODS

Survey design

Systematic surveys maximised coverage and minimised off-effort time over four strata (Fig. 1) for the purposes of design-based multi-species density estimation as seen in Thomas *et al.* (2007). Zigzag configurations were applied over the open strata (1) and (2), with sub-stratification for the more topographically complex strata (2). For the narrower strata (3) and (4), parallel lines oriented perpendicular to the long axis reduced edge effects. The four inlet strata were further subdivided into primary sampling units (PSUs) so that for a given season, a random sub-sample of PSUs was selected for surveying (Table 2). To estimate density, effort-weighted means were used for all strata, except stratum (4), which was derived from the un-weighted mean of the PSUs. Detailed survey design and strata are described in Thomas *et al.* (2007) and Williams and Thomas (2007).

Field methods

Field methods have been previously described in detail by Williams and Thomas (2007), but are summarized here. Two vessels were used to collect survey information. The 21m motorsailor *Achiever* was used in 2004, 2006, 2007, and

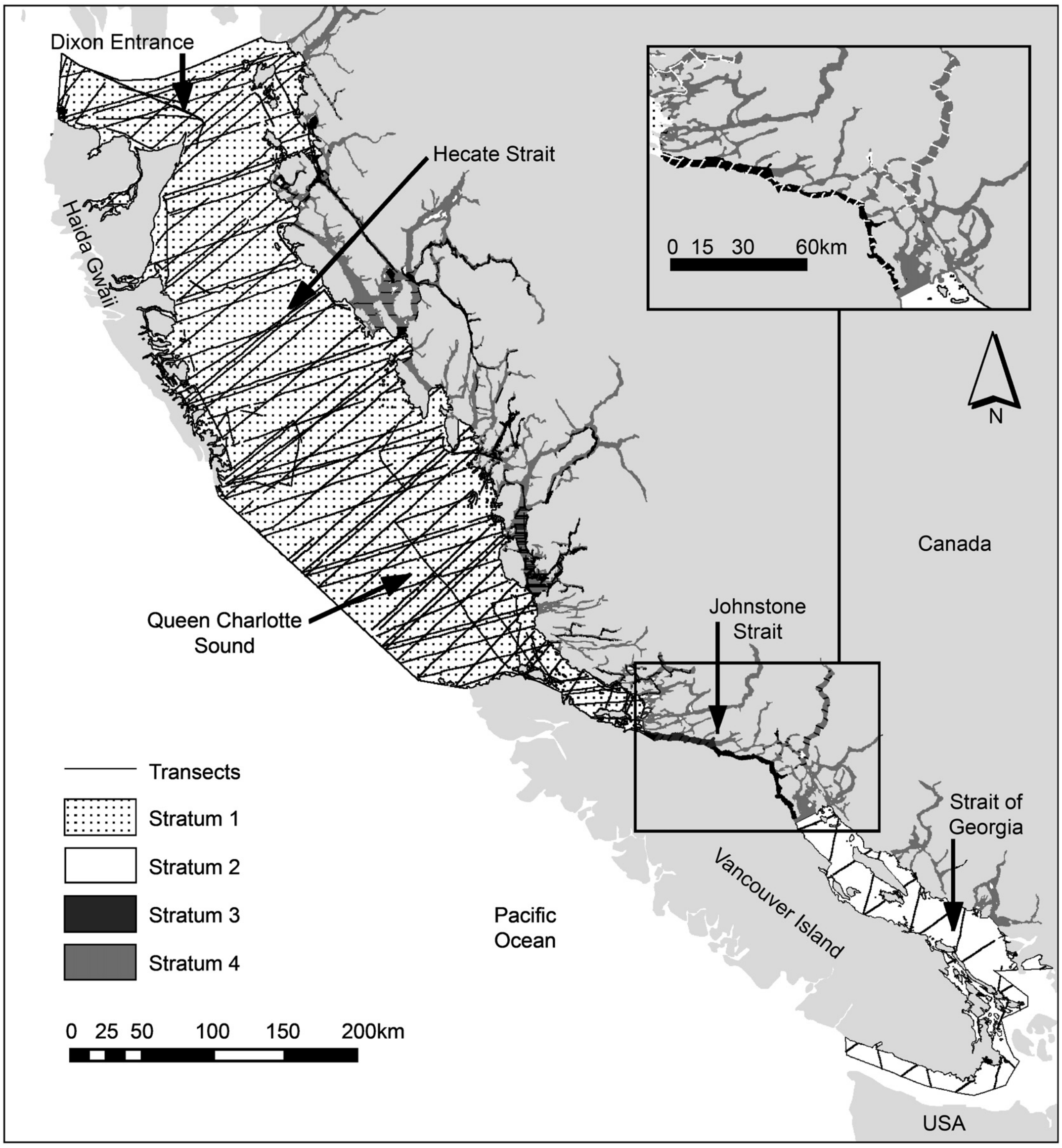

Fig. 1. Stratum identification and on-effort transects, including transit legs, between design-based transects (2004–2008) corresponding to Queen Charlotte Basin (Stratum 1), Straits of Georgia and Juan de Fuca (Stratum 2), Johnstone Strait (Stratum 3) and mainland inlets (Stratum 4) of coastal British Columbia.

2008 and the 20m powerboat, *Gwaii Haanas*, was used in 2005. Vessels actively surveyed at a relatively constant 15kmh^{-1}. On both survey vessels, observer eye height was approximately 5m. On *Achiever*, a platform was constructed over the boom and main cabin to allow for unobstructed sightings (with the exception of the mast, but observers were placed as far port and starboard to see past the mast).

A rotating group of six individuals primarily served as the observation team, although this number ranged from four to seven. A port and starboard observer searched the vessel's path, each person responsible for a sector that ranged from 30° on one side of the trackline to 90° on the other side but concentrating most of their effort on the trackline (0°). The use of two observers positioned at port and starboard also addressed any issues arising from the obstruction of sightings due to the mast. Observers used 8 × 50 and 7 × 50 binoculars to scan the area. A third team member was positioned between the observers; this individual recorded data when a sighting was made and assisted in identification and data collection. Sighting information was relayed by the data collector to a fourth team member (the computer operator) located inside the vessel. The vessel's Global Positioning System (GPS) was connected to the survey computer that logged the vessel's position every 10 seconds, using *Logger 2000* software (developed by International Fund for Animal Welfare). In addition to sightings information and position, environmental conditions were recorded every 15min, or sooner if conditions were changeable. Environmental conditions recorded were: Beaufort sea state; cloud cover percentage; precipitation; and a ranking code based on overall sightability. The fifth team member functioned as deck hand, to assist as required and the sixth team member held a rest position. Positions rotated every hour and observer identity was recorded.

Sighting information was relayed by the data recorder to the computer operator via a two-way radio or by direct verbal communication. Two angle boards mounted to the port and starboard were used to measure the radial angle to the marine mammal school. Radial distance to the school was measured using: 7 × 50 reticle binoculars; a perpendicular sighting

Table 2

Realised survey effort by year and strata for line transect surveys of British Columbia's coastal waters. Note the sample unit for stratum 4 is based on primary sampling units (PSU), not number of transects.

Stratum/location	PSU	Year	Season	Length (km)	Number of transects	Area (km^2)
1: Queen Charlotte Basin		2004	Summer	1,672	17	62,976
		2005	Summer	1,693	18	
		2006	Summer	605	9	
		2007	Spring	1,694	17	
			Autumn	897	13	
		2008	Summer	1,692	17	
2: Strait of Georgia		2004	Summer	479	24	8,186
3: Johnstone Strait		2005	Summer	74	29	420
4: Mainland inlets						11,965
	4	2004	Summer	24		
	10			84		
	17			47		
	21			98		
	29			79		
	17	2006	Summer	44		
	21			104		
	7	2007	Spring	49		
	13			39		
	17			32		
	21			119		
	23			13		
	7	2007	Autumn	51		
	13			39		
	17			33		
	21			123		
	23			13		
	8	2008	Summer	20		
	14			46		
	17			30		
	21			125		
	25			39		

gauge; a laser range finder; or by a visual estimate. For each school the following information was recorded: radial distance; radial angle; species; school size; behaviour (travel, forage, avoid, approach, breach, unknown and other); cue type (body, blow, seabird activity); and heading relative to the ship (profile, head-on, tail-on or uncertain). Off-transect data (e.g., when the vessel was re-positioning for another transect) were routinely collected while still actively observing (i.e., on-effort). This information was used to increase sighting number for detection functions but was not used in calculating encounter rate for the CDS density estimates. Density surface models were not constrained by the need to maximise coverage and did not limit detections to on-transect data, so off-transect on-effort data were used in modelling encounter rate (Miller *et al.*, 2013; Williams *et al.*, 2011b).

Data analysis and abundance estimation using conventional distance analysis

Data were analysed in the program *Distance* version 6 Beta 3 (Thomas *et al.*, 2010). CDS was used to generate marine mammal abundance estimates (Buckland *et al.*, 2001). This approach replicates the methods of Williams and Thomas (2007) for the entire 2004–08 survey to generate new and revised abundance estimates for 10 marine mammals inter-annually and for novel seasons. During the 2006 survey, observer effort within the inlet stratum 4 was not part of a designed survey and only included effort while on passage, so these data were excluded from the estimation of abundance estimates. Abundance was estimated as the density of animals multiplied by the applicable study area or stratum. To estimate density ($\hat{D}$), the following formula was used:

$$\hat{D} = \frac{n\hat{s}}{L2w\hat{p}}$$

Where the encounter rate (*n/L*) or number of schools seen (*n*) over the length of the transect (*L*), is multiplied by twice the truncation distance (*w*) to obtain an area and the estimated school size ($\hat{s}$). In line transect surveys, the probability of detecting a school decreases with increase in distance. Accounting for this probability of detection ($\hat{p}$) helps to form the basis of CDS by fitting a detection function (Buckland *et al.*, 2001).

Detection functions were estimated using the software *Distance*, which can apply several key functions (uniform, half-normal or hazard rate) and series expansion terms (polynomial or cosine) to estimate the shape of the function. The observers recorded radial distance (*d*) and angle (θ) during the field surveys. These relative values are then converted to perpendicular distance from the trackline using simple geometry, $sin(\theta) \times d$. All on-effort sightings (i.e., periods when the observers were actively observing for animals), including off-transect observations, were used for detection model fitting. Models that minimise the Akaike Information Criterion (AIC) score were generally selected, which provides an explanation of deviance while penalising the addition of terms to achieve the most parsimonious model (Akaike, 1974). In addition, the Kolmogorov-Smirnov goodness-of-fit test was employed to provide a measure of agreement between the model and the data (Buckland *et al.*, 2004). If species exhibit an attraction to the survey vessel, then a spike is typically seen near the trackline, which can cause positive bias in the density estimates. Observations were truncated to within the perpendicular distance (w) used in Williams and Thomas (2007).

These detection functions all assume certain detection on the trackline, meaning $g(0) = 1$. A probability of availability is typically divided by the density to account for the fact that marine mammals are often below the water surface and not detected even when directly on the trackline of the vessel. Estimating this probability requires tracking of individuals to estimate proportion of time spent underwater (e.g., Laake *et al.*, 1997) or multiple platforms of simultaneous, independent observation. The research vessel was not large enough to offer two platforms for isolated observers, and $g(0)$ could therefore not be estimated. Due to this factor, the abundance estimates developed will underestimate the true population size, but the estimates should be consistent over the years the study took place, thereby allowing trends to be examined.

School size bias was estimated in *Distance* using the default CDS method. The natural logarithm of group size is regressed on the probability of detection and the value of *ln*() at zero distance is back-transformed to obtain the expected school size (E(s)).

Abundance estimates using\ density surface modelling (DSM)

Spatial patterns in animal density were modelled using a suite of geographic and environmental predictors (Density Surface Modelling (DSM); Miller *et al.*, 2013). This technique was performed using the software program *Distance* (Buckland *et al.*, 2004), which relies on a Generalised Additive Models (GAM) to associate environmental variables to the rate of encounter. This approach has the potential to improve precision of the final estimate (De Segura *et al.*, 2007) and can be used to identify areas of high animal density that may inform spatial management of natural resources. Because DSM methods do not require systematic or random sampling of the survey region (i.e. uniform coverage of the transects), they have the additional benefit of allowing inclusion of effort and sightings data when observers were on-effort but off-transect (i.e. 'transit-leg' segments).

Transects were segmented into one nautical mile (1,852m) in order to be at a scale relative to the underlying environmental data (Miller *et al.*, 2013). The response variable in this analysis is the estimated number of schools encountered per segment i, $\hat{N}_i$, given by the Horvitz-Thompson estimator (Horvitz and Thompson, 1952):

$$\hat{N}_i = \sum_{j=1}^{n_i} \frac{1}{\hat{p}_{ij}}, i =, \ldots, v \ .$$

Here, the inverse of the detection probability ($\hat{p}$) for the j^{th} detected school in the i^{th} segment is summed across all detected schools n_i, per segment. Data was then merged to segments without sightings ($N = 0$), so a GAM was fitted using the quasi-Poisson distribution and a logarithmic link function to relate N to the environmental predictor variables:

$$\hat{N}_i = \exp\left[\alpha + \sum_{k=1}^{q} s_k(z_{ik}) + \log(a_i)\right] + e_i$$

Here, the predictor variables, z_{ik} are fitted by a smoothing function s_k, and subsequently summed with intercept α and an offset a_i, which represents the segment's area ($2wL_i$). The estimation of the smoothing function was performed by the R library MGCV (Wood, 2001).

Once the model was fitted to the observed environmental conditions, a prediction was made over the entire study area based on a single period of the input environmental data (z). So far the response $\hat{N}$ is the number of schools detected over the area, or the school density. To obtain an estimate of abundance ($\hat{A}$), we must then multiply by the estimated school size ($\hat{s}$).

Variance on the abundance estimate is calculated using the Delta method (Seber, 1982) to combine the variance of the school density ($CV(\hat{N})$) with the detection function ($CV(\hat{p})$) and the mean school size ($CV(\hat{s})$):

$$\hat{A} = \sum_{i=1}^{n} \hat{N}_i$$

$$CV(\hat{A}) = \sqrt{CV(\hat{p})^2 + CV(\hat{N})^2 + CV(\hat{s})^2}$$

To estimate variance of just $\hat{N}$ (e.g., CV($\hat{N}$) term above), the *Distance* software historically used a moving block bootstrap resampling technique. Even for only 400 replicates, this technique can be very time consuming and frequently failed before reaching completion. As an alternative, the coefficients and variance from the fitted model were used to simulate predictions were generated using a multivariate normal sampler on the Bayesian posterior covariance matrix. From these simulated predictions confidence intervals were extracted. This method is described by Wood and Augustin (2002) and in the *R* documentation for the predict.gam function and has since been incorporated (in principle) into the latest density surface modelling variance estimation software under development[7].

The set of covariates used in the final model are selected to explain the greatest deviance while minimising unnecessary addition of parameters. Many criteria exist that weight these two factors against each other (e.g., AIC). For GAMs that have a dispersion term, as with the quasi-Poisson response dispersion used in these models, the lowest Generalised Cross-Validation (GCV) value is the preferred model selection tool (Wood *et al.*, 2008). The number of knots that govern the degree of smoothing, are further reduced in most of these models by using the non-default thin-plate spline with shrinkage (basis = 'ts') function, which adds a small penalty to additional knots, so that the whole term can be shrunk to zero, removing any contribution from the predictor. Term plots were inspected and any terms with confidence bounds spanning zero were removed to allow the process to test for a model with a lower GCV score. Models would sometimes fail to converge using this approach. In this situation, attempts were then made to limit the possible number of knots to five and to implement the default thin-plate spline (tp) without the shrinkage term. In addition to environmental covariates, the longitude-latitude bivariate term provided a spatial estimator, which can act as a proxy for unmeasured variables that influence hotspots not accounted for by the other predictors. Categorical variables

[7] *See: https://github.com/dill/dsm/blob/master/R/dsm.var.gam.R.*

such as season (summer, autumn, or spring) and inlet (in or out) were also tested using this approach.

Density surface model detection functions

The detection functions generated using CDS could not be reused for estimating $\hat{p}$ because the DSM module in the software program *Distance* is only compatible with the multiple covariate distance sampling (MCDS) function available through the mark recapture distance sampling (MRDS) R library, which at the time of the analysis only allowed for half-normal (hn) and hazard rate (hr) key functions. Based on the CDS analysis, the same truncation distances were used with the half-normal key function, unless a hazard rate model was used. The logic of this process is that as the school size increases, it should become easier to detect. This was accounted for by adding a covariate of size with detection function, which is possible with the MCDS function and not with CDS approach. When the use of size covariate was not possible, the detection function was chosen during our CDS model selection.

Environmental variables

The manipulation of spatial data was performed with ESRI ArcGIS 9.2 using the Spatial Analyst toolbox (ESRI 2009). Midpoints of the transect segments were used to extract the values of the environmental layers and then sampled for use in the GAM. To predict the seascape with the fitted model, a 5km prediction grid was generated using the NAD 83BC Environment Albers projection to correspond with the available environmental data. The raster grid was converted to a polygon vector layer and the cells were clipped to the coastline and strata areas. The areas were calculated per cell to be used as the offset value during prediction. The centroid location of each cell was used to extract values from the environmental layers.

Static environmental variables included bathymetric depth, slope, and distance to shore. Latitude and longitude were used as separate variables and as a co-varying term. Shoreline data were extracted from the Global Self-consistent, Hierarchical, High-resolution Shoreline (GSHHS) database (Wessel and Smith, 1996). Bathymetry data were extracted from the SRTM30 Plus 30-arc second resolution dataset (Becker *et al.*, 2009). Euclidean distance from shore and the local slope of the bathymetry surface were calculated in ArcGIS. The log of these predictors was tested in cases for which model convergence with a GAM was otherwise prohibitive.

The marine environment is highly dynamic, requiring the capture of this variability over the survey periods to build more temporally meaningful models. These models represent proxies for physiological or biological constraints (e.g., sea surface temperature) and prey patterns (e.g., primary productivity) associated with the species. However, attempts to incorporate dynamic variables, such as sea surface temperature (SST) and Chlorophyll *a* (Chl*a*), into the predictive model proved unsuccessful. Due to the continuous cloud cover experienced and the nearness to shore, sufficient satellite data matched to the specific observation periods of this analysis were not available for this study. After spatially interpolating these data with kriging and summarising inputs across seasons, it was still found that none of the DSM models with these dynamic data outperformed the environmentally static models that were to be chosen in the final model selection. Consequently, all subsequent analyses considered only the static variables described above as candidate covariates.

RESULTS

Survey effort

On-effort transects for the surveys (2004–08) occurred in the open waters of Queen Charlotte Basin (stratum 1), Strait of Georgia (stratum 2), Johnstone Strait (stratum 3) and mainland inlets (stratum 4; Fig. 1). Realised transect effort, in terms of kilometres covered, varied by stratum and year (Table 2). A number of complete transects in stratum 1 were cancelled in autumn 2007, due to extremely poor weather conditions and portions of transects that occurred in US waters in stratum 2 (2004) were cancelled due to transboundary permitting reasons. In addition, several small transect segments were excluded due to being non-navigable by the survey vessels and/or poor environmental conditions.

Sightings

Ten species were sighted with sufficient frequency for analysis (Fig. 2). The final detection models (Figs 3 and 4) and associated information for CDS and DSM were generated (Tables 3 and 4). School sighting information was also generated (Table 5). Species abundance and density estimates with 95% confidence intervals (CIs) and percentage coefficient of variation (%CV) were calculated across all surveys and strata using CDS (Fig. 5 and online supplement for detailed information).

Responsive movement can be a problem, in terms of both avoidance or attraction, but analyses to date suggest the field protocols generally allowed observers to search far enough ahead of the vessel to record distance and angle prior to responsive movement occurring. Using methods described by Palka and Hammond (2001), Williams and Thomas (2007) examined data on swimming direction of animals for evidence of responsive movement and found that only Pacific white-sided dolphins approached the boat before being detected by observers. A greater proportion of approaching behaviour for Dall's porpoise and prominent spike in the data warranted similar methods for coping with responsive movement in this study, namely not fitting the spike near zero. For all other species, no evidence for responsive movement was found, and was therefore ignored in the analysis.

Harbour porpoise

Combining all surveys, 128 harbour porpoise groups were sighted (Table 3). This species was distributed widely across the northern and southern extents of the study area, and were more common in nearshore and inlet waters (Fig. 2). Most (122/128 = 95%) exhibited travelling/foraging behaviour, with the remaining two feeding and two avoiding; no obvious response to the observer vessel is indicated with these data.

Restricting the observations to a truncation distance of 600m excluded 10 observations, or 8% of the sightings

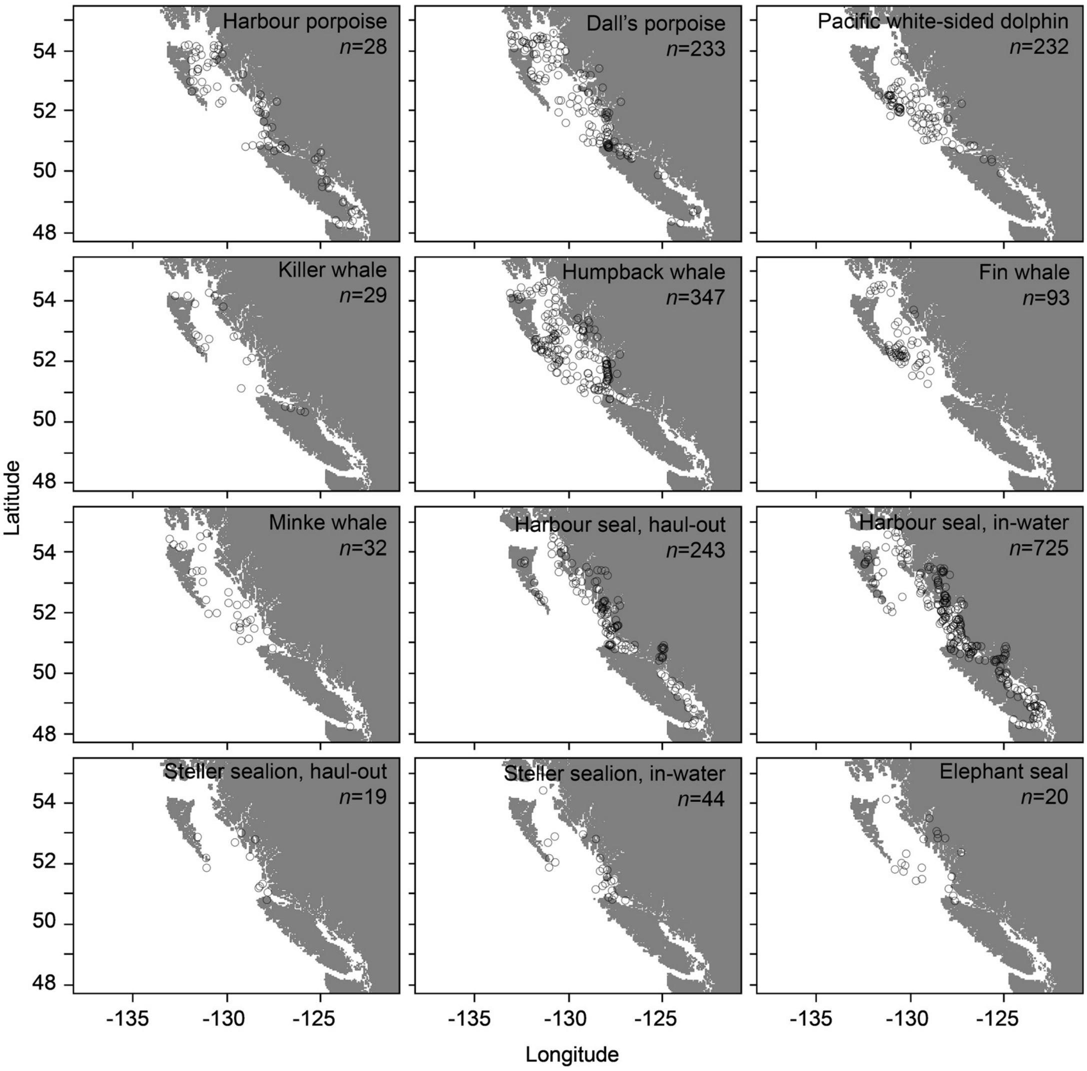

Fig. 2. Sightings of ten marine mammal species from surveys of British Columbia's coastal waters in summer 2004, 2005 and 2008 and spring and autumn 2007.

(Table 3). The preferred detection function was the hazard rate model with no adjustment terms (Table 3). The data show a spike near zero (Fig. 3). These spikes are typically linked with attractive movement, but none was noted in the field or in the data collected on behaviour or orientation relative to the ship, so alternate models that ignored the spike were not considered. The steeply declining detection function is likely to accurately reflect the cryptic nature of this species; that is, observers really did cover only a narrow strip for this species. All the other models tested with higher AIC values produced smoother fits than the data or the hazard rate model, which produced a higher $\hat{p}$ and lower abundance estimate. For example, the next lowest-AIC model (ΔAIC = 8.53), uniform with five cosine adjustments, produced a $\hat{p}$ 41% larger (0.284 vs. 0.201).

Dall's porpoise

Of the 239 Dall's porpoise school sightings (Table 3), most occurred in the offshore waters of the northern and southern portions of the Queen Charlotte Basin with relatively few schools within the inlets or the southern straits (Fig. 2). Whereas most observations (212/239 = 88.7%) were travelling/foraging, a small proportion (11/239 = 4.6%) were approaching and the same number feeding. Other behaviours included socialising (2/239 = 0.8%), avoidance (1/239 = 0.4%), and unknown (2/239 = 0.8%).

A truncation distance of 700m excluded 18 observations, or 8% of the observations, from model fitting. The hazard rate function with one cosine adjustment fit the data best according to the AIC criteria, but exhibited a sharp spike near zero. Given that a small proportion of Dall's porpoise were recorded with attractive behaviour and are known to bow-ride (including our survey vessel), we believe that the spike near zero reflects responsive movement. Following Williams and Thomas (2007), we chose a half-normal model with two cosine adjustments having the next lowest AIC (ΔAIC = 7.02). Turnock and Quinn (1991) also found that a half-normal model corrected most for the attractive movement, using simulations and data from Dall's porpoises in Alaska. The half-normal model for Dall's porpoise detection was also chosen by Williams and Thomas (2007), except the approaching behaviours were less numerous (2/11 = 18% versus 11/239 = 4.6%) which presumably contributed to not having to override the AIC selected hazard rate model with the half-normal. To further quantify a correction factor, a secondary platform of observation is recommended but that could not be accomplished on our survey vessel.

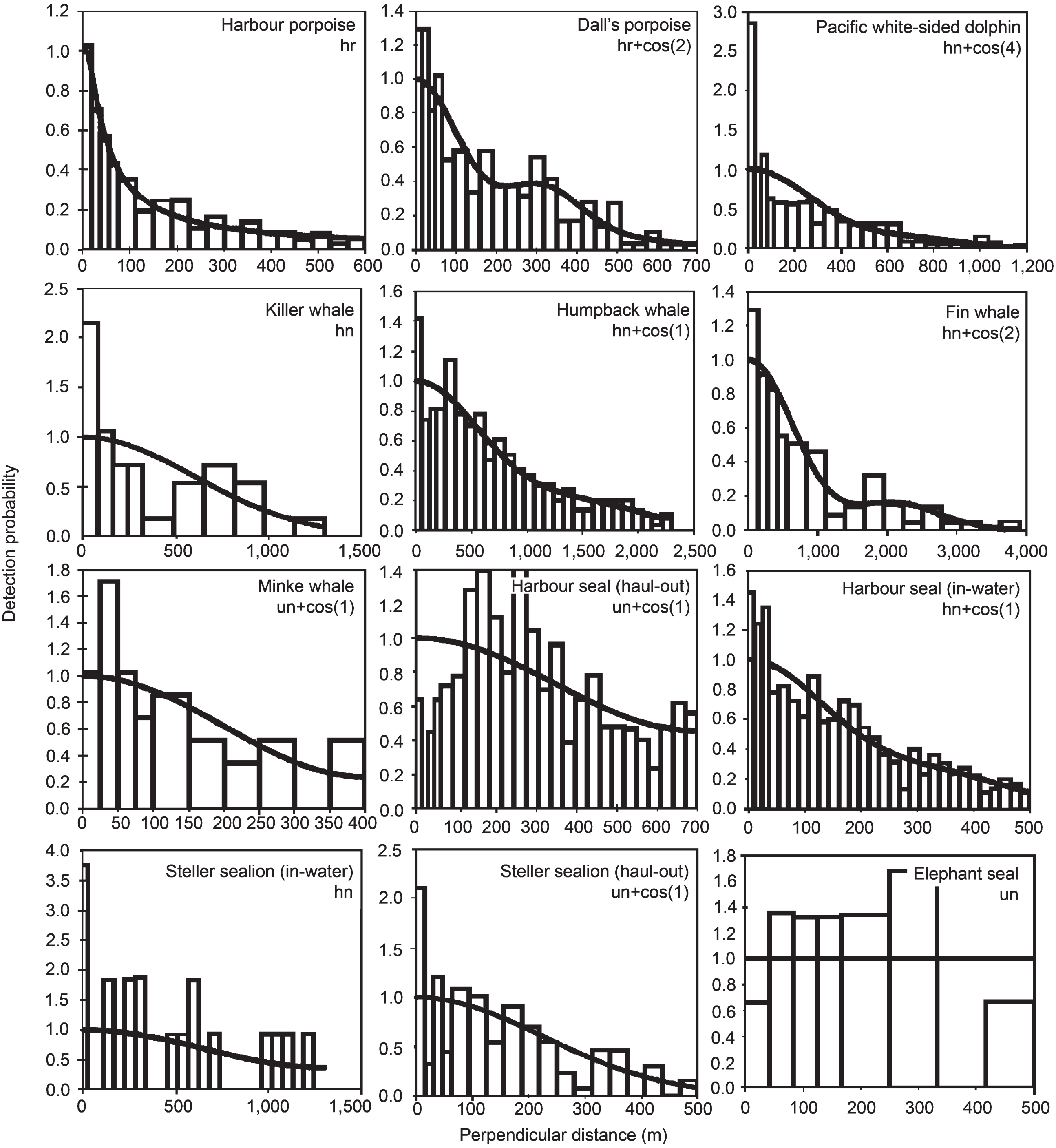

Fig. 3. Detection functions for marine mammal species generated using Conventional Distance Sampling (CDS) analysis for coastal British Columbia 2004–08 surveys.

Pacific white-sided dolphin

Of the 233 schools of Pacific white-sided dolphin, most were seen throughout the southern portion of the Queen Charlotte Basin, particularly near Haida Gwaii, with several additional sightings in the inlets and northern end of the southern straits (Fig. 2). This species exhibits the strongest approaching behaviour (47/233 = 20.2%). Other behaviours include: travelling/foraging (151/233 = 64.8%); feeding (18/233 = 7.7%); breaching (13/233 = 6%); socialising (1/233 = 0.4%); avoidance (1/233 = 0.4%); and uncertain (2/233 = 0.8%).

Using a truncation distance of 1,200m (Table 3), the lowest AIC values were achieved with a hazard rate model, which followed the spike of the data near zero distance. To minimise the bias of attractive movement, the model with the 2nd lowest AIC (ΔAIC = 23.89) was achieved with a half-normal model with four cosine adjustments to avoid fitting the spike (Fig. 3). This is a similar strategy for model selection as used with Dall's porpoise.

Humpback whale

The highest number of cetacean school sightings (n = 352) was attributed to humpback whale (Table 3). These sightings occurred exclusively in Queen Charlotte Sound and inlets, but not in the southern straits (Fig. 2). Most sightings were in deep water, with some preference towards the southern Haida Gwaii region and the southeastern portion of Queen

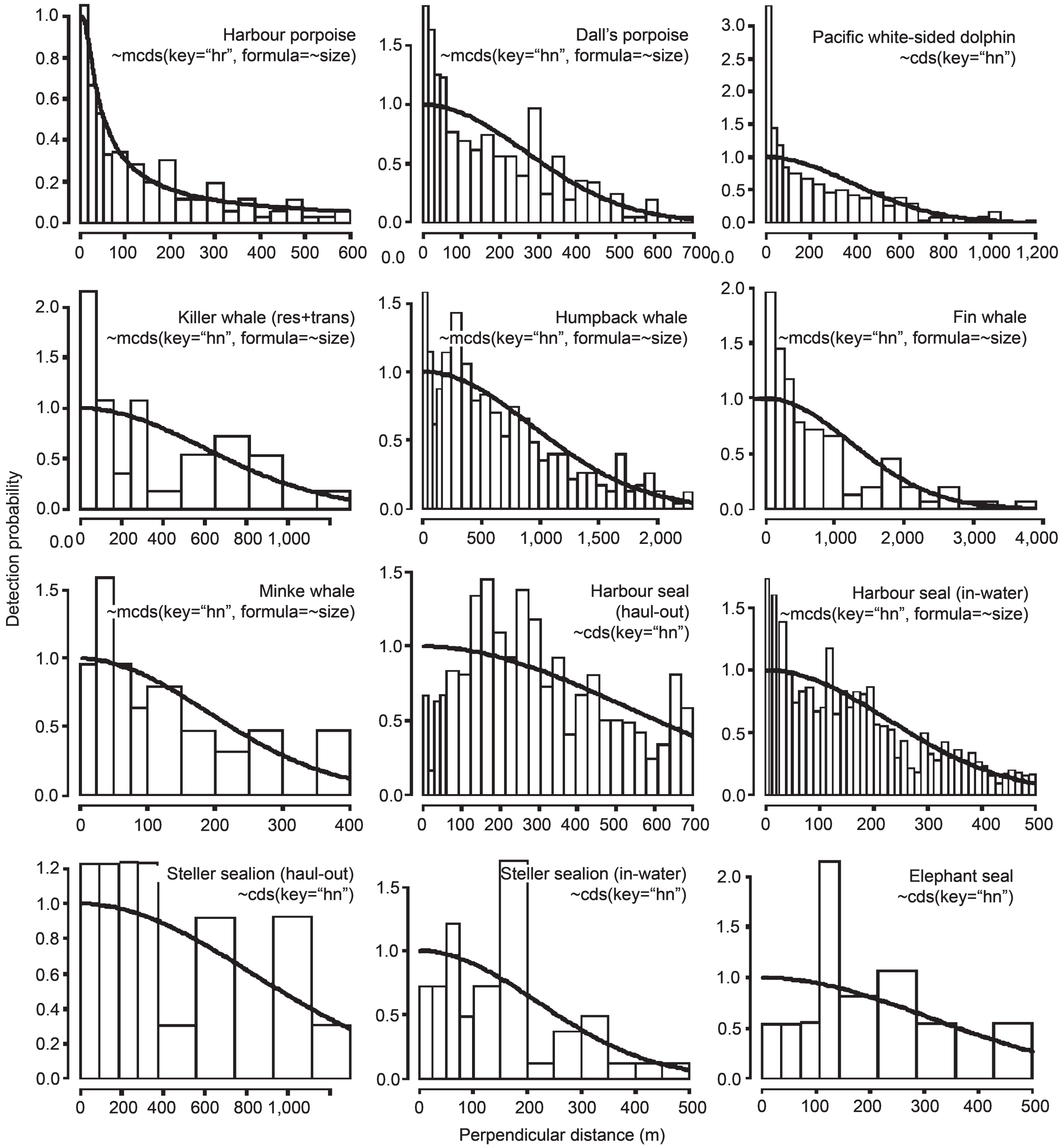

Fig. 4. Average detection probabilities for Density Surface Modeling (DSM) using the Multiple Covariates Distance Sampling (MCDS) engine with the covariate size where possible, otherwise using Conventional Distance Sampling (CDS) without a covariate. The detection function uses either a half-normal (hn) or hazard rate (hr) key functions. Marine mammal sighting information was obtained from line transect surveys in coastal British Columbia (2004–08).

Charlotte Sound. Only one observation was noted for approaching behaviour (1/352 = 0.2%) and the rest included: travelling/foraging (265/352 = 75.3%); feeding (41/352 = 11.6%); breaching (25/352 = 7.1%); socialising (3/352 = 8.5%); and unknown (5/352 = 1.4%). Using a 2,300m truncation distance, the lowest-AIC model selected used a half-normal model with one cosine adjustment term (Fig. 3).

Fin whale

All of the 91 school sightings of fin whale were found in the Queen Charlotte Basin, with the exception of two observations in Grenville Channel, located on the North Coast of BC (Fig. 2). Most offshore sightings were located off southeastern Haida Gwaii, with another large cluster of sightings in the northern portion of the Sound (Fig. 2). The behaviours of sightings include: travelling/foraging (73/91 = 80.2%); feeding (3/91 = 3.3%); socialising (1/91 = 1.1%); and other/uncertain (4/91 = 4.4%). A 3,900m truncation distance was applied (Table 3). The hazard rate model obtained the lowest AIC, but exhibited a spike near zero, so a half-normal model with two cosine adjustment terms (ΔAIC = 1.4) was used instead (Fig. 3).

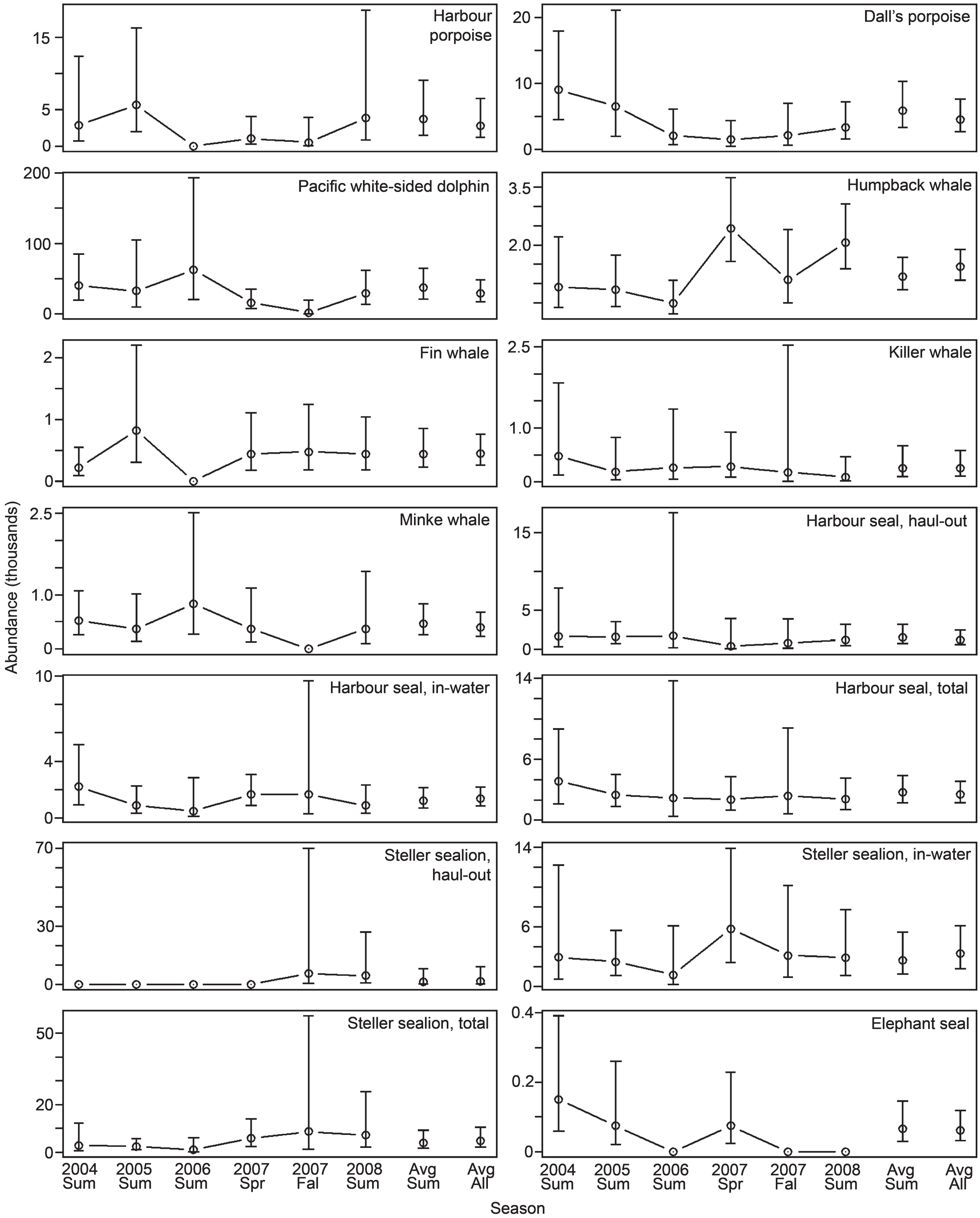

Fig. 5. Abundance estimates with 95% confidence intervals generated using Conventional Distance Sampling (CDS) over surveyed years and seasons in stratum 1 only, including the average of all seasons. Summer averages are included for seasonal comparison with 2007 autumn and spring in coastal British Columbia.

Killer whale

At 29 school sightings, the killer whale is the least frequently seen of the whale species analysed (Table 3). Most targeted killer whale studies differentially treat the ecotypes (Zerbini *et al.*, 2006), but data constraints forced the grouping of the resident, transient, and offshore types together for this analysis. Most sightings occurred in the Queen Charlotte Basin and Johnstone Strait, most commonly in the nearshore (Fig. 2). Observed behaviours include: travelling/foraging (24/29 = 82.7%); feeding (2/29 = 6.7%); socialising (1/29 = 3.4%); and other (2/29 = 6.7%). A truncation distance of 1,300m was applied to provide a monotonically decreasing tail, while retaining as many observations as possible (25/29 = 86%). A hazard rate model best fit these data, but to offset

Table 3

Detection function summary statistics using Conventional Distance Sampling (CDS) for marine mammal species surveyed in coastal British Columbia (2004–08). Truncation distance (w) with number of sightings (n) before and after truncation. Model described by key function (hazard-rate (hr), half-normal (hn), or uniform (un) with optional series expansion terms (polynomial (poly), or cosine (cos)). The p-value for the goodness-of-fit Kolmogorov-Smirnov (K-S), and the final probability of detection ($\hat{p}$) and its percent coefficient of variation (%CV ($\hat{p}$)).

Common name	w(m)	n before	n after	Model	K-S p	$\hat{p}$	%CV ($\hat{p}$)
Harbour porpoise	600	128	118 (–8%)	hr	0.899	0.201	24.29
Dall's porpoise	700	239	221 (–8%)	hn + cos(3)	0.190	0.344	9.86
Pacific white-sided dolphin	1,200	233	219 (–6%)	hn + cos(4)	0.001	0.253	8.63
Humpback whale	2,300	352	325 (–8%)	hn + cos(1)	0.951	0.421	6.43
Fin whale	3,900	91	82 (–10%)	hn + cos(2)	0.375	0.270	11.01
Killer whale	1,300	29	25 (–14%)	hn	0.302	0.558	16.71
Minke whale	400	32	29 (–9%)	un + cos(1)	0.641	0.620	13.81
Harbour seal (haul-out)	700	244	212 (–13%)	un + cos (1)	0.326	0.728	6.69
Harbour seal (in-water)	500	774	732 (–5%)	hn + cos (1)	0.030	0.477	4.74
Steller sea lion (haul-out)	1,300	20	17 (–15%)	un + cos (1)	0.639	0.686	21.57
Steller sea lion (in-water)	500	123	114 (–7%)	hn	0.047	0.548	7.71
Elephant seal	500	20	18 (–10%)	un	0.572	1.000	0.00

Table 4

Generalised Additive Model (GAM) formulation with truncation distances (w) and distance model type (Detection) for given stratum with generalized cross-validation score (GCV), deviance explained (DE) and GAM model terms for marine mammals surveyed in coastal British Columbia (2004–08). The Detection function is indicated by the key function of either hazard rate (hr) or half-normal (hn).

Common name	w	Detection	Strata	GCV	DE (%)	GAM model terms
Harbour porpoise	600	hr	1–4	0.486	25.6	lon,lat + depth + distcoast + slope + season + inlet
Dall's porpoise	700	hn	1–4	0.345	19.1	lon,lat + depth + distcoast + slope + season + inlet
Pacific white-sided dolphin	1,200	hn	1–4	0.377	33.4	lon,lat + depth + distcoast + slope + season + inlet
Humpback whale	2,300	hn	1	0.521	19.0	lon,lat + depth + distcoast + slope + season
			4	0.265	11.0	depth† + distcoast† + slope†
Fin whale	3,900	hn	1–4	0.145	41.8	lon,lat + depth + distcoast + slope
Killer whale (all ecotypes)	1,300	hn	1–4	0.040	39.5	lon,lat†
Minke whale	400	hn	1–4	0.045	32.5	lon,lat + depth + distcoast + slope
Harbour seal (haul-out)	700	hn	1–4	0.188	35.6	lon,lat + depth + distcoast + slope + season + inlet
Harbour seal (in-water)	500	hn	1	0.157	43.4	lon,lat + depth + distcoast + slope + season
			2–4	1.366	23.9	lon,lat + depth + distcoast + slope + inlet
Steller sea lion (haul-out)	1,300	hn	1–4	0.025	26.5	log(depth)* + distcoast* + log(slope)*
Steller sea lion (in-water)	500	hn	1–4	0.062	47.1	lon,lat + depth + distcoast + slope + inlet
Elephant seal	500	hn	1–4	0.018	51.8	lon,lat + depth + distcoast + slope + season

*Terms were limited to 5 knots. †Terms were used with a basis 'ts', which is the default thin-plate smooth but allowing for shrinkage to zero.

Table 5

Observed and estimated school sizes ($\hat{s}$) for marine mammal species from 2004–08 surveys in coastal British Columbia waters using Conventional Distance Sampling (CDS).

	Estimated school size		Observed school size		
Species	$\hat{s}$	%CV($\hat{s}$)	Mean	%CV	Maximum
Harbour porpoise	1.67	4.56	1.81	4.53	5
Dall's porpoise	2.41	4.54	2.43	5.55	15
Pacific white-sided dolphin	13.53	14.77	38.27	20.41	1,200
Humpback whale	1.51	2.79	1.57	3.75	8
Fin whale	1.78	6.86	1.99	12.73	20
Killer whale (all ecotypes)	3.67	18.26	3.80	15.27	28
Minke whale	0.99	2.36	1.03	3.33	2
Harbour seal (haul-out)	5.58	9.51	6.82	9.77	90
Harbour seal (in-water)	1.11	1.20	1.20	2.83	18
Steller sea lion (haul-out)	70.29	66.86	37.77	49.25	300
Steller sea lion (in-water)	6.11	20.31	14.41	26.89	370
Elephant seal	1	0	1	0	1

the spike near zero the half-normal model without adjustment terms (ΔAIC = 0.53) was chosen.

Common minke whale

Only slightly more frequently seen (n = 32) than killer whales is the common minke whale (Table 3). Sightings were widely distributed within Queen Charlotte Basin, generally offshore (Fig. 2). All sightings were recorded as travelling/foraging behaviour, although minke whales are at surface less than other species so detailed behaviour is often difficult to determine. Of the 32 observations only three exceeded 400m in perpendicular distance from the transect line (2,377m, 1,888m and 1,532m), so a truncation distance of 400m was used. The lowest-AIC model, a uniform model with one cosine adjustment term, was chosen in this case.

Harbour seal

The most commonly sighted of all marine mammals (n = 1,018; Table 3), harbour seals were typically sighted in nearshore waters throughout all strata (Fig. 2). They exhibited the following behaviours: travelling/foraging (701/1,018 = 68.9%); socialising (75/1,018 = 7.4%); feeding (13/1,018 = 1.3%); approaching (1/1,018 = 0.1%); and other/unknown (110/1,018 = 10.8%). Detectability is expected to vary as a function of whether the animal is in or out of water, hence the separation between in-water and haul-out observations for truncation distances and detection functions (Table 3). Roughly, one quarter of the sightings were haul-out versus three quarters in-water. For in-water observations, a truncation distance of 500m was used and the lowest-AIC model selected was a half-normal model with one cosine adjustment term (Fig. 3). For haul-out observations, a 700m truncation was used, indicative of greater visibility when out of water, and the lowest-AIC model selected was a uniform model with one cosine adjustment. The distance readings for haul-out observations exhibit a peak around 200m rather than monotonically increasing towards zero. Because most haul out sightings are to the side during along-shore transects, this off-zero peak was anticipated.

Steller sea lion

A total of 123 in-water sightings of Steller sea lions were recorded and an additional 20 on land (Table 3). All of these sightings were generally made in the nearshore and inlets of the southern Queen Charlotte Basin (Fig. 2). In-water animals appeared to exhibit slight responsiveness to the ship (avoidance: 30/123 = 24.4%; approach: 2/123 = 1.6%), otherwise found travelling/foraging (67/123 = 54.5%), socialising (10/123 = 8.1%), feeding (3/123 = 2.4%), or other/unknown (38/123 = 30.9%). For in-water observations, a 500m truncation distance was used and the lowest-AIC model selected was a half-normal model. For haul-out observations, a 1,300m truncation distance was used and the lowest-AIC model selected was a uniform model with one cosine adjustment.

Northern elephant seal

The least frequently sighted of all marine mammal species analysed (group sightings = 20; Table 3), the northern elephant seal was observed in the open waters of Queen Charlotte Basin as well as the southern and central coast inlets (Fig. 2). A 500m truncation distance was used, and the final model selected was a uniform model, which corresponds to a strip transect, i.e., density is assumed to not vary with distance from transect. In this case, there were too few observations to construct a robust distance detection function, as further evidenced by the unrealistic $\hat{p}$ value of 1 (Table 3).

Other species

Besides the marine mammals already mentioned, other species were observed during the survey, albeit too rarely to estimate abundance or without sufficient taxonomic specificity. The number of sightings broken down to season, years and strata are listed in supplementary Table 7: gray whale (*Eschrichtius robustus*; n = 7), sei whale (*Balaenoptera borealis*; n = 1; reported previously in (Williams and Thomas, 2007)), sea otter (*Enhydra lutris*; n = 36), sunfish (*Mola mola*; n = 27) and sharks (n = 106). A high-density shark aggregation was described previously (Williams *et al.*, 2010). Sea otters were excluded from assessment because relatively few observations were made and their distribution is elsewhere better described by dedicated surveys conducted by Fisheries and Oceans Canada (Nichol *et al.*, 2009).

Comparison of estimates and uncertainty

Compared with previous abundance estimates by Williams and Thomas (2007), who relied on survey data from 2004 and 2005 alone, our analyses resulted in altered abundance estimates and tighter confidence intervals, often substantially so, for all mean abundance estimates over the study region (Fig. 6) and within stratum (see online supplement). For some species, mean abundance estimates for the entire study area (Fig. 6 and online supplement) are lower than earlier estimates (Williams and Thomas, 2007): harbour porpoise (6,631 and 34.9% CV vs. 9,120 and 40.5% CV); fin whale (446 and 26.4% CV vs. 496 and 45.8% CV); and harbour seal (in-water) (10,394 and 6.5% CV vs. 13,524 and 15.3% CV). The remainder of mean abundance estimates are higher, as with Dall's porpoise (6,232 and 20.0% CV vs. 4,913 and 29.2% CV), Pacific white-sided dolphin (32,637 and 24.6% CV vs. 25,906 and 35.3% CV), humpback whale (1,541 and 12.9% CV vs. 1,313 and 27.5% CV), killer whale (308 and 38.2% CV vs. 161 and 67.4% CV), minke whale (430 and 25.2% CV vs. 388 and 26.8% CV) and harbour seal (haul-out) (7,060 and 12.9% CV vs. 5,852 and 25.9% CV). Abundance estimates for Steller sea lions and elephant seals were available in this analysis and not in Williams and Thomas (2007) due to the limited sample size generated from 2004 and 2005 surveys.

Comparing 95% confidence intervals of abundance estimates between surveys for stratum 1, we see that with one exception, all of the estimates have overlapping confidence intervals (Fig. 5 and online supplement). This suggests no significant population changes occurred over the 2004–08 sampling period. The only clearly non-overlapping confidence interval was found for humpback whales, which have the lowest estimated abundances in summer 2006 (486 and 95% CI 219–1,081) and highest estimated abundances in the following spring survey in 2007 (2,431 and 95% CI 1,577–3,747). The second highest abundance estimate was in summer 2008 (2,057 and 95% CI 1,382–3,062). Notably, summer 2006 had the least amount of realised survey effort at 605km versus nearly 1,700km for all other summer surveys. In the case of humpback whales, a simple linear trend is non-significant, either by summer surveys (p = 0.276) or inclusive of 2007 autumn and spring (p = 0.204). Nonetheless, mean abundance estimates are appreciably higher in 2007–08 compared with the earlier period of 2004–06. Bayesian methods may suit a future study having more observational data to estimate trends in population abundance (Moore and Barlow, 2011; 2013).

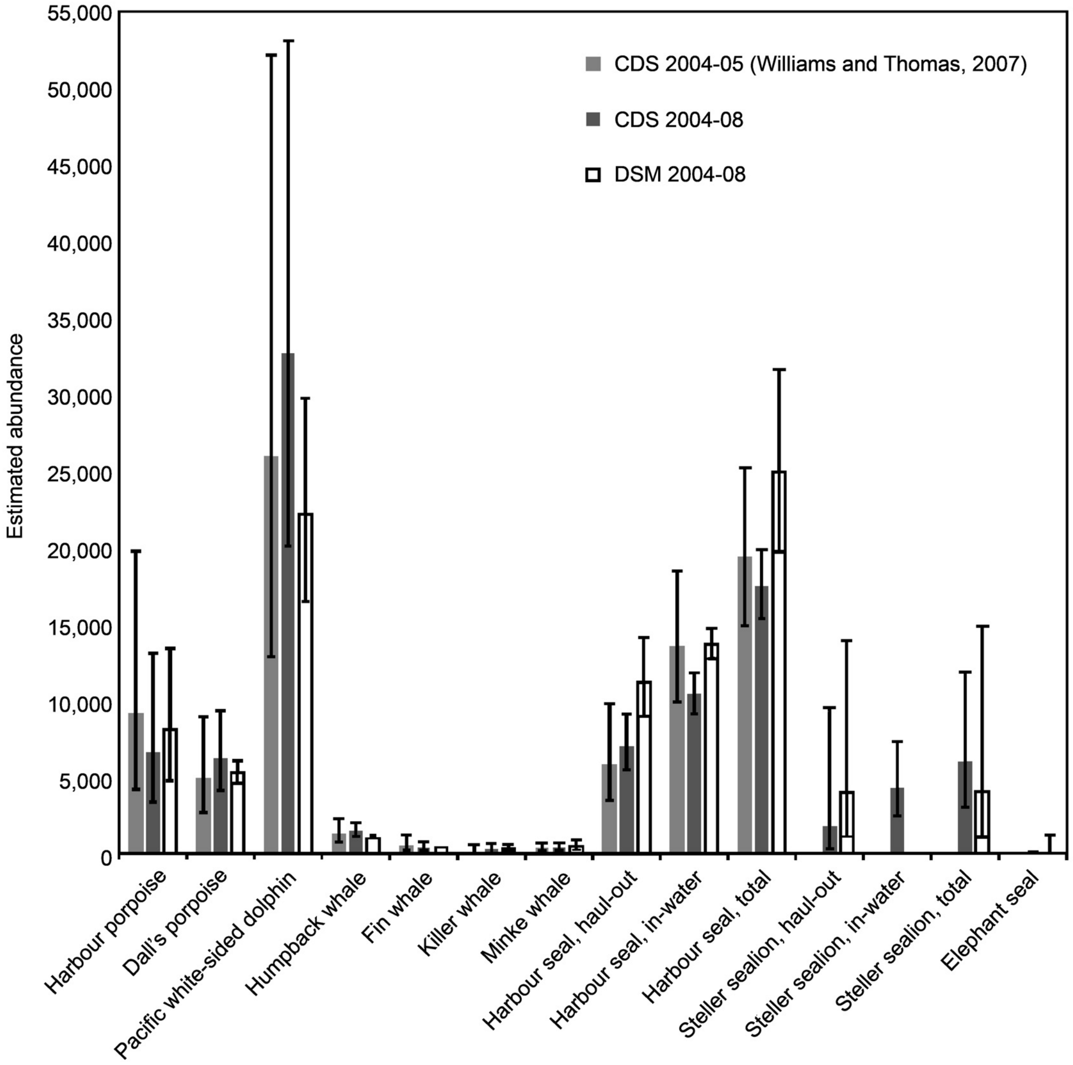

Fig. 6. Abundance estimate comparisons ±95% confidence intervals of the updated 2004–08 survey data pooled across all strata and seasons using Conventional distance Sampling (CDS) and Density Surface Models (DSM) and compared to Williams and Thomas (2007) estimates generated from the 2004–05 surveys in coastal British Columbia. Species abbreviations are for harbour porpoise, Dall's porpoise, Pacific white-sided dolphin, killer whale, humpback whale, common minke whale, fin whale, harbour seal, Steller sea lion, and elephant seal.

Density surface modelling abundance estimates

For harbour seals (in-water), separate models had to be fitted for stratum 1 and the other strata 2, 3 and 4. The humpback whale model had to be fitted with separate models for stratum 1 and stratum 4, excluding strata 2 and 3 where no observations were made. For Steller sea lion (haul-out), the log terms of depth and slope were used to obtain a fitted model (Table 4).

In general, differences between abundance estimates using our CDS and DSM approaches were minor, with significant differences for harbour seals (in water) only. When comparing the CVs between our CDS and DSM abundance estimates for the entire region (Fig. 6 and online supplement), the gain in precision is seen for almost all of the individual species: harbour porpoise (26.2% vs 34.95%); Dall's porpoise (6.8% vs 20.0%); Pacific white-sided dolphin (15.1% vs 24.6%); humpback whale (4.8% vs 12.9%); fin whale (9.3% vs 26.4%); killer whale (26.7% vs 38.2%); harbour seal haul-out (11.5% vs 12.9%); harbour seal in-water (3.7% vs 6.5%); Steller sea lion haul-out (70.3% vs 99.9%); and Steller sea lion in-water (24.2% vs 27.9%). Species where this was not the case were the minke whale (29.9% vs 25.2%) and the elephant seal (2,452.4% vs 29.9%). The CV for the elephant seal is exceptionally high, mainly due to the high variance being divided by a very small mean value. Due to so few observations being made ($n = 20$) while so many more segments were zero, DSM is less reliable than estimates derived using CDS.

Spatial distributions

Density surface models are useful for identifying potential high-use areas or hotspots (see Fig. 7) where any conflicting human use should be avoided, highlighting low-use areas (blue in Fig. 7) where these activities may more safely be relocated. Comparing the observations (Fig. 2), we see general agreement with the distribution of the density surface models (Fig. 7). Much of the predictive power from the models is derived from the bivariate spatial location predictor (i.e., latitude, longitude).

Dall's porpoise is most highly concentrated in the northeastern section of the study region and the model is influenced most positively by medium range depths (Fig. 7a). Harbour porpoises are distributed heavily in the southern strata and some northern areas of Queen Charlotte Basin near

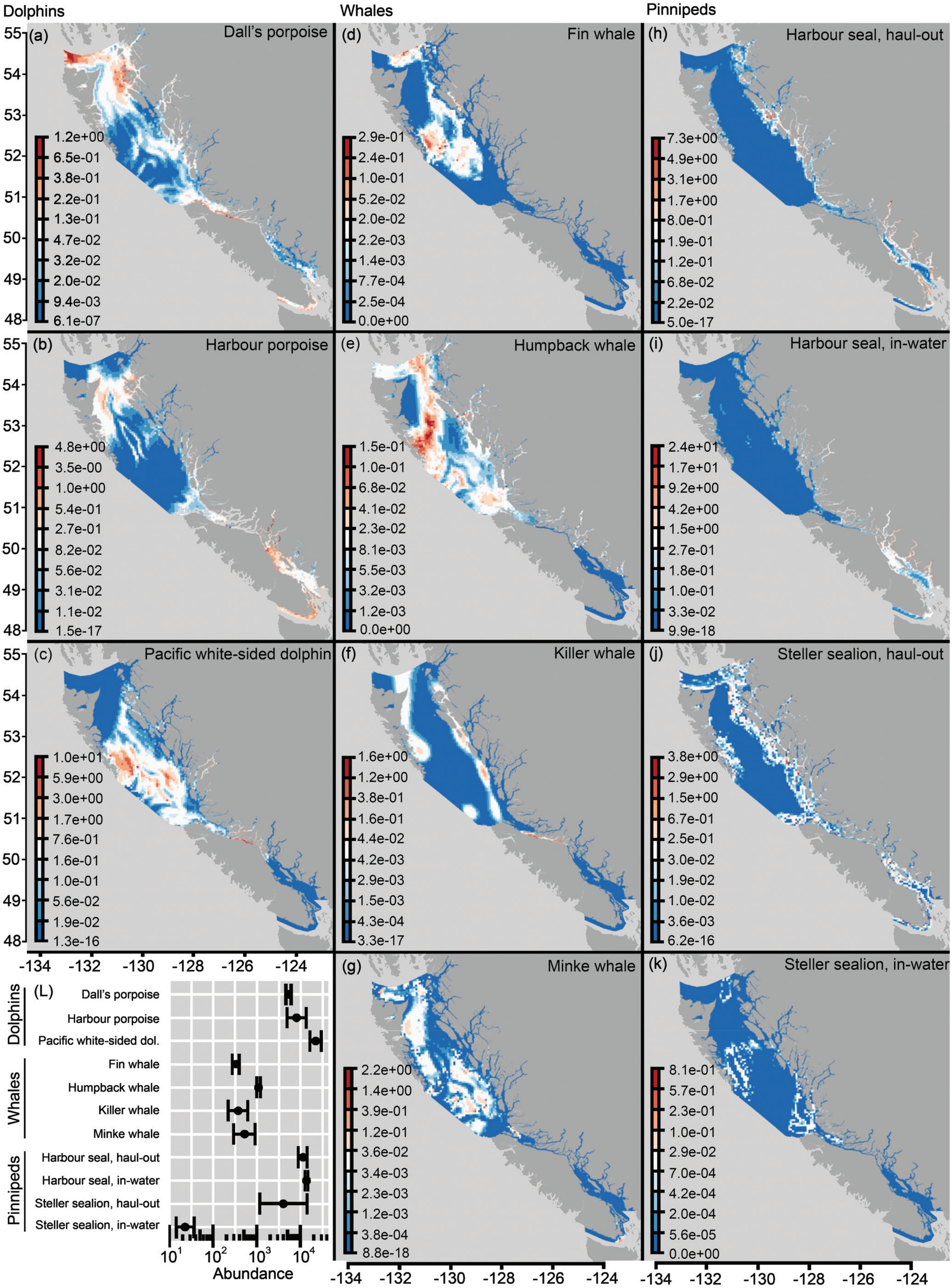

Fig. 7. Density surface models for marine mammals in coastal British Columbia reported as density (# animals/km^2) for dolphins (a–c), whales (d–g) and pinnipeds (h–k), which are further differentiated between in water and hauled out populations. Colour breaks diverge above (red) and below (blue) the mean density (white) based on Jenk's natural breaks to maximise spatial differentiation. Note that the break intervals are unequal. Plotted in geographic coordinate space using cells generated in Albers BC. The whisker plot (L) of mean and 95% confidence interval of total abundance for the study area (Supplemental Tables 5 and 6) compares population sizes between species. Note the log 10 axis for abundance.

Prince Rupert (Fig. 7b). Because only encounter rate is spatially modelled, observations with larger groups are not heavily weighted for the density surface. The Pacific white-sided dolphin dominates the southern and central portion of the basin, with another 'hotspot' in Johnstone Strait (Fig. 7c). Distance from the coast is a dominant term positively influencing density, offset by the negative contribution of depth and slope.

Fin whales are clustered at the southern portion of Haida Gwaii and the northernmost section of the basin (Fig. 7d). Humpback whale distribution (Fig. 7e) is positively influenced by distance to coast and depth, with animals most prominently found off the southern portion of Haida Gwaii and along the tidally driven Hecate Strait Front, which is known to aggregate prey from spring to autumn (Clarke and Jamieson, 2006), and which corresponds with other humpback survey results (Dalla Rosa *et al.*, 2012). Killer whales are found in coastal pockets in the south and central basin (Fig. 7f). For this species, spatial location (latitude, longitude) was the only selected predictor. Common minke whales were spread throughout the basin at a low density with greater concentrations offshore (Fig. 7g).

Harbour seals hauled out (Fig. 7h) are found most in the south central portion of the nearshore basin and inlet waters. In-water harbour seals (Fig. 7i) are also distributed nearshore and in the southern strata. Steller sea lions haul-out (Fig. 7j) and in-water (Fig. 7k) are also found nearshore, but more widely throughout the basin. For all pinniped spatial models, distance to shore and depth were strong predictors in the model, reducing the in-water density of the hauled-out surfaces to negligible values. A single density surface per species is preferable for management. The in-water and hauled-out density surfaces could be summed with the hauled-out group truncated to nearshore cells. The full spatial surfaces, however, were retained separately to allow for later recombination given double platform estimates on the trackline *g*(0) and to account for small islands and rocks present within the coarse 5km prediction grid.

The density surface map for elephant seals was omitted because of poor model performance due to few sightings and preference for the conventional distance sampling abundance results (supplemental Tables 2 and 4).

DISCUSSION

This study provides abundance estimates for 10 marine mammals that inhabit the coastal waters of British Columbia; two represent new abundance estimates for the region and eight represent improved and updated abundance estimates. With often substantial reductions in CIs, whether using conventional or model-based approaches, our revised abundance estimates offer greater precision and accuracy than previous estimates and provide new estimates for spring and fall seasons. A key finding is that humpback whale abundance was highest in spring, which suggests that our surveys sampled whales migrating through BC waters on their way to Alaska. This is particularly relevant because humpback whale abundance is often estimated using mark-recapture statistics from photo-identification. As a secondary objective, a larger, longer-term distributional dataset has also been generated, with relevance for future marine mammal habitat preference studies and further improvement of abundance estimates using either CDS or DSM (Marques and Buckland, 2003). This study's density surface model-based abundance estimates, with the exception of elephant seals, should be viewed as the most reliable abundance estimates, mainly because this approach accounts for spatial heterogeneity over strata and can theoretically improve abundance estimates by narrowing confidence intervals relative to those generated by CDS methods (De Segura et al., 2007; Burt and Paxton, 2006; Hedley and Buckland, 2004).

The most significant and immediate uses of these improved marine mammal distribution and abundance estimates relate to conservation and management. In British Columbia's coastal waters and surrounding regions, marine mammals face numerous threats including: ship strikes (Williams and O'Hara, 2010); bycatch (Williams *et al.*, 2008); pollution and bio-accumulation of toxins (Ross, 2006; Ross *et al.*, 2004); exhaust emissions (Lachmuth *et al.*, 2011); marine noise (Morton and Symonds, 2002; Williams *et al.*, 2013); marine debris (Williams *et al.*, 2011a); competition with fisheries (Matthiopoulos *et al.*, 2008); climate change (Huntingdon and Moore, 2008); and habitat modification/destruction (Johannessen and Macdonald, 2009). These threats affect many populations that are experiencing reduced population sizes due to the long-term consequences of historical commercial whaling, predator control programs, and other factors. Information generated from a subset of these surveys has already contributed to spatial assessments of likely interaction between 11 marine mammal species and debris (Williams *et al.*, 2011a) and ship strike risk for fin, humpback, and killer whales (Williams and O'Hara, 2010). Although still uncertain, a proposal for an oil pipeline terminus and associated supertanker traffic on the north coast of BC represents an emergent and poorly understood threat to marine mammals and their habitat. The Northern Gateway Pipeline project is a proposal that joins a host of other energy developments which, in combination, signal increasing industrialisation of coastal BC. Lacking from most if not all of these projects is the quality baseline distribution and abundance information required to quantitatively assess risks to marine mammal species.

Given the number of threats faced by marine mammals and the relative paucity of baseline distribution and abundance information, these data provide opportunities for extensive future conservation, research management and decision-making. Further, baseline data represents a benchmark against which future population changes can be monitored, which is a crucial issue in the monitoring and management of marine mammals, particularly for those species that do not benefit from targeted census. As with any type of information regarding species assessment, the need to revise, improve, and subsequently apply updated information for more effective conservation and management strategies should be an ongoing priority. Our future research priorities are to, *inter alia*: expand spatial and seasonal coverage; use model averaging on the detection function to improve our estimates for rare species (Williams and Thomas, 2009); to integrate previously unpublished *in situ* data on temperature, salinity and zooplankton abundance and diversity; develop better methods for gauging distance to marine mammals at sea from small boats when the horizon is not visible (Williams *et al.*, 2007); and explore potential to conduct surveys near land-based observation sites to conduct benign, non-invasive studies to assess the point at which cetaceans begin to avoid or approach our research vessel. Notwithstanding these limitations, the updated distribution and abundance estimates presented here are timely and important, given the backlog of SARA-listed species for which critical habitat has not been identified or fully protected (e.g., Taylor and Pinkus 2013, Favaro *et al.*, 2014).

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ONLINE SUPPLEMENT

Table 1

Abundance and density estimates generated using Conventional Distance Sampling (CDS) for cetaceans in stratum 1 (Queen Charlotte Basin, coastal British Columbia, 2004–08) over all survey periods and cumulative pooled estimates for stratum 1.

	Stratum 1							
Estimate	2004 – Summer	2005 – Summer	2006 – Summer	2007 – Spring	2007 – Autumn	2008 – Summer	Average – all	Average – summers
Harbour porpoise								
D	0.157	0.309	0	0.056	0.027	0.211	0.153	0.202
95%CI(D)	0.036–0.675	0.108–0.887	0	0.014–0.221	0.003–0.216	0.044–1.023	0.066–0.355	0.083–0.492
N	2,874	5,677	0	1,032	487	3,874	2,806	3,704
95%CI(N)	667–12,391	1,980–16,279	0	263–4,054	60–3,964	799–18,785	1,209–6,514	1,518–9,040
%CV	79.4	54.9	0	73.4	125.1	87.5	43.2	45.9
Dall's porpoise								
D	0.492	0.354	0.113	0.081	0.115	0.182	0.247	0.318
95%CI(D)	0.248–0.978	0.109–1.152	0.039–0.332	0.027–0.240	0.035–0.379	0.085–0.391	0.147–0.416	0.180–0.560
N	9,038	6,507	2,083	1,487	2,105	3,350	4,540	5,838
95%CI(N)	4,549–17,956	2,001–21,159	711–6,098	503–4,399	638–6,950	1,562–7,184	2,700–7,632	3,313–10,289
%CV	33.8	60.9	50.1	55.1	59.7	37.7	25.5	27.8
Pacific white-sided dolphin								
D	2.196	1.762	3.415	0.858	0.085	1.582	1.566	2.013
95%CI(D)	1.048–4.600	0.544–5.705	1.107–10.536	0.387–1.901	0.007–1.041	0.745–3.361	0.928–2.642	1.152–3.517
N	40,316	32,345	62,708	15,755	1,565	29,054	28,759	36,958
95%CI(N)	19,243–84,464	9,988–104,747	20,327–193,448	7,111–34,905	128–19,113	13,680–61,706	17,047–48,517	21,153–64,573
%CV	37.2%	61.1	53.9	40.0	166.2	37.8	26.4	28.1
Humpback whale								
D	0.049	0.046	0.026	0.132	0.06	0.112	0.078	0.065
95%CI(D)	0.020–0.121	0.022–0.095	0.012–0.059	0.086–0.204	0.027–0.131	0.075–0.167	0.059–0.103	0.045–0.092
N	909	839	486	2,431	1,093	2,057	1,431	1,186
95%CI(N)	373–2,213	406–1,737	219–1,081	1,577–3,747	496–2,405	1,382–3,062	1,085–1,888	835–1,684
%CV	44.1	35.7	36.2	21.0	37.7	19.3	13.6	17.0
Fin whale								
D	0.012	0.045	0	0.024	0.026	0.024	0.024	0.024
95%CI(D)	0.005–0.030	0.017–0.120	0	0.010–0.060	0.010–0.068	0.010–0.057	0.014–0.041	0.012–0.047
N	223	820	0	441	476	442	446	443
95%CI(N)	91–548	305–2,199	0	176–1,108	182–1,242	188–1,040	262–760	229–859
%CV	44.9	50.0	0	46.2	47.1	42.7	26.4	32.7
Killer whale								
D	0.026	0.01	0.014	0.015	0.01	0.005	0.014	0.014
95%CI(D)	0.007–0.100	0.002–0.045	0.003–0.073	0.005–0.050	0.001–0.138	0.001–0.025	0.006–0.032	0.005–0.036
N	476	188	263	282	177	94	251	253
95%CI(N)	124–1,829	43–829	51–1,346	86–921	12–2,527	19–463	107–585	96–666
%CV	72.0	81.3	83.6	62.1	186.3	88.6	43.4	49.9
Minke whale								
D	0.029	0.02	0.045	0.02	0	0.02	0.022	0.025
95%CI(D)	0.014–0.058	0.007–0.055	0.015–0.136	0.007–0.061	0	0.005–0.078	0.013–0.037	0.014–0.045
N	526	371	830	371	0	371	396	466
95%CI(N)	258–1,071	136–1,013	275–2,505	123–1,119	0	96–1,431	231–678	261–829
%CV	35.4	51.1	52.1	56.5	0	71.2	26.7	28.6

Table 2

Abundance and density estimates generated for pinnipeds in stratum 1 (Queen Charlotte Basin, coastal British Columbia, 2004–08) over all survey periods generated using Conventional Distance Sampling (CDS) and cumulative pooled estimates for stratum 1.

Estimate	Stratum 1							Average – summers
	2004 – Summer	2005 – Summer	2006 – Summer	2007 – Spring	2007 – Autumn	2008 – Summer	Average	
Harbour seal, hauled out								
D	0.09	0.089	0.093	0.022	0.042	0.067	0.066	0.083
95%CI(D)	0.019–0.428	0.041–0.192	0.009–0.954	0.002–0.215	0.008–0.212	0.025–0.175	0.033–0.133	0.039–0.176
N	1,651	1,630	1,712	407	769	1,224	1,212	1,523
95%CI(N)	347–7,863	753–3,527	167–17,517	42–3,939	152–3,894	467–3,209	600–2,450	717–3,236
%CV	85.2	38.4	133.4	146.7	86.5	48.4	34.6	37.2
Harbour seal, in water								
D	0.119	0.047	0.026	0.09	0.089	0.047	0.074	0.066
95%CI(D)	0.051–0.282	0.018–0.121	0.004–0.155	0.048–0.167	0.015–0.528	0.018–0.125	0.046–0.118	0.038–0.117
N	2,192	866	485	1,644	1,634	866	1,350	1,217
95%CI(N)	929–5,172	336–2,227	82–2,849	880–3,072	275–9,690	326–2,300	839–2,172	690–2,145
%CV	42.3	47.2	89.8	30.3	97.5	48.7	22.8	27.3
Harbour seal, total								
D	0.209	0.136	0.12	0.112	0.131	0.114	0.14	0.149
95%CI(D)	0.089–0.491	0.075–0.246	0.019–0.750	0.053–0.235	0.035–0.495	0.057–0.226	0.093–0.210	0.092–0.241
N	3,842	2,496	2,197	2,052	2,403	2,090	2,562	2,740
95%CI(N)	1,638–9,016	1,379–4,516	350–13,778	974–4,323	635–9,087	1,052–4,154	1,704–3,852	1,697–4,426
%CV	43.8	29.9	105.8	37.9	71.9	34.8	20.3	24.0
Steller sea lion, hauled out								
D	0	0	0	0	0.301	0.24	0.082	0.072
95%CI(D)	0	0	0	0	0.024–3.821	0.039–1.462	0.013–0.497	0.012–0.438
N	0	0	0	0	5,530	4,399	1,503	1,314
95%CI(N)	0	0	0	0	436–70,158	721–26,845	248–9,119	215–8,036
%CV	0	0	0	0	179.6	109.6	108.9	109.6
Steller sea lion, in water								
D	0.16	0.135	0.063	0.316	0.17	0.158	0.18	0.142
95%CI(D)	0.038–0.664	0.060–0.307	0.012–0.334	0.132–0.758	0.052–0.553	0.059–0.422	0.098–0.333	0.067–0.297
N	2,936	2,485	1,160	5,797	3,126	2,901	3,314	2,601
95%CI(N)	706–12,200	1,096–5,634	219–6,129	2,415–13,914	963–10,145	1,087–7,746	1,796–6,116	1,239–5,460
%CV	76.7	41.8	85.1	44.7	60.0	50.4	31.3	37.7
Steller sea lion, total								
D	0.16	0.135	0.063	0.316	0.471	0.398	0.262	0.213
95%CI(D)	0.038–0.664	0.060–0.307	0.012–0.334	0.132–0.758	0.071–3.117	0.114–1.388	0.121–0.567	0.091–0.498
N	2,936	2,485	1,160	5,797	8,656	7,301	4,817	3,915
95%CI(N)	706–12,200	1,096–5,634	219–6,129	2,415–13,914	1,309–57,235	2,092–25,483	2,230–10,403	1,675–9,153
%CV	76.7	41.8	85.1	44.7	116.8	69.0	40.2	44.5
Elephant seal								
D	0.008	0.004	0	0.004	0	0	0.003	0.004
95%CI(D)	0.003–0.021	0.001–0.014	0	0.001–0.012	0	0	0.002–0.006	0.002–0.008
N	151	74	0	74	0	0	61	67
95%CI(N)	58–391	21–260	0	24–228	0	0	31–119	30–146
%CV	47.4	64.9	0	56.8	0	0	32.0	38.3

Table 3

Abundance and density estimates generated using Conventional Distance Sampling (CDS) for cetaceans in stratum 2 (Strait of Georgia), 3 (Johnstone Strait) and 4 (mainland inlets) over all survey periods and averaged estimates for the entire survey region (strata 1–4) in coastal British Columbia (2004–08).

	Stratum 2	Stratum 3	Stratum 4				
Estimate	2004 – Summer	2005 – Summer	2004 – Summer	2007 – Autumn and Spring	2008 – Summer	Average	Entire region – average
Harbour porpoise							
D	1.342	0	0.24	0.049	0.247	0.178	0.272
95%CI(D)	0.540–3.334	0	0.006–9.643	0.001–1.616	0.006–9.903	0.012–2.709	0.138–0.536
N	3,203	0	838	170	861	622	6,631
95%CI(N)	1,289–7,957	0	21–33,641	5–5,639	21–34,546	41–9,449	3,366–13,065
%CV	47.4%	0	225.0	317.2	225.0	213.6	34.9
Dall's porpoise							
D	0.358	0.695	0.252	0.335	0.028	0.216	0.256
95%CI(D)	0.289–0.443	0.562–0.860	0.009–7.159	0.015–7.550	0.001–1.125	0.011–4.390	0.171–0.383
N	855	85	879	1,168	96	752	6,232
95%CI(N)	691–1,058	69–105	31–24,973	52–26,339	2–3,926	37–15,315	4,165–9,324
%CV	10.9	10.9	182.0	238.4	223.9	267.7	20.0
Pacific white-sided dolphin							
D	0.16	20.675	0	0.151	0.916	0.277	1.34
95%CI(D)	0.114–0.223	14.803–28.875	0	0.005–4.997	0.030–27.527	0.011–7.093	0.825–2.177
N	381	2,532	0	525	3,195	965	32,637
95%CI(N)	273–533	1,813–3,536	0	16–17,433	106–96,029	38–24,744	20,087–53,029
%CV	17.2	17.1	0	316.7	189.2	322.8	24.6
Humpback whale							
D	0	0	0.062	0.004	0.047	0.031	0.063
95%CI(D)	0	0	0.002–1.711	0.000–0.145	0.004–0.615	0.002–0.436	0.049–0.082
N	0	0	216	15	164	110	1,541
95%CI(N)	0	0	8–5,967	0–505	13–2,146	8–1,521	1,187–2,000
%CV	0	0	178.5	316.3	117.1	199.0	12.9
Fin whale							
D	0	0	0	0	0	0	0.018
95%CI(D)	0	0	0	0	0	0	0.011–0.031
N	0	0	0	0	0	0	446
95%CI(N)	0	0	0	0	0	0	263–759
%CV	0	0	0	0	0	0	26.4
Killer whale							
D	0	0.469	0	0	0	0	0.013
95%CI(D)	0	0.287–0.766	0	0	0	0	0.006–0.027
N	0	57	0	0	0	0	308
95%CI(N)	0	35–94	0	0	0	0	146–649
%CV	0	24.8	0	0	0	0	38.2
Minke whale							
D	0.014	0	0	0	0	0	0.018
95%CI(D)	0.011–0.019	0	0	0	0	0	0.011–0.029
N	34	0	0	0	0	0	430
95%CI(N)	26–45	0	0	0	0	0	259–712
%CV	14.0	0	0	0	0	0	25.2

Table 4

Abundance and density estimates generated using Conventional Distance Sampling (CDS) for pinnipeds in stratum 2 (Strait of Georgia) 3 (Johnstone Strait) and 4 (mainland inlets) over all survey periods and averaged estimates for the entire survey region (strata 1–4) in coastal British Columbia (2004–08).

	Stratum 2	Stratum 3	Stratum 4				
Estimate	2004 – Summer	2005 – Summer	2004 – Summer	2007 – Autumn and Spring	2008 – Summer	Average	Entire region – average
Harbour seal, hauled out							
D	1.217	0	1.567	0.3	1.437	0.844	0.29
95%CI(D)	0.968–1.529	0	0.090–27.386	0.033–2.773	0.059–34.745	0.067–10.642	0.225–0.374
N	2,904	0	5,467	1,047	5,014	2,944	7,060
95%CI(N)	2,311–3,649	0	313–95,538	113–9,673	207–121,210	233–37,126	5,477–9,101
%CV	11.7%	0	138.8	128.1	166.4	185.0	12.9
Harbour seal, in water							
D	1.934	0.647	1.631	1.225	0.902	1.246	0.427
95%CI(D)	1.754–2.133	0.588–0.713	0.134–19.808	0.220–6.830	0.088–9.234	0.240–6.480	0.375–0.485
N	4,617	79	5,689	4,275	3,145	4,348	10,394
95%CI(N)	4,187–5,090	72–87	468–69,099	767–23,827	307–32,212	836–22,606	9,143–11,816
%CV	5.0%	4.9	111.8	88.4	101.2	93.6	6.5
Harbour seal, total							
D	3.151	0.647	3.198	1.526	2.339	2.09	0.717
95%CI(D)	2.832–3.506	0.588–0.713	0.553–18.492	0.373–6.237	0.303–18.047	0.424–10.309	0.631–0.814
N	7,521	79	11,156	5,322	8,159	7,292	17,454
95%CI(N)	6,760–8,367	72–87	1,929–64,510	1,302–21,757	1,057–62,957	1,479–35,964	15,362–19,831
%CV	5.4%	4.9	88.7	75.4	109.4	93.2	6.5
Steller sea lion, hauled out							
D	0	0	0.323	0	0	0.073	0.072
95%CI(D)	0	0	0.009–11.304	0	0	0.002–2.923	0.013–0.391
N	0	0	1,126	0	0	256	1,759
95%CI(N)	0	0	32–39,433	0	0	6–10,196	324–9,534
%CV	0	0	234.4	0	0	474.3	99.9
Steller sea lion, in water							
D	0	0	0.261	0.43	0	0.271	0.175
95%CI(D)	0	0	0.013–5.410	0.022–8.249	0	0.015–4.804	0.101–0.301
N	0	0	910	1,499	0	946	4,260
95%CI(N)	0	0	44–18,874	78–28,777	0	53–16,760	2,472–7,341
%CV	0	0	155.6	213.7	0	240.4	27.9
Steller sea lion, total							
D	0	0	0.583	0.43	0	0.345	0.247
95%CI(D)	0	0	0.051–6.618	0.022–8.249	0	0.024–4.860	0.125–0.487
N	0	0	2,035	1,499	0	1,202	6,019
95%CI(N)	0	0	179–23,087	78–28,777	0	85–16,956	3,056–11,853
%CV	0	0	147.1	213.7	0	214.5	35.3
Elephant seal							
D	0	0	0	0.003	0	0.001	0.003
95%CI(D)	0	0	0	0.000–0.093	0	0.000–0.051	0.001–0.005
N	0	0	0	10	0	4	65
95%CI(N)	0	0	0	0–324	0	0–176	35–121
%CV	0	0	0	316.2	0	469.0	29.9

Table 5

Abundance and density estimates generated using Density Surface Modelling (DSM) for cetaceans all strata (1, Queen Charlotte Basin; 2, Strait of Georgia; 3, Johnstone Strait; and 4, mainland inlets) over all survey periods and average estimates for the entire survey region in coastal British Columbia (2004–08).

	Strata				
Estimate	1	2	3	4	Entire region – average
Harbour porpoise					
D	0.058	0.368	0.21	0.11	0.097
95%CI(D)	0.035–0.096	0.222–0.610	0.127–0.350	0.066–0.183	0.058–0.160
N	3,647	3,053	92	1,298	8,091
95%CI(N)	2,202–6,041	1,843–5,058	55–153	783–2,153	4,885–13,401
%CV	26.2	26.2	26.4	26.2	26.2
Dall's porpoise					
D	0.067	0.063	0.17	0.041	0.063
95%CI(D)	0.059–0.077	0.055–0.072	0.143–0.203	0.035–0.046	0.055–0.073
N	4,232	518	75	478	5,303
95%CI(N)	3,701–4,839	452–595	63–89	418–548	4,638–6,064
%CV	6.9	7.0	9.0	7.0	6.8
Pacific white-sided dolphin					
D	0.313	0.001	2.704	0.106	0.265
95%CI(D)	0.233–0.419	0.000–0.002	1.996–3.664	0.079–0.144	0.198–0.356
N	19,715	7	1,183	1,256	22,160
95%CI(N)	14,699–26,441	3–18	873–1,603	931–1,693	16,522–29,721
%CV	15.1	52.6	15.6	15.3	15.1
Humpback whale					
D	0.016	–	–	0.008	0.013
95%CI(D)	0.014–0.017	–	–	0.007–0.009	0.012–0.014
N	995	–	–	97	1,092
95%CI(N)	905–1,094	–	–	87–107	993–1,200
%CV	4.8	–	–	5.3	4.8
Fin whale					
D	0.005	0	0	0.001	0.004
95%CI(D)	0.004–0.006	0	0	0.001–0.002	0.003–0.005
N	314	0	0	15	329
95%CI(N)	262–377	0	0	11–19	274–395
%CV	9.3	0	0	12.5	9.3
Killer whale					
D	0.004	0	0.118	0.005	0.004
95%CI(D)	0.003–0.007	0	0.071–0.199	0.003–0.008	0.003–0.007
N	264	0	52	55	371
95%CI(N)	158–442	0	31–87	33–93	222–621
%CV	26.7	0	26.8	27.2	26.7
Minke whale					
D	0.008	0.003	0	0	0.006
95%CI(D)	0.004–0.014	0.001–0.005	0	0.000–0.001	0.004–0.011
N	498	21	0	4	522
95%CI(N)	281–883	11–39	0	2–7	295–927
%CV	29.9	32.3	0	38.9	29.9

Table 6

Abundance and density estimates generated using Density Surface Modelling (DSM) for pinnipeds in all strata (1, Queen Charlotte Basin; 2, Strait of Georgia; 3, Johnstone Strait; and 4, mainland inlets) over all survey periods and average estimates for the entire survey region in coastal British Columbia (2004–08).

	Strata				
Estimate	1	2	3	4	Entire region – average
Harbour seal, haul-out					
D	0.048	0.436	0.051	0.387	0.134
95%CI(D)	0.038–0.060	0.348–0.547	0.040–0.066	0.308–0.485	0.107–0.168
N	3,040	3,613	22	4,558	11,233
95%CI(N)	2,423–3,815	2,881–4,530	18–29	3,635–5,715	8,965–14,076
%CV	11.6	11.6	12.7	11.6	11.5
Harbour seal, in-water					
D	0.018	0.441	0.352	0.741	0.164
95%CI(D)	0.017–0.019	0.413–0.471	0.304–0.407	0.680–0.807	0.152–0.176
N	1,141	3,652	154	8,736	13,683
95%CI(N)	1,068–1,219	3,420–3,900	133–178	8,017–9,520	12,734–14,703
%CV	3.4	3.4	7.5	4.4	3.7
Harbour seal, total					
D	0.066	0.877	0.403	1.128	0.298
95%CI(D)	0.052–0.084	0.693–1.110	0.302–0.537	0.885–1.436	0.235–0.378
N	4,181	7,265	176	13,294	24,916
95%CI(N)	3,301–5,296	5,740–9,195	132–235	10,439–16,930	19,666–31,569
%CV	12.1	12.1	14.8	12.4	12.1
Steller sea lion, haul-out					
D	0.042	0.128	0.023	0.023	0.048
95%CI(D)	0.012–0.147	0.037–0.442	0.007–0.081	0.007–0.080	0.014–0.166
N	2,673	1,057	10	273	4,014
95%CI(N)	771–9,262	305–3,664	3–36	79–948	1,158–13,908
%CV	70.3	70.4	70.4	70.3	70.3
Steller sea lion, in-water					
D	0.0003	0	0	0.0004	0.0003
95%CI(D)	0.000–0.000	0	0	0.000–0.001	0.000–0.000
N	19	0	0	4	23
95%CI(N)	12–30	0	0	3–7	15–37
%CV	24.1	0	0	24.4	24.0
Steller sea lion, total					
D	0.043	0.128	0.023	0.024	0.048
95%CI(D)	0.012–0.157	0.035–0.468	0.006–0.086	0.006–0.087	0.013–0.177
N	2,692	1,057	10	278	4,037
95%CI(N)	733–9,882	288–3,876	3–38	76–1,021	1,100–14,815
%CV	74.4	74.3	74.3	74.5	74.3
Elephant seal					
D	0.00007	0.000005	0	0.0004	0.0001
95%CI(D)	0.000–0.000	0.000–0.014	0	0.000–0.065	0.000–0.015
N	5	0	0	4	9
95%CI(N)	3–7	0–116	0	0–770	0–1,248
%CV	22.2	411,476.5	0	3,497.3	2,452.4

Table 7

Sightings of other species observed but not modelled by season, year, and stratum from surveys in coastal British Columbia (2004–08).

Species	Season	Year	Stratum	Sightings
Gray whale	Spring	2007	1	3
		2007	4	1
	Summer	2004	1	3
Total				**7**
Sunfish	Summer	2004	1	8
		2005	1	9
		2006	1	8
		2008	1	2
Total				**27**
Shark	Summer	2004	1	21
		2005	1	57
		2006	1	27
		2008	1	1
Total				**106**
Sei whale	Summer	2005	1	1
Sea otter	Autumn	2007	1	5
		2007	4	7
	Spring	2007	1	5
		2007	4	3
	Summer	2005	1	2
		2006	1	7
		2008	1	6
		2008	4	1
Total				**36**

Observations of movement and site fidelity of white-beaked dolphins (*Lagenorhynchus albirostris*) in Icelandic coastal waters using photo-identification

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ABSTRACT

The white-beaked dolphin (*Lagenorhynchus albirostris*) is the most commonly sighted delphinid species in Icelandic coastal waters. However, little is known about the species' abundance, site fidelity and movements throughout its range. Photo-identification studies were conducted from April–October (2002–10) during whalewatching operations in Faxaflói and Skjálfandi bays on the southwest and northeast coasts of Iceland, respectively. Minimum abundance, annual site fidelity and movement between bays were calculated. A total of 154 and 52 individuals were identified in Faxaflói and Skjálfandi bays, respectively. The annual re-sighting rate was 21.4% in Faxaflói bay while only one individual was re-sighted in Skjálfandi bay (1.7%). A total of five dolphins (2.3%) were matched between Faxaflói and Skjálfandi bays with the period between re-sightings ranging from 272 to 821 days (mean 28.16 days, SD = 5.94). Low site fidelity rates observed likely signify a much larger home range than the present study area, into either other coastal or offshore zones, or alternatively may be explained by a large natural population size and/or the opportunistic nature of sampling during this study. Therefore, expansion of the study area is required. The matches between bays suggest that white-beaked dolphins inhabit a large-scale coastal range of the Icelandic coast and can be considered highly mobile and transient possibly due to scarce and patchy resources. Alternatively it could be due to a large population size.

KEYWORDS: WHITE-BEAKED DOLPHIN; PHOTO-ID; SITE FIDELITY; MOVEMENTS; NORTH ATLANTIC; ICELAND; NORTHERN HEMISPHERE

INTRODUCTION

The white-beaked dolphin (*Lagenorhynchus albirostris*) is endemic to the North Atlantic (Kinze *et al.*, 1997; Northridge *et al.*, 1997; Reeves *et al.*, 1999) and present in Icelandic coastal waters all year round (Magnúsdóttir, 2007). Although white-beaked dolphins have been studied in Icelandic waters (e.g. Bertulli *et al.*, 2012; Rasmussen *et al.*, 2013; Rasmussen and Miller, 2002), there has been insufficient data to fully understand their abundance and habitat use.

Higher occurrences of white-beaked dolphins have been observed on the southwest coast, on the northeast coast and on the southeast coast, based on aerial surveys conducted from 1986 to 2001 covering Icelandic coastal waters (Gunnlaugsson *et al.*, 1988; Pike *et al.*, 2009). Based upon opportunistic sightings from whalewatching boats, white-beaked dolphins are routinely found in the southwest as the second most common species encountered; common minke whales (*Balaenoptera acutorostrata*) are the most sighted species (Bertulli, 2010). In the northeast they are the third most commonly sighted species in the Skjálfandi bay (hereafter 'Skjálfandi'); the most sighted species is the humpback whale (*Megaptera novaeangliae*) and the second most sighted is the common minke whale (Cecchetti, 2006), with a reported increase of sightings from 2004 to 2007 (Cooper, 2007). On the west coast of Iceland, sightings have also been reported (whalewatching operator, Láki Tours[5]). The east coast of Iceland remains inadequately surveyed.

[5] *http://www.lakitours.com.*

The only available abundance estimate (Pike *et al.*, 2009) for white-beaked dolphins in Icelandic waters dates back to 2001 (NASS surveys conducted from 1986–2001), resulting in an estimated 31,653 animals (95% CI: 17,679–56,672).

Previous studies indicate site fidelity (Bertulli, 2010) and movement patterns of white-beaked dolphins in Icelandic waters spanning *ca*. 300km or greater (Rasmussen *et al.*, 2013; Tetley *et al.*, 2006).

The aim of this paper is to present opportunistic data on residency patterns (inter-annual site fidelity), observed movements between two Icelandic bays, Faxaflói Bay (southwest, hereafter 'Faxaflói') and Skjálfandi (northeast) and to evaluate the minimum abundance of white-beaked dolphin using photo-identification in these two study areas.

MATERIALS AND METHODS

Study area

Faxaflói (64°24'N, 22°00'W) and Skjálfandi (66°05'N, 17°33'W) are two relatively wide bays respectively located on the southwest and northeast coast of Iceland, approximately 600km apart from each other (see Fig. 1). Faxaflói is *ca*. 50km long and 90km wide (Stefansson and Guðmundsson, 1978; Stefánsson *et al.*, 1987) and covers about 4,400km^2. Skjálfandi is about 25km long and 10km wide (Gíslason, 2004) and covers about 1,100km^2 (Bertulli *et al.*, 2012). Both bays were used as locations to collect data because of the predictable seasonal occurrence of dolphins close to the shore in relatively high numbers and

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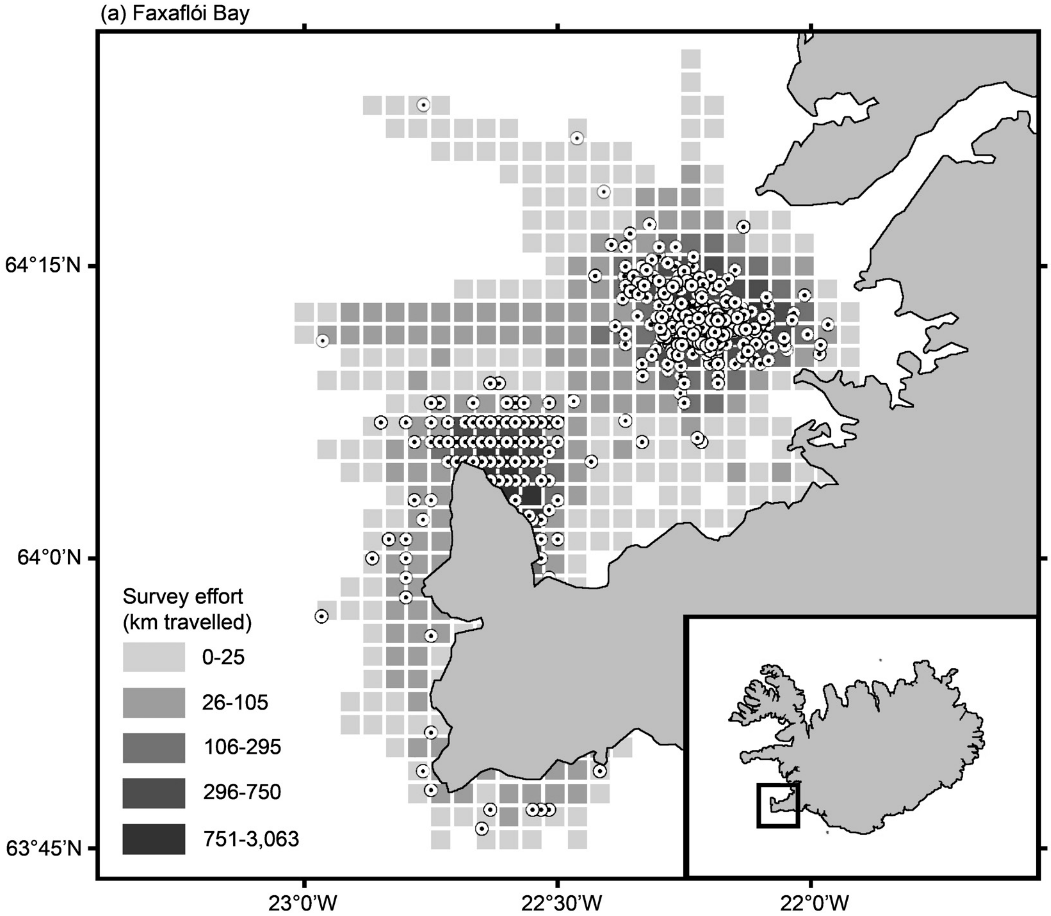
(a) Faxaflói Bay



(b) Skjálfandi Bay

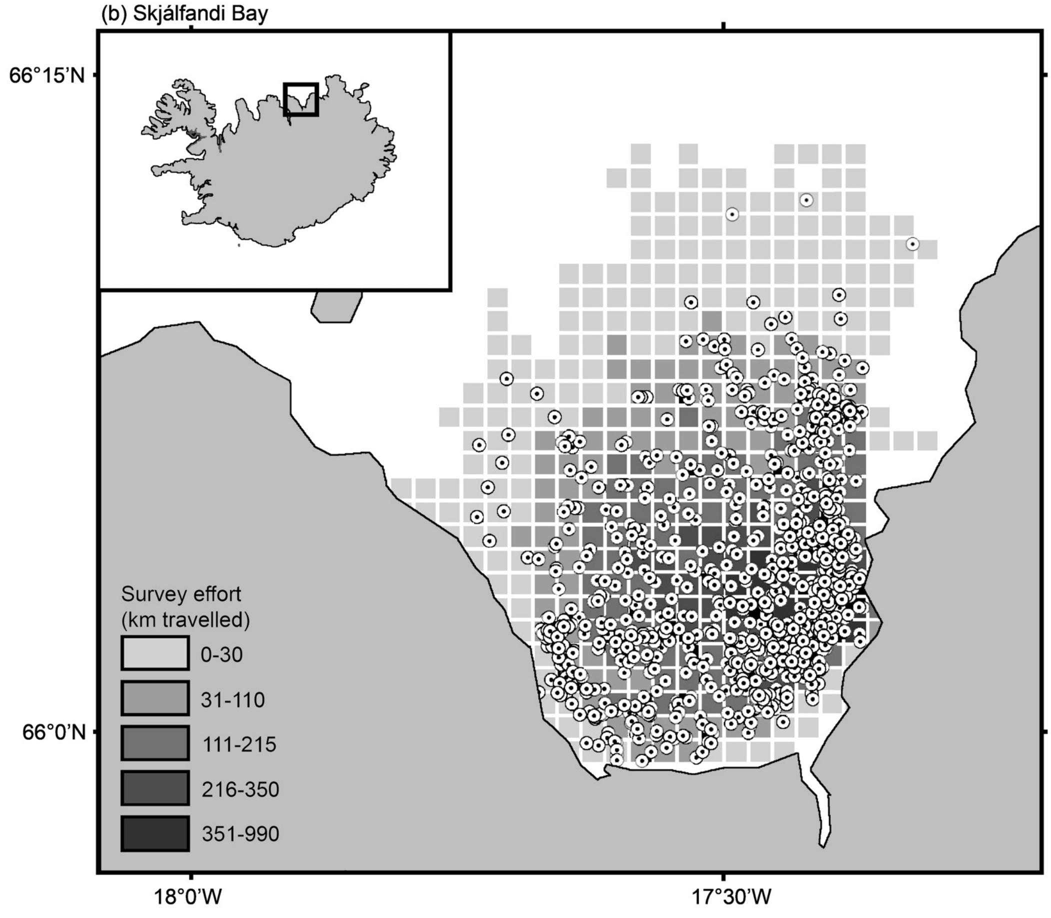


Fig. 1. Location of white-beaked dolphin sightings from 2002 to 2010 in Faxaflói (Top) and in Skjálfandi (Bottom). Searching effort (expressed in km travelled) using whale-watching vessels and white-beaked dolphin sightings (white circles) are shown.

for the presence of whalewatching operations giving multiple tours daily.

Data collection

Photo-identification was undertaken from April–September (2002–10) from two whalewatching boats based in Faxaflói, Reykjavik, and from May–October (2002–10) from three boats in Skjálfandi, Húsavík, Iceland. The whalewatching tours were generally conducted between the hours of 9:00 and 21:00 (at least three trips were scheduled daily lasting approximately three hours) across mainly the spring and summer seasons. Due to the high latitude of the study sites, daylight lasts between approximately 7:00–20:00 hours in April and September, and *ca.* 5:00–22:00 hours in May and August with almost constant daylight from mid-June till early July (see US Naval Observatory Astronomical Applications Department website[6]). Non-systematic boat surveys based on whalewatching boats in Beaufort sea states of zero to three were conducted in both bays. Observations were collected from the roof of the wheelhouse (5–8m above sea level in Faxaflói, 2.7 to 4.5m in Skjálfandi) of two vessels (length 25–26m) in Faxaflói and three vessels (length 20–25m) in Skjálfandi. Every 15 minutes data forms were used to enter environmental data (sea state, swell, visibility and glare), the vessel position (GPS) was recorded at 5-min intervals. Throughout the surveys there were specific cues utilised to detect animals, including the occurrence of bird feeding flocks and/or feeding whales (often associated with the presence of dolphins) and direct animal observations, either from their surfacing bodies or from their tall and curved dorsal fins. At times the location of animals was reported from other vessels operating in the same area.

At each dolphin sighting, the following information was recorded: species, time, position, environmental conditions, behaviour, and group size/composition (see Bertulli, 2010). Encounter duration was ultimately dependent on the captain's decision to stay with the animals or leave the area (Bertulli *et al.*, 2013). When possible, the vessel would run parallel to the dolphin group, allowing researchers to systematically photograph the whole surfacing pattern of each individual, including the dorsal fin (primary feature used). Secondary features such as the dorsum, flanks and peduncle carrying skin lesions were also used (e.g. Bertulli *et al.*, 2012).

In order to obtain an impartial estimate of the amount of animals encountered, an attempt was made to photo-identify every dolphin within each group without giving preference to obviously marked over unmarked individuals (Currey *et al.*, 2008; Gormley *et al.*, 2005; Williams *et al.*, 1993).

A range of digital cameras were used in both study areas with zoom lenses ranging from 55–200mm to 70–300mm for Faxaflói and from 28–135mm to 40–150mm for Skjálfandi. Images were taken in both JPG (300 pixel/inch) and RAW formats. The number of photographers varied from one to four, usually the principle investigator (CB) and three assistants, who were stationed 360° around the survey vessel in Faxaflói. In Skjálfandi, surveys were conducted by one or two teams, with a total of six different investigators being involved (on rotation) in data collection, also covering an area of 360° around the survey vessel.

Photo-identification analysis

Each photo-identification picture was allocated a quality rating (Q) from Q1 to Q6 (Q6 being the highest), taking into consideration focus, exposure, angle and proportion of the frame occupied by the body of the animal. The Q-value attributed to each image was not dependent of the marks visible on each individual. Only images rated $Q \geq 5$ were considered good enough for the analysis (Elwen *et al.*, 2009; Gowans and Whitehead, 2001; Rosso *et al.*, 2011). Considering the distinctiveness of each image, only distinctive and very distinctive dorsal fins were used in the analysis (Zaeschmar *et al.*, 2014). In order to identify individual white-beaked dolphins from photographs, a previously adopted classification was used (Tscherter and Morris, 2005) which used dorsal fin edge marks (DEMs) as primary features and body marks as secondary features (but these were solely used in addition to DEMs). In fact, due to the lack of studies on the stability over time of secondary features (such as skin marks in white-beaked dolphins) only individuals marked on the fin (DEM) were used for the analysis. Notches have already proven to be reliable permanent marks in other dolphin species (Auger-Méthé and Whitehead, 2007; Rosso *et al.*, 2011; Wilson *et al.*, 1999).

Analysis was only carried out on adult individuals. All images were viewed using Adobe *Photoshop CS2/CS3* imaging software to identify unique permanent markings. Photographs were sorted into chronological order of collection, allowing researchers to detect the evolution of skin marks over time, making them a valid support to DEMs and therefore confirming the identity of different individuals. Additionally, during the matching process a single qualified person was responsible to quality-grade each photo-identification image which was also systematically evaluated by up to two people (i.e. CB or MHR) throughout each field season (Davies *et al.*, 2001; Sears *et al.*, 1990).

Data analysis

Three independent analyses were carried out: (1) estimate of minimum abundance (minimum number of individuals identified in each study area); (2) '*annual re-sighting proportion*' (the proportion of individual dolphins identified in more than one year among all years of study); and (3) matching of individual dolphins between Faxaflói and Skjálfandi bays. A '*re-sighting proportion*' is defined as the number of animals re-sighted in multiple years in both areas divided by the total number of individuals identified in these areas (Bertulli *et al.*, 2013).

The shortest distance between the two bays for the annual re-sighted white-beaked dolphins identified was determined using the 'ruler' tool provided by *Garmin MapSource* (version 6.14) as the direct route by sea (avoiding land) between Reykjavik (Faxaflói) and Húsavík (Skjálfandi) following Bertulli *et al.* (2013).

To describe the white-beaked dolphins visiting the Faxaflói and Skjálfandi study areas the word 'population' was used with no genetic or absolute abundance associations (Weir *et al.*, 2008; de Boer *et al.*, 2013).

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[6] *http://aa.usno.navy.mil.*

Table 1

Survey effort for white-beaked dolphin surveys conducted in: (a) Faxaflói between March and November 1999 to 2010; and in (b) Skjálfandi between May and October 2002 to 2010. N/A = data not available. During the years 2005 in Faxaflói and 2003 in Skjálfandi, photo-IDs were not collected. Effort data was also not recorded in 2002 in Skjálfandi.

Study period	Survey effort (days)	Survey effort (trips)	Survey effort (hours)	Observation (days)	Observation (trips)	Observation (hours)
(a) Faxaflói						
2002	105	134	402	94	112	336
2003	119	163	489	94	119	357
2004	135	188	564	99	130	390
2005	191	401	1203	98	127	381
2006	69	130	390	53	75	225
2007	77	167	311.34	42	62	123.13
2008	102	198	395.43	65	96	180.42
2009	85	172	354.25	46	61	130.34
2010	79	143	254.34	43	55	97.10
Total	962	1,696	4,364.16	634	837	2,220.47
(b) Skjálfandi						
2002	N/A	N/A	N/A	N/A	N/A	N/A
2003	48	51	156.03	15	15	42.42
2004	28	28	99.21	12	12	33.20
2005	71	75	192.17	45	46	125.19
2006	79	84	198.48	29	29	65.10
2007	105	105	257.31	36	36	89.14
2008	103	110	280.28	28	29	73.06
2009	103	132	286.11	24	34	84.31
2010	115	181	353.37	58	77	185.20
Total	652	766	1,803.23	247	278	699.42

RESULTS

Photo-identification effort and white–beaked dolphin encounters

Between April 2002 and October 2010, 881 (54.6%) days were spent observing white-beaked dolphins in both study areas, with a total of 837 tours in Faxaflói and 278 in Skjálfandi (Table 1). Dolphin encounters were distributed throughout the surveyed coastline, with particular clusters of sightings in the Garður (64°4’0”N 22°38’0”W) and Kollafjörður (62°7’6”N, 6°54’20”W) areas in Faxaflói and in the inner coastal part of Skjálfandi (Fig. 1).

In the Faxaflói area the number of surveys where white-beaked dolphins were sighted seem to show an increase until 2004, then a drastic decrease in numbers (with the exception of the year 2008 which shows the highest number of tours in that area when dolphins were encountered since the year 2006). Conversely, in Skjálfandi, surveys showed an increase in numbers almost every other year (see Table 1).

Minimum abundance

A total of 524 high quality colour digital photographs were analysed ($n = 415$ in Faxaflói, $n = 109$ in Skjálfandi). As a result, a total of 154 individuals could be identified in Faxaflói, 52 in Skjálfandi and 5 individuals in both bays (Fig. 2).

Of the 211 individual dolphins identified in both areas in Faxaflói, 56 (35.2%) were left side identifications, 55 (34.6%) were right side identifications and 43 (27.0%) where both sides were identified. In Skjálfandi 23 (44.2%) were left side identifications, 18 (34.6%) were right side and 11 (21.2%) both sides. The 5 individuals photographed in both bays consisted of 1 right side identification (20.0%) and 4 both sides (80.0%).

Overall, in both study sites the cumulative number of identified individuals (‘rate of discovery’ curve) of white-beaked dolphins did not decrease (Fig. 2). The number of photo-identified images collected counted an overall average of 3.75 ± 2.89 (± SD) new white-beaked dolphins per day (every year) in Faxaflói and 2.97 ± 1.86 (± SD) in Skjálfandi.

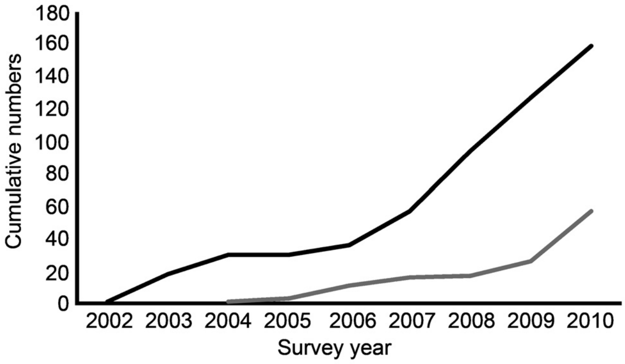

Fig. 2. The Discovery curve is established by plotting the cumulative number of newly marked (DEM) identified and catalogued white-beaked dolphins each year, in Faxaflói from 2002 to 2010 (black line) and in Skjálfandi from 2004 to 2010 (grey line) inclusive.

Annual re-sighting proportion

The annual re-sighting proportion was 21.4% ($n = 34$) in Faxaflói, with the majority of identified dolphins observed only one year ($n = 125$, 78.6%), followed by 31 individuals recorded two years (19.5%), and 3 seen for three years (1.9%) between April and September 2002 to 2010 (Fig. 3). Of the 34 animals re-sighted annually, 21 (61.8%) were re-sighted in consecutive years; the highest number was re-sighted between 2007 and 2010. Only one individual (DEM57) was inter-annually re-sighted in Skjálfandi (annual proportion of 1.7%), this individual was first sighted in 2007 and then re-sighted in 2010.

Overlap between the Faxaflói and Skjálfandi white-beaked dolphin ‘populations’

Both photo-identified catalogues include images of 211 distinctive individuals ($n = 154$ in Faxaflói, $n = 52$ in

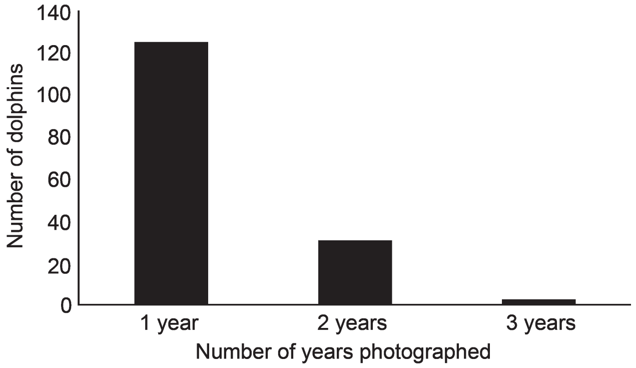

Fig. 3. Distribution of annual re-capture frequencies between years for all white-beaked dolphins identified in Faxaflói between April and October 2002 to 2010.

Skjálfandi) and five of these have been seen in both areas. This equates to an overall *re-sighting proportion* of 2.4%. Of the five re-sighted dolphins, three (60.0%) were first identified in Faxaflói and two (40.0%) in Skjálfandi. The time between re-sightings ranged from 272 to 821 days (mean of 411.20 days, SD = 230.43) (Table 2). The observed distances between re-sightings ranging from Faxaflói to Skjálfandi are *ca*. 600 km.

DISCUSSION

Minimum abundance

Stable conclusions on abundance and site fidelity are predictably restricted by the use of opportunistic platforms. However, despite its opportunistic nature, this study has given an insight into the population of white-beaked dolphins occurring on the SW and NE coasts of Iceland. Photo-identification indicates there were at least 211 individuals using the Faxaflói and Skjálfandi areas from 2002 to 2010. The absence of a plateau in the ‘discovery’ curve suggests that the white-beaked dolphins found are likely part of a larger population, as is confirmed by systematic aerial surveys which have reported a relative abundance of around thirty thousand animals in Icelandic coastal waters (Pike *et al.*, 2009). Additionally, by 2010 the ‘discovery’ curve for both areas was still ascending, indicating that further photo-identification effort is still required within these waters. This may be important as the study area of Faxaflói surveyed was only a small part of the whole bay. Lastly, an analysis on group size estimates and numbers of photo-identification images would also offer clarification on the proportion of individuals identified during each encounter and consequently also help to explain the minimum abundance estimates found in this study.

There are currently three other existing photo-identification catalogues of white-beaked dolphins: one with 20 photo-identified individuals collected during the summer 2001–10 (Caroline Weir, unpublished data) in Aberdeenshire waters Scotland, one curated by MARINELife, in which eighty individuals were documented between 2007 and 2012 (Brereton, pers. comm.) in Lyme Bay and surrounding waters off south-west England and another detailing 26 identifications collected between 2003 and 2012 (by MARINELife; Kitching, pers. comm.) along the Northumberland coast of England. In comparison to these other white-beaked dolphin catalogues, the photo-identification results provided in this study represent the largest existing photo-identification catalogue of white-beaked dolphins in the North Atlantic.

The most successful identification criteria used for individual dolphins has proven to be notches which are prominent markings with a low gain and loss rate (Auger-Méthé *et al.*, 2010; Auger-Méthé and Whitehead, 2007; Gowans and Whitehead, 2001). To be able to use their body marks, an accurate analysis of their stability over time needs to be conducted in order to know whether these marks can robustly be used to identify individuals (Auger-Méthé *et al.*, 2010). In the present study, several different body marks (summarised by Bertulli *et al.*, 2012) were used as secondary features with the identification of DEMs. However, individuals identified by using only these secondary features were not included in the final abundance estimates (Berghan *et al.*, 2008).

An unbiased estimate of minimum abundance was ensured by using excellent quality images ($Q \geq 5$) as well as high distinctiveness of each dorsal fin (Nicholson *et al.*, 2012). Misidentifications (e.g. false positive and negative errors) were avoided by considering only notches on the dorsal fin as long-lasting and stable identification features. The data set has shown that photo-identification can be a useful technique for the individual recognition of white-beaked dolphins in the coastal waters of Iceland if a strict quality controlled protocol is followed. However, photo-identification can be important in not only obtaining accurate estimates of abundance and survival rates but also study of social interactions and health status of a species, for which photographic quality rules can be relaxed.

Annual re-sighting proportion

Dolphin habitat use (i.e. site fidelity) can be altered by both food availability and predation risk (Heithaus and Dill, 2002). Thus, it is beneficial for a dolphin species to reside in a small area if the food is plentiful and is therefore easily located (Baird *et al.*, 2008); if the food becomes scarce, the size of its home-range might increase (e.g. Defran *et al.*, 1999; Silva *et al.*, 2008).

As an indication of this, three individuals (DEM62, DEM93, DEM163) out of the five re-sighted between

Table 2

Summary of white-beaked dolphin sightings and re-sightings between Faxaflói and Skjálfandi.

No. animals identified	ID-name	1st sighting date Faxaflói	Lat.	Long.	1st sighting date Skjálfandi	Lat	Long	Time (days)
1	DEM62	29/07/2009	64.174	–22.394	19/06/2010	66.098	–17.611	325
2	DEM93	16/05/2008	64.206	–22.042	15/08/2010	66.040	–17.519	821
3	DEM65	16/07/2007	64.250	–22.000	03/08/2006	66.072	–17.625	337
4	DEM174	09/05/2010	64.207	–22.294	10/08/2009	66.046	–17.4791	272
5	DEM163	16/08/2009	64.222	–22.265	13/06/2010	66.119	–17.392	301

Faxaflói and Skjálfandi were sighted in Skjálfandi for the first time in 2010 but they had previously shown site fidelity to the Faxaflói area during 2007–2009. Similarly, 37 dusky dolphins (*Lagenorhynchus obscurus*) in New Zealand waters showed residency off Kaikoura during summer and spring months, when they were also recorded venturing *ca*. 200 km further north in the Marlborough Sounds area during the winter (Markowitz, 2004; Markowitz *et al.*, 2004).

Overlap between the Faxaflói and Skjálfandi white-beaked dolphin 'populations'

This study indicates that white-beaked dolphins inhabit a large-scale coastal range of the Iceland coastline. Dolphins are capable of performing seasonal migrations (e.g. Constantine, 1995; Markowitz *et al.*, 2004; Wood, 1998), mid-distance movements (around 300km; Bearzi *et al.*, 2010; Silva *et al.*, 2008) and long-distance movements (up to 650km; O'Brien *et al.*, 2009). Two more recent findings showed a short-beaked common dolphin (*Delphinus delphis*) mother and calf pair travelling at least 1,000km (Genov *et al.*, 2012), and common bottlenose dolphins covering a minimum distance of 1,277km between UK and Ireland (Robinson *et al.*, 2012).

The reasons for the continual change in distances travelled by the Icelandic white-beaked dolphins are not known. Previous studies suggest how changes in temperature and the occurrence of oceanographic events (e.g. el Niño) could encourage animals to expand their home ranges (e.g. Hansen and Defran, 1990; Neumann, 2001). Since 1997, gradual changes including increased temperature and salinity in the Icelandic marine ecosystem (Marine Research Institute, 2008; 2012) have resulted in visible alterations in distribution and abundance of many fish species (e.g. Astthórsson *et al.*, 2007; as summarised by Björnsson and Pálsson, 2004; Gudmundsdottir and Sigurdsson, 2004; Vilhjálmsson *et al.*, 1997), some of which [e.g. cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*) mackerel, (*Scomber scombrus*), and whiting (*Merlangius merlangus*)] are known to be part of the white-beaked dolphins' diet (Canning *et al.*, 2008; Van Bree and Nijssen, 1964; Víkingsson and Ólafsdóttir, 2004). The recent findings of movements of individuals from the southwest to the northeast coast of Iceland could support these recent changes in the Icelandic coastal marine environment.

Evidence of long distance movements has been previously documented on two occasions in Icelandic waters. In 2006, Tetley *et al.* (2006) reported a white-beaked dolphin sighted twice, 361km apart, in only 6 days. In the same year, a male white-beaked dolphin was tagged with a satellite transmitter in Faxaflói (Rasmussen *et al.*, 2013) and was found to be travelling back and forth between the south and the west coasts, covering a total minimum distance of 5,280km. Opportunistic photo-identification images taken on the west coast of Iceland on 22 June 2008 were re-matched with a photo-identified individual (DEM184) which was photographed on 1 August 2010 in Faxaflói. More photographs taken on 24 February 2012 on the west coast resulted in another rematch with an individual (DEM247, Q4 quality so not included in this analysis) previously identified in Faxaflói on 11 July 2011. When compared to these photo-identifications and to the satellite tagged dolphin data, the present study suggests that white-beaked dolphins in Icelandic waters reside in particular coastal areas, which they regularly explore. One of these areas might range between the southwest and northeast coast of Iceland.

To carefully review all results presented and assess the potential of this study in the long-term, a number of caveats should be highlighted regarding the methods adopted for this study. There were days when dolphins were sighted in the bay but photo-identification images were not collected due to the boats interest in other species (e.g. common minke whales, humpback whales) not associating with the dolphins at that time. White-beaked dolphins showing signs of disturbance and performing avoidance behaviour (e.g. frequent change of direction while surfacing, long dives, further re-surfacing) negated photo-identification being conducted.

Similarly to other 'core user' species, white-beaked dolphins in coastal Icelandic waters may exhibit site fidelity to an area, but they can also travel far through different geographical territories (e.g. Baird *et al.*, 2008; Bearzi *et al.*, 2010; Markowitz *et al.*, 2004; Tezanos-Pinto, 2009; Wilson *et al.*, 2004). The results of this study demonstrate the potential of photo-identification as a technique for studying long-distance movements of this species. A continual use of this technique is, therefore, recommended for future studies to facilitate further inter-regional collaboration between different research institutions in Iceland, and to improve current understanding of white-beaked dolphin abundance, movement patterns and distribution within the region. It is also suggested that an expansion of the area studied into other similar coastal areas on the west coast, could highlight an important connecting area between the southwest and the northeast territories. A focused, long-term, year-round study is needed to verify suggestions about dolphin movements as observed opportunistically from whalewatching boats.

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Correction factors account for the availability of bowhead whales exposed to seismic operations in the Beaufort Sea

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ABSTRACT

The accuracy of estimates of cetacean density from line-transect survey data depends in large part on how visible the target species is to the observer. Behavioural data (i.e. surface and dive times) from government- and industry-funded aerial observation programmes (1980–2000) were used to calculate availability correction factors needed to estimate the number of bowhead whales (*Balaena mysticetus*) from aerial survey sighting data. Correction factors were calculated for bowhead whales exposed and not exposed to seismic operations. Travelling non-calf whales were found to be less likely to be available for detection than other whales, and their availability further declined in the presence of seismic operations. Non-calves were also less available to observers during autumn when exposed to seismic operations than when not exposed, regardless of activity (travelling or otherwise). Such differences in availability appear to reflect behavioural responses to the sound of seismic operations that alters the surfacing and diving patterns of bowhead whales. Localised abundance estimated from aerial surveys may range from 3% to as much as 63% higher in areas ensonified by seismic operations if correction factors are applied to account for differences in availability associated with the presence of seismic operations, compared to abundance estimates derived from assessments that only account for changes in availability of undisturbed whales. These results provide the first empirical estimates of availability for bowhead whales exposed to seismic operations and highlight the implications of not correcting for disturbance-related availability in density assessments in the vicinity of seismic operations.

KEYWORDS: *g*(0); SURVEY-AERIAL; NOISE; BEAUFORT SEA; BOWHEAD WHALE; LINE-TRANSECT; BEHAVIOUR; DIVING; MONITORING

INTRODUCTION

Aerial surveys are a common means to assess the abundance of animals that range over wide areas (Edwards *et al.*, 2007; Evans *et al.*, 2003; Forcada *et al.*, 2004; Hain *et al.*, 1999; Huber *et al.*, 2001; Laake *et al.*, 1997; Pollock *et al.*, 2006; Richard *et al.*, 2010; Southwell *et al.*, 2007). Such surveys typically use systematic line-transect methods and consist of one or more observers recording the numbers, locations and distances from the transect line of detected animals. These data are then analysed using methods such as distance sampling (Thomas *et al.*, 2010) to estimate the density of individuals that were present within the surveyed area. However, the accuracy of these estimates depends on the reliability with which the animals can be detected (Caughley, 1974; Marsh and Sinclair, 1989; Steinhorst and Samuel, 1989).

Distance sampling methodology incorporates a detection function $g(x)$ for modelling the effect of the perpendicular distance (x) from the transect line on the probability of detection. The quantity $g(0)$ is central to the concept of distance sampling (Buckland *et al.*, 2001), and denotes the probability of detecting an object given that it is on or near the transect line. Conventional line-transect methodology assumes that all animals on the transect line are detected (i.e. $g(0) = 1$; Buckland *et al.*, 2001). Hence, a source of negative bias in density estimates can occur when animals along the transect line either cannot be seen or are missed by observers (i.e. when $g(0)<1$).

The probability of failing to detect an animal is composed of two components, perception bias (animals that are potentially visible to observers but not seen) and availability bias (animals that are not available to observers because they are submerged or concealed) (Laake and Borchers, 2004; Marsh and Sinclair, 1989; Samuel and Pollock, 1981). These probabilities may be functions of animal behaviour, survey platform specifications and environmental factors (e.g. sea state and ice cover) (Caughley, 1974). It is therefore necessary to estimate and correct for any biases associated with perception and availability to obtain unbiased density estimates (e.g. Heide-Jørgensen *et al.*, 2010; Marsh and Sinclair, 1989).

Differences in availability make it particularly difficult to obtain unbiased estimates of cetacean abundance from aerial survey observations. Individuals or groups of cetaceans are generally considered available when they are at or near the surface of the water, and considered unavailable to be seen when submerged below the surface (Laake and Borchers, 2004). Availability for a species of cetacean may be estimated as a function of the proportion of time that individuals would be expected to spend at the surface, and the duration of time that the animal, even if submerged, would be within the range of detectability of the observer (described as the time-in-view). The expected proportion of time at the surface can be calculated from surface-respiration-dive (SRD) behaviour data (Hain *et al.*, 1999). The time that an animal may be in view can in turn be determined by survey speed, altitude and the field of view (Fig. 1) from the survey platform (Caughley, 1974; Forcada *et al.*, 2004; Hain *et al.*, 1999; Laake and Borchers, 2004). Consideration of these variables allows correction factors for

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availability to be estimated and incorporated into density estimates.

In the Beaufort Sea, aerial surveys are commonly used to study the distribution of the Bering-Chukchi-Beaufort Seas' population of the bowhead whale (*Balaena mysticetus*). Line-transect sightings data from industry-sponsored aerial surveys have also been used to monitor for effects of offshore industrial activities and estimate localised densities. These density estimates have been used to provide management with estimates of the number of animals exposed to different received levels of seismic sound (Brandon *et al.*, 2011). In the Beaufort Sea, offshore industrial activities occur primarily during the late summer and autumn when the waters are often ice-free and most easily accessible. Hence, industry-sponsored aerial surveys have also occurred during that time.

The westward migration of this bowhead population also occurs during the late summer and autumn (Moore and Reeves, 1993). The migration occurs in pulses (Blackwell *et al.*, 2007), segregated both temporally and spatially by age class, and bowhead distribution is influenced by sea-ice conditions and water depth (Koski and Miller, 2009; Ljungblad *et al.*, 1986; Moore *et al.*, 2000; Treacy *et al.*, 2006). While the predominant activity of bowhead whales at that time of year is travel, they sometimes pause to feed along the migration corridor at places and times where prey is abundant (Koski *et al.*, 2009). Activity state, age class, ice conditions and water depth influence the surface-respiration-dive behaviour of bowhead whales (Dorsey *et al.*, 1989; Richardson *et al.*, 1995; Robertson *et al.*, 2013; Würsig *et al.*, 1984), and potentially the proportion of time that they spend at the surface.

The durations of surfacings and dives of bowhead whales are also influenced by industry operations such as seismic exploration (Ljungblad *et al.*, 1988; Richardson *et al.*, 1986; Robertson *et al.*, 2013). The availability for bowhead whales was first assessed by Davis *et al.* (1982), who recognised the need to account for bowhead whales missed due to variations in their surface and dive behaviour. Davis *et al.* (1982) calculated the correction factors for availability following the method derived by McLaren (1961). More recently, Thomas *et al.* (2002) expanded the earlier work and calculated availability correction factors for presumably undisturbed bowhead whales engaged in different activities. Availability correction factors have not been previously published for bowhead whales or other cetacean species exposed to seismic or other industry operations.

Disturbance and other factors are known to influence surface-respiration-dive behaviour, but it is not known whether they also affect availability and the density estimates of bowhead whales calculated from line-transect surveys. While changes in the surfacing and diving variables noted above would be expected, they do not necessarily correspond with changes in availability. For example, the availability of whales would not change appreciably if they reduced (or increased) both their surfacing and dive times by ~25%. The objective of this study was therefore to assess whether the availability of bowhead whales to aerial observers differs in the presence and absence of seismic operations in the Beaufort Sea. Availability correction factors for bowhead whales in different reproductive states that were engaged in different activities during summer and autumn while in the presence and absence of seismic operations were estimated. The extent to which the presence of seismic operations could result in over- or under-estimates of the local abundance of whales, if this potential source of bias were not accounted for, was also assessed.

METHODS

Data sources and collection

Bowhead behaviour data were obtained from five studies conducted from 1980 to 2000 in the southern Beaufort Sea during summer and autumn. Summaries of these studies are provided by Koski and Johnson (1987), Richardson *et al.* (1986) and Richardson and Thomson (2002). All behavioural observations were made using the same standardised procedures as Würsig *et al.* (1985) and Richardson *et al.* (1985). In brief, the data were collected from fixed-wing aerial observation platforms in a manner that ensured whales were not appreciably disturbed by the observation aircraft (Patenaude *et al.*, 2002; Richardson *et al.*, 1985; 1987; Richardson and Thomson, 2002; Würsig *et al.*, 1985). The observations included whales that had not been recently exposed to seismic operations or other types of human activity (presumably undisturbed behaviour), as well as whales that were exposed to industrial or experimental sources of seismic sounds (potentially disturbed behaviour) (Dorsey *et al.*, 1989; Richardson *et al.*, 1985; 1987; Richardson and Thomson, 2002; Würsig *et al.*, 1985). The data included surface and dive durations. A dive, as recognised here, is based on the definition of a sounding dive by Würsig *et al.* (1984); a sounding dive is when a whale was submerged below the surface and out of sight for ≥60 seconds in duration.

Mean surface and dive durations were calculated for disturbed and presumably undisturbed whales in different reproductive states (non-calf whales, including adult and subadult whales, and cows with a dependent calf), for non-calves engaged in different activities (travelling, socialising and feeding), and for non-calves during summer and autumn. Sample sizes for surface and dive data are summarised in Table 1. Note that all whales classified as undisturbed were presumed to be undisturbed because no seismic activities or other human or industrial activities were occurring or had recently occurred in the region (this was determined if no air-gun pulses, or other industry related sounds were detected on sonobuoys) and the observation aircraft was >457m altitude. Data on surface and dive duration are key components in the calculation of bowhead whale availability.

Assessing the field of view from a Twin Otter

The field of view for an observer in a de Havilland Twin Otter aircraft was determined during September and October 2012. Twin Otter aircraft are one of the main platforms used for government- and industry-sponsored surveys for bowhead whales and other marine mammals in the Beaufort Sea. Visibility is often reduced within a certain lateral distance of the transect line and also forward and aft for these aircraft (Thomas *et al.*, 2002); therefore, complete detection on or near the transect line cannot be assumed even if all whales present were at the surface and available to be seen.

Table 1

Categories for which bowhead whale availability [$a(x)$] correction factors were calculated and the corresponding sample sizes of surface and dive data available. Only dives ≥60s were included for analysis. Correction factors by season and by activity state were calculated for non-calf whales only. Non-calf whales included all whales without a dependent calf.

	Seismic		Undisturbed		Total	
Category	Surface	Dive	Surface	Dive	Surface	Dive
Reproductive status:						
Non-calf	504	106	1,070	333	1,574	439
Cow with dependent calf	29	18	80	67	109	85
Season*						
Summer (3–24 August)	281	71	414	84	695	155
Autumn (25 August–10 October)	223	35	656	249	879	284
Whale activity						
Travel	79	18	120	77	199	95
Feed-shallow (≤20m depth)	46	21	258	97	304	118
Feed-deep (>20m depth)	38	20	213	47	251	67
Social	326	44	369	66	695	110

*25 August delineates the average start of the B-C-B bowhead population's migration west through the central Beaufort Sea (Richardson and Thomson, 2002).

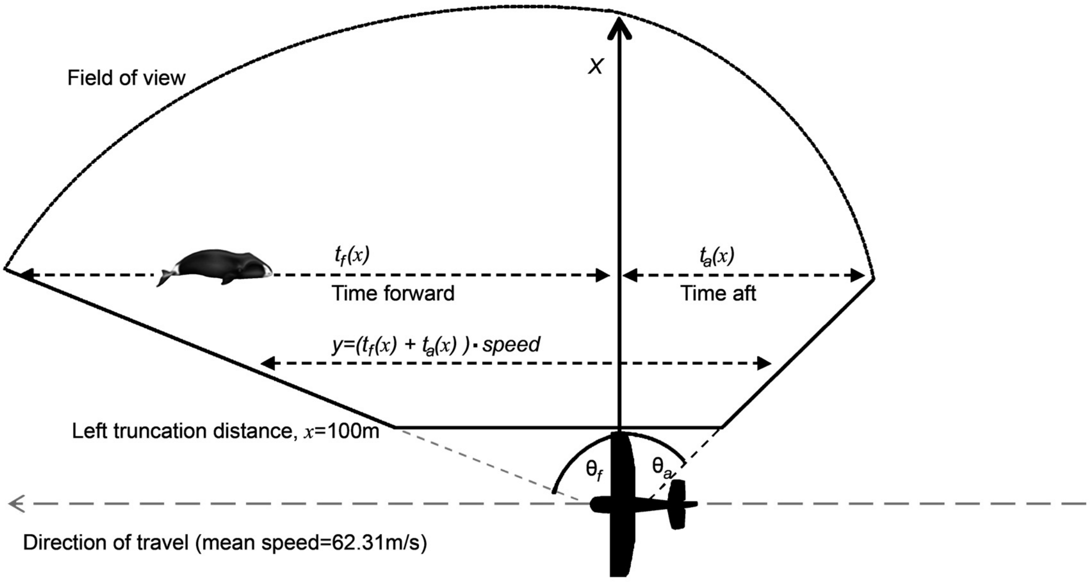

Fig. 1. A depiction of the field of view of an observer from a Twin Otter aircraft. The maximum visible range is denoted by *X*. Observers generally scan an area from $90 - \theta_f$ to $90 + \theta_a$, which gives a maximum angle of view. The field of view aft is smaller than might be expected because search effort is generally focused forward of the plane and perpendicular to it. The total time-in-view (time forward plus time aft) is a function of the perpendicular distance (x), survey speed and altitude, and was evaluated at $x = 100$m, the distance at which bowhead sighting data are generally left truncated. The lateral distance (y) is the swath of the sea surface that is within the observer's field of view.

For this reason, bowheads are only available for detection within a certain viewing area, an area referred to as the field of view.

The field of view is a function of the forward (θ_f) and aft (θ_a) angles-of-view, and a perpendicular distance representing the maximum visible range (X) from the transect line (Forcada *et al.*, 2004) (see Fig. 1). The survey platform, altitude and the scanning behaviour of the observer can affect the parameters of the field of view.

The field of view was estimated by combining the results of a dedicated experiment with a trigonometric modelling approach, similar to that presented by Forcada *et al.* (2004). The experiment to estimate the time-in-view for the Twin Otter aircraft consisted of flying the aeroplane along parallel tracks past a static object (in this case a small structure) at pre-selected discrete distances, increasing from 160m to 1,600m from the object. Each experiment was performed at a standard survey speed of 220km/h (averaging 62.3ms^{-1}) and an altitude of 305m above surface level. A single observer (FCR) was used to collect the data in this experiment. For each parallel track, the discrete distance was randomly selected and only known to the pilots, ensuring that the observer was not cued into a particular search pattern. The observer was asked to maintain their 'normal' search pattern (i.e. to avoid actively searching for the object) and record three time measures: (1) the time at which the object first came into view ahead of the aircraft (t_1); (2) the time when the object was perpendicular to the aircraft (t_2); and (3) the time when the object left the observer's view to the rear of the aircraft (t_3). Two time measures were calculated from these data: (1) time forward: $t_f = t_2 - t_1$ and (2) time aft: $t_a = t_3 - t_2$.

Linear models were fitted separately to the forward time-in-view and aft time-in-view data as a function of perpendicular distance (x), assuming normal sampling error on recorded times.

$$t_i = \alpha_i + \beta_i x \qquad (1)$$

where i denotes either forward or aft (i = a or f) of the line perpendicular to the transect line, and α and β are the model coefficients, where β is the gradient of the line fit to the data. The forward and aft angles of view can then be derived from a trigonometric model using the model coefficient β_i:

$$\tan\theta_i = \beta_i \cdot speed \qquad (2)$$

The dimensions of the field of view allowed forward and aft view times to be evaluated at each perpendicular distance (x) from 0–2,000m, at 100m increments. A maximum perpendicular distance of 2,000m (X) was selected because bowhead sighting data are often truncated at a perpendicular distance of ~2,000m from the transect line (Fig. 1).

$$t_i(x) = \alpha_i + \frac{x \cdot \tan\theta_i}{speed} \qquad (3)$$

This allowed the lateral distances (y) at each perpendicular distance to be determined, where the lateral distance was the swath of sea surface within the observer's field of view in which a whale would have to be at the surface to be detected (Fig. 1). Based on previous aerial survey studies of bowhead whales in the Beaufort Sea (e.g. Funk *et al.*, 2011), sighting data collected from Twin Otter aircraft have been left-truncated at 100m; therefore, for the purposes of this study, we assumed that perfect detection (conditional on the animal being at the surface) should occur at 100m rather than on the transect line itself. Hence we evaluated t at a perpendicular distance of 100m from the transect line. Similar assumptions have been made by Forcada *et al.* (2004) and Hain *et al.* (1999).

Correction factors for availability

Availability correction factors [$a(x)$] were calculated for bowhead whales in the presence and absence of seismic operations and for whales of different reproductive states and for non-calf whales during summer and autumn and while engaged in different activities. Calves were excluded from the analysis because they had different dive profiles and were in close association with an adult whale (the mother). Observers often detect calves after their attention has been drawn to the mother. Correction factors for availability were thus calculated for whales in the presence and absence of seismic operations to determine whether the presence of seismic operations affected the probability of a bowhead whale being available to be seen during an aerial survey.

Availability correction factors were calculated following the method outlined by Laake *et al.* (1997) to describe the availability of harbour porpoise (*Phocoena phocoena*) during an aerial survey study in the coastal waters of Washington State. Their model treats the animals' surfacing and diving behaviour as an alternating Poisson process of being available (time at the surface, s) or unavailable (the length of the dive, d) (Laake and Borchers, 2004). Laake *et al.* (1997) assumed the lengths of the intervals s and d were independent exponential random variables with μ the rate parameter of s and λ the rate parameter of d. Thus the expected values of s and d are $E(s) = 1/\mu$ and $E(d) = 1/\lambda$. Under this model, $E(s) + E(d)$ is the expected length of the surface-dive cycle. Therefore, availability at perpendicular distance x, defined as the probability that an animal at perpendicular distance x will be at the surface at some point while within the observer's field of view, is:

$$P(x) = \frac{\lambda}{\lambda+\mu} + \frac{\mu\left[1-e^{\{-\lambda t(x)\}}\right]}{\lambda+\mu} \qquad (4)$$

Time $t(x)$ in Eqn. 4 is the amount of time the ocean at perpendicular distance x is in the observer's view; Eqn. 4 can be re-written as:

$$P(x) = \frac{E(s)}{E(s)+E(d)} + \frac{E(d)\left[1-e^{\{-\lambda t(x)\}}\right]}{E(s)+E(d)} \qquad (5)$$

(Laake *et al.*, 1997). Substituting sample means for expected values and $t(x)$ yields the availability correction factors:

$$a(x) = \frac{\bar{s}}{\bar{s}+\bar{d}} + \frac{\bar{d}\left[1-e^{\{-t(x)/\bar{d}\}}\right]}{\bar{s}+\bar{d}} \qquad (6)$$

where $t(x)$ is time-in-view (t) evaluated at 100m (estimated using Eqn. 3). Correction factors were calculated for the different categories (e.g. reproductive status, activity state, season and exposure to seismic operations) based on their SRD data (Table 2). The Laake *et al.* (1997) method for estimating the probability that a whale would be at the surface and available for detection is suitable for animals that are considered to be intermittently available (e.g. a marine mammal). Intermittent availability is defined as occurring when an animal is available for more than an instant and its availability can change when it is within the field of view (Laake and Borchers, 2004).

The effect of not applying the correct availability correction factor to bowhead whale sighting data collected in the presence of seismic operations was investigated. The percentage change for abundance estimates was calculated using two correction factors. These were based on SRD estimates from: (i) presumably undisturbed whales; and (ii) those when seismic operations were present:

$$\%change = \frac{N_s - N_{ns}}{N_{ns}} \cdot 100 \qquad (7)$$

where N_{ns} is the estimated abundance of whales obtained when applying the availability correction factor for presumably undisturbed whales and N_s is the abundance estimate for whales in the presence of seismic operations when the appropriate availability correction factor for disturbed whales is applied.

The same approach was used to illustrate how much correction factors themselves vary, when they incorporate a field of view that has been estimated under different assumptions. Correction factors derived with our estimated field of view, $a(x_l)$ were compared to correction factors derived with a field of view that assumed a constant 1km

Table 2

Availability [a(x)] correction factors for presumably undisturbed bowhead whales and those exposed to seismic operations, as calculated from Eqn. (6). Bowhead behaviour data were collected from the southern Beaufort Sea; mean surface ($\bar{s}$) and dive durations ($\bar{d}$) are recorded in seconds and time-in-view (t) (40.85s) is evaluated at a perpendicular distance of 100m. Only sounding dives (≥60s) were included in the dive category in accordance with Würsig *et al.* (1984). Variance estimates (V) were calculated based on the multivariate delta method (Eqns. 9–10). The percentage by which abundance would be underestimated if the incorrect correction factor were applied is also given.

	Seismic				Undisturbed				
Category	$\bar{s}$	$\bar{d}$	*a(x)*	*se*	$\bar{s}$	$\bar{d}$	*a(x)*	*se*	% Change in abundance estimates
Reproductive status									
Non-calf	61.1	528.7	0.170	0.16	74.2	504.7	0.196	0.16	15
Cow with dependent calf	96.4	740.5	0.163	0.13	121.7	656.8	0.207	0.12	27
Season									
Summer	56.4	371.0	0.222	0.18	66.6	394.2	0.229	0.19	3
Autumn	67.0	848.6	0.117	0.10	78.9	542.0	0.190	0.16	63
Whale activity									
Travel	53.0	645.9	0.132	0.14	92.3	705.3	0.165	0.12	25
Feed shallow	55.8	408.5	0.204	0.16	69.5	373.3	0.244	0.21	20
Feed deep	72.6	639.8	0.157	0.18	66.3	524.6	0.179	0.20	14
Social	62.3	507.1	0.178	0.12	73.8	326.2	0.281	0.13	57

swath along the transect line, $a(x_2)$. For a plane travelling at a standard survey speed of 220km/h (averaging 62.3ms^{-1}), a 1km swath will be in view for 16.1 seconds. The difference between correction factors derived from different field of view estimates was calculated as:

$$\% difference = \frac{a(x_1) - a(x_2)}{a(x_2)} \cdot 100 \qquad (8)$$

Variance calculations

Variances specific to each estimated correction factor $a(x)$ were estimated using the multivariate delta method. From the multivariate delta method the variance is:

$$V = \left[\nabla^T P(\boldsymbol{X})\right]|_{X=\gamma} \sum \left[\nabla P(\boldsymbol{X})\right]|_{X=\gamma} \qquad (9)$$

where [$\nabla P(\boldsymbol{X})$] is defined by Eqn. 10 [$\nabla^T P(\boldsymbol{X})$] and is its transpose. The rewritten version of $P(\boldsymbol{X})$ makes clear that it is a function of the random variables s, d and $t(x)$, which are independent by assumption – which is further simplified in Eqn. 10 by writing t in place of $t(x)$. Therefore $\boldsymbol{X}$ is a column vector with elements s, d and t; $\boldsymbol{\gamma}$ is a column vector with elements the estimated mean values $\bar{s}$, $\bar{d}$ and t; and $\sum$ is a three by three diagonal matrix with the variances $V(\bar{s})$, $V(\bar{d})$ and $V(t)$ on its diagonal. The notation $|_{X=\gamma}$ means that the corresponding vector of the partial derivatives of the re-written version of $P(\boldsymbol{X})$ with respect to s, d and t is to be evaluated at $\boldsymbol{X} = \boldsymbol{\gamma}$.;

$$\left[\nabla P(\boldsymbol{X})\right]|_{X=\gamma} \begin{bmatrix} -\frac{d\left(1-e^{\left(-t/d\right)}\right)}{(d+s)^2} - \frac{s}{(d+s)^2} + \frac{1}{d+s} \\ -\frac{d\left(1-e^{\left(-t/d\right)}\right)}{(d+s)^2} - \frac{s}{(d+s)^2} + \frac{1-e^{\left(-t/d\right)}}{d+s} - \frac{e^{\left(-t/d\right)}t}{d(d+e)} \\ \frac{e^{\left(-t/d\right)}}{d+s} \end{bmatrix} \qquad (10)$$

RESULTS

The field of view for a Twin Otter

The experiment to determine the field of view for a Twin Otter was conducted opportunistically 18 times over a two-month period with the same observer (FCR) on each occasion. Line-transect surveys were conducted at a mean survey speed of 62.31ms^{-1}. Linear models fitted to the forward and aft time-in-view data provided the coefficients used to estimate the fore and aft angles (θ) that determined the boundaries of the area searched by the observer (Fig. 2). The coefficients estimated for the forward time-in-view data were 31.41 (SE = 7.17) for α and 0.02 (SE = 0.007) for β, while the coefficients for the aft time-in-view data were 6.37 (SE = 1.42) for α and 0.01 (SE = 0.001) for β. Hence the total time-in-view on the trackline was estimated to be 37.78s. This resulted in a search sector that spanned from 37.4° forward to 121.2° aft (where 0° is ahead of the plane and 90° is perpendicular to the transect line) for the Twin Otter survey aircraft used in this experiment (Fig. 1). Given the assumption that perfect detection occurs at a perpendicular distance of 100m from the transect line, the time that a whale could be within the field of view at an average survey speed of 62.31ms^{-1} and 305m survey altitude was 40.85s (95%CI = 32.89–48.82s). The corresponding distance parallel to the track line and in view to an observer given t at a perpendicular distance of 100m was 2.55km.

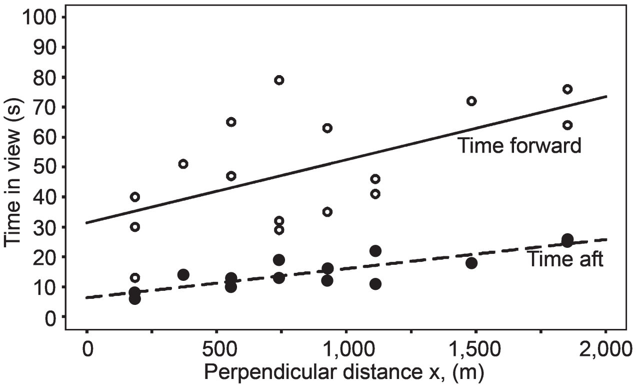

Fig. 2. Linear models fitted to the forward and aft time-in-view data collected during the 18 sampling occasions. The resulting *a* and *b* coefficients were incorporated into the trigonometric model used to estimate the field of view that observers scan while surveying (Eqn. 1–3).

The effect of exposure to seismic operations on availability of bowhead whales

The presence of seismic operations resulted in a lower probability of bowhead whales being available for visual detection within the observer's field of view (Table 2). For a presumably undisturbed non-calf whale, the overall probability of it being available for detection was $a(x)$ = 0.196; however this dropped to $a(x)$ = 0.170 in the presence of seismic operations. The probability of a cow with a dependent calf being at the surface and available for detection was $a(x)$ = 0.207, and higher than that for the average non-calf whale in presumably undisturbed conditions. In the presence of seismic operations, however, the availability of whales with dependent calves declined to $a(x)$ = 0.163 (Table 2). Both non-calf whales and cows accompanied by dependent calves displayed a lower probability of being available for visual detection in the presence of seismic operations. Not correcting for this difference in availability (i.e. failing to apply the appropriate correction factors for whales potentially disturbed by seismic operations) would have resulted in an underestimation of the estimated number of whales by 15% for non-calves and 27% for cows with dependent calves.

The presence of seismic operations had little effect on the availability of non-calves in the summer. In the autumn, however, the availability of non-calf bowhead whales decreased by almost one third in the presence of seismic operations (Table 2). Non-calves exposed to seismic operations were the least available for visual detection in the autumn. Abundance estimates of non-calf whales exposed to seismic operations in the autumn would be underestimated by 63% if the effects of seismic operation activity on whale behaviour were not accounted for.

There was a similar effect of seismic operations on non-calves that were travelling, socialising and feeding. The probability of being available for detection declined for all behaviours in the presence of seismic operations (Table 2). When whales were presumably not disturbed, travelling whales had the lowest probability of being available for detection ($a(x)$ = 0.165). Their availability dropped further when seismic operations were present to $a(x)$ = 0.132 (Table 2). Abundance estimates of travelling whales in the presence of seismic operations would be underestimated by 25% if appropriate correction factors were not applied. Undisturbed socialising whales exhibited the greatest probability of being available for detection, but their availability declined by 57% in the presence of seismic operations. Seismic operations also resulted in a lower probability of feeding whales being available for detection, although the effect was less than that for travelling or socialising whales (Table 2). Numbers of feeding whales exposed to seismic operations would be underestimated by 20% for whales feeding in shallow waters and 14% for whales feeding in deep waters if appropriate correction factors were not used (Table 2). Overall, estimates of abundance for bowhead whales may range from three, to as much as 63% higher in areas ensonified by seismic operations if correction factors were not applied to account for behavioural changes.

Correction factors derived with the time-in-view estimated for this study ($a(x_1)$, t = 40.85s) and a time-in-view that assumed the field of view was a constant 1km swath of water ($a(x_2)$, t = 16.1s) varied by 17%–34% (Table 3). These results highlight the effect of the field of view on availability correction factors. The results of the experiment to determine the field of view for a Twin Otter suggested that t increased as a linear function of perpendicular distance (Fig. 2). This implies that estimates of bowhead whale density derived

Table 3

A comparison of the availability [$a(x)$] correction factors for presumably undisturbed bowhead whales and those exposed to seismic operations derived from a time-in-view (t) of 16.1s for a lateral distance of 1km, and a t of 40.85s calculated using the methods proposed by this study, equating to a lateral distance of 2.55km.

	Seismic			Undisturbed		
	a(x)			*a(x)*		
Category	t = 16.1	t = 40.9	% Difference in *a(x)*	t = 16.1	t = 40.9	% Difference in *a(x)*
Reproductive status						
Non-calf	0.130	0.170	30	0.155	0.196	26
Cow with dependent calf	0.134	0.163	21	0.177	0.207	17
Season						
Summer	0.169	0.222	32	0.179	0.229	28
Autumn	0.091	0.117	29	0.153	0.190	25
Whale activity						
Travel	0.099	0.132	34	0.136	0.165	22
Feed shallow	0.154	0.204	32	0.192	0.244	27
Feed deep	0.124	0.157	27	0.139	0.179	29
Social	0.137	0.178	30	0.224	0.281	25

from aerial surveys should account for survey specific variables (such as survey platform, survey speed, observer search patterns and altitude) as well as whale behavioural changes.

DISCUSSION

This is the first study to investigate and quantify availability for bowhead whales exposed to seismic operations. The results indicate that the probability that a bowhead whale will be available for visual detection is lower when whales are exposed to seismic operations. Hence, if appropriate correction factors are not taken into account, the number of bowhead whales estimated to be in seismic survey areas exposed to various sound levels from seismic operations would be underestimated. Conversely, estimates of avoidance of seismic operations would be overestimated. The probability of detecting a bowhead whale within the field of view of an observer is lowest in the autumn when whales are migrating west through areas of the Beaufort Sea where there are (at some places and times) offshore industry activities, including seismic surveys. In general, at least during the autumn migration, the presence of seismic operations leads to a lower probability of bowhead whales being available for visual detection. A similar potential bias may exist for other whale species exposed to seismic operations.

Availability correction factors calculated in earlier studies were for bowhead whales that were presumed to be undisturbed (e.g. Davis *et al.*, 1982; Thomas *et al.*, 2002) and were specific to the aerial survey protocols of those individual studies. The field of view, and therefore the time-in-view (t) for observers to detect an animal at the surface, on or near the transect-line, is specific to the survey platform and is a function of platform specifications, survey speed, altitude and the individual observers (Caughley, 1974). Therefore, t may vary between surveys, especially if different observers, survey platforms, survey speeds, altitudes and strip widths or scanning patterns are used; availability correction factors derived for one survey may lead to inaccurate results if used in the analysis of data collected from a different platform under differing conditions (Marsh and Sinclair, 1989; Pollock and Kendall, 1987).

Earlier studies conducted in the Beaufort Sea estimated the time-in-view (t) to be between 18s (Davis *et al.*, 1982) and 21.6s (Thomas *et al.*, 2002). These estimates of time-in-view are shorter than the time-in-view at 100m from the trackline of 40.85s that we calculated for a Twin Otter aircraft (with bubble windows) flying at an altitude of 305m, at a standard survey speed of 220km/h. Likewise, the correction factors calculated with different field-of-view assumptions explored in these analyses differed by 17% to 34%. Despite these differences, as long as sightings data are limited to the field of view used to derive an availability correction factor, the application of that correction factor to those data is appropriate. On the other hand, if there is a difference between the field of view used to collect sightings data and that assumed to derive an availability correction factor, bias can be introduced into resulting estimates of densities and abundance. The experimental data used here to model t confirmed that the field of view was not constant across increasing perpendicular distances for a Twin Otter with bubble windows. It is thus important to consider survey specific data and observer search patterns when calculating t to obtain accurate density estimates of whale numbers within survey areas.

The proportion of time that a whale spends at the surface during a typical surface-respiration-dive (SRD) cycle and the time-in-view (t) of a location on the water are the key components needed to assess the availability of a whale for visual detection. Variations in SRD behaviour affect the overall proportion of time that whales spend at the surface, such that a whale that spends a higher proportion of its time submerged, and is therefore unavailable for detection, will decrease the probability of this whale being available for detection. Activity state, season, reproductive status and exposure to seismic operations all influence the availability of a whale for visual detection.

Subtle variations in SRD behaviour of bowhead whales exposed to seismic operations have been identified in early behavioural response studies (Koski and Johnson, 1987; Ljungblad *et al.*, 1988; Richardson *et al.*, 1985; 1986). During the autumn when whales are migrating west through the central Beaufort Sea and have been exposed to seismic operations there, travelling is the primary activity, interspersed with occasional feeding bouts (Koski *et al.*, 2009; Richardson and Thomson, 2002). It is during this time and for travelling whales that the more recent analysis of pooled behavioural data (from studies conducted during 1980 to 2000) found non-calf bowhead whales to be most responsive to seismic operations (Robertson *et al.*, 2013). Our correction factors based on the same behavioural data are consistent with this finding and suggest that non-calf bowhead whales are the least available for visual detection while travelling and in the autumn when exposed to seismic operations. Variation in the availability of a whale for visual detection may result in underestimates of the number of whales exposed to various levels of seismic operations in the Beaufort Sea, especially in autumn, and for travelling bowhead whales.

The surface and dive behaviour of bowhead whales varies with activity state. Differences in behaviours among activity states are also reflected in a whales' availability for visual detection. Thomas *et al.* (2002) determined that travelling whales had the lowest probability of detection while whales engaged in social activities had the highest probability of detection. Our study corroborates this finding for presumably undisturbed bowhead whales. However, the availability for detection declines by over a third when socialising whales are exposed to seismic operations, a level that is below that of whales feeding in shallow waters in the presence of seismic operations.

A large seasonal effect of seismic operations on the availability of bowhead whales was also determined. Most notably, seismic operations had little effect on whale availability during summer when feeding is the predominant activity (Würsig *et al.*, 1985). However, during autumn, seismic operations had a notable effect on the availability of whales when travelling becomes increasingly more common as the whales begin their westward migration. Previous assessments of availability (e.g. Davis *et al.*, 1982; Thomas *et al.*, 2002) focussed on presumably undisturbed bowhead whales, and therefore, are not applicable in analyses of sighting data collected in the presence of seismic and possibly other industrial operations.

During autumn, non-calves exposed to seismic operations have a low probability of being available for detection, followed by presumably undisturbed non-calves that are travelling. This is consistent with the finding that whales observed in the autumn or engaged in travel are more sensitive to seismic operations than are whales engaged in feeding (Koski and Miller, 2009; Robertson *et al.*, 2013). Undisturbed bowhead whales in the eastern and central Beaufort Sea spend the majority of the late summer and early autumn feeding, but also spend approximately one-third of their time travelling (Würsig *et al.*, 2002). During years of particularly low prey density, the time whales spend travelling increases as whales continue their westward migration rather than stopping to feed (Würsig *et al.*, 2002).

Bowhead whales react to seismic operations by subtly changing their SRD behaviour (Koski and Johnson, 1987; Ljungblad *et al.*, 1988; Richardson *et al.*, 1985; 1986; Robertson *et al.*, 2013), which affects the proportion of time that they spend at the surface. These changes are reflected in the probability of the whales being available for detection during an aerial survey. Aerial surveys are commonly part of environmental monitoring programmes for oil and gas exploration in the US Beaufort Sea (Funk *et al.*, 2011). These surveys monitor marine mammal presence and distribution relative to the industry's operations. Some surveys have applied alternate correction factors to account for bowhead whale activity (Thomas *et al.*, 2002). More recent surveys have begun to use availability correction factors that also account for the presence of active seismic operations (Brandon *et al.*, 2011). Nevertheless, results from earlier surveys that did not apply availability correction factors that account for seismic activity likely underestimated the numbers of whales potentially exposed to seismic operations and overestimated avoidance of seismic operations.

The presence or absence of industrial operations and the activity states of the whales seen during surveys will dictate which $a(x)$ estimate should be incorporated into the density analyses. For example, should a survey yield adequate sighting data where the majority of whales were observed feeding in an area with active seismic operations, then it is appropriate to select the correction factor for potentially disturbed feeding whales adjusted by the their value of $a(x)$. Alternatively, analyses of surveys without information on activity states would be stratified by season with the appropriate correction factor selected depending on whether or not seismic operations were present. Selection and use of the appropriate correction factors during analysis will lead to improved estimates of the number of whales exposed to different received levels of seismic sound, as required by regulators, for example, in the USA.

There are a number of limitations to the approach used in this paper to calculate the availability correction factors for bowhead whales exposed to seismic operations. The highly visible nature of the sighting object used in the time-in-view experiment meant that the field of view estimates likely represent the maximum potential detectability, and therefore the maximum time-in-view. The data collected during the time-in-view experiment influenced the choice to fit a linear model to the data. Ideally the pre-selected discrete perpendicular distances should have encompassed the transect line (0m), and the fact that it did not resulted in a lack of experimental observations on and very close to the transect line that may have influenced the overall fit of the model. Future experiments to estimate field of view should be designed so that pre-selected distances encompass the transect line, as well as utilise more realistic sighting objects, such as buoys on the sea surface. The latter would also allow, in principal, potential environmental effects (as discussed further below) to be incorporated in estimates of correction factors. The use of time recorded when the sighting object was perpendicular to the plane in both the calculation for time forward, $t_f = t_2 - t_1$ and time aft: $t_a = t_3 - t_2$ will have led to correlated errors. Future analysis of data collected under such a sampling design should consider the use of a joint-regression where the errors of t_1 and t_3 are independent but the errors of t_2 is the same for each calculation of t_f and t_a.

The time-in-view experiment also did not allow an investigation of the influence of environmental variables (e.g. sea state, sea ice coverage and glare) on the boundaries of the search area. During high sea states, for instance, observers may reduce their search area because it takes longer to decide whether a potential sighting is a marine mammal. Observer scanning behaviour and individual variation are also likely to influence the duration of detectability, and the time-in-view is based on measurements from a single observer. Future studies could likewise use a mixed-effects modelling framework to account for variation due to individual observer scanning behaviour, and also might produce better estimates of variance around the correction factors. Despite the limitations associated with this experiment, these results represent a first attempt to estimate a survey-specific time-in-view at the location where detection is assumed to be 1.0 for the Twin Otter aircraft commonly used for bowhead surveys in the Alaskan Beaufort Sea. These analyses have built on previous methods that have only estimated time-in-view based on aircraft speed (e.g. Davis *et al.*, 1982) or predetermined measures of the forward and aft angles of view (e.g. Forcada *et al.*, 2004).

The methods available to estimate the parameters associated with the field of view are an area of active research (Borchers *et al.*, 2013). A review of different methods may be warranted to understand their limitations and how differences between methods may influence overall estimates of availability. We acknowledge that there are limitations with the approach presented here resulting in a degree of uncertainty surrounding the final time-in-view estimates. However, this experimental approach has highlighted the need for further research into methods that can provide improved accuracy in field of view estimates, and ultimately detection patterns for marine mammals during aerial surveys.

Group size can influence how available whales are to being seen by observers. Groups of two or more whales, for example, tend to be more detectable to observers than single individuals. Surface-active groups of North Atlantic right whales (*Eubalaena glacialis*) have been found to have the highest availability with a mean of 93%, while the availability of individual right whales ranged from 40–60%

(Hain *et al.*, 1999). Bowhead whales engaged in surface skim feeding or socialising activities are often observed in groups of two or more whales (Würsig *et al.*, 1985; 1989). Such group activities by socialising bowhead whales and by whales feeding in shallow waters tend to increase disturbance of the surface waters, leading to higher probabilities of detection. The detection factors presented here are for individual whales.

Environmental, observer and whale related variables inevitably influence both the time-in-view as well as the overall availability of a bowhead whale for visual detection by an aerial observer. Although we were unable to account for the effects of many of these variables, these correction factors could be considered to be better than past values, but not optimal values for bowhead whales within each of the categories examined. Future measurements of the time-in-view in marine areas and subsequent estimates of bowhead whale availability should investigate and incorporate the effects of environmental, observer and whale related variables so that more accurate measures of detectability can be determined for a wider range of conditions.

Understanding how the behaviour, distribution and habitat use of bowhead whales are affected by industry operations is needed to evaluate the potential effects of oil and gas exploration and development activities on individual whales and their populations. These analyses have shown that seismic operations generally resulted in whales being less available for visual detection by aerial observers. Although these methods are specific to aerial observations of bowhead whales in the Beaufort Sea during summer and autumn, the same principles apply to aerial surveys and vessel-based surveys for other seasons, species and regions. Future studies investigating the effects of anthropogenic activities on cetacean distribution, local abundance and behaviour should calculate availability correction factors specific to the species of interest at the time and in the circumstances of exposure. This is necessary to avoid under- or over-estimating the number of whales exposed to potential sources of disturbance and to avoid over- or under-estimating the degree of avoidance around those activities. Such assessments require situation-specific data on surfacing and dive behaviour of the cetaceans, which can be obtained by visual methods (as shown here) or by tagging and telemetry methods. This information is needed to calculate appropriate correction factors for sighting data to better estimate the numbers of cetaceans that may have been exposed to disturbances (such as seismic operations). This information is needed in turn to determine how exposure to industrial activities influences the distribution of cetaceans and their choice of habitat.

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Abundance and distribution of marine mammals in nearshore waters off New Jersey, USA

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ABSTRACT

Marine mammal abundance and distribution in New Jersey's nearshore waters are not well known due to limited dedicated studies. The first year-round systematic surveys were conducted to determine the spatial/temporal distribution and estimate the abundance of marine mammals in this region prior to wind power development. Eight marine mammal species were observed: North Atlantic right whale (*Eubalaena glacialis*), humpback whale (*Megaptera novaeangliae*), minke whale (*Balaenoptera acutorostrata*), fin whale (*Balaenoptera physalus*), bottlenose dolphin (*Tursiops truncatus*), common dolphin (*Delphinus delphis*), harbour porpoise (*Phocoena phocoena*) and harbour seal (*Phoca vitulina*). Results indicate clear seasonal patterns in distribution and abundance. The fin whale, humpback whale and bottlenose dolphin were sighted during all seasons. The abundance of large whales in the study area was relatively low while the abundance of dolphin and porpoise species was high and largely seasonal. The bottlenose dolphin was the most abundant species; however, abundance was high only during spring and summer. Common dolphins and harbour porpoises were common in the study area during winter and spring. These baseline data will be used to assess potential environmental impacts of the construction and operation of offshore wind power facilities in this region.

KEYWORDS: ABUNDANCE ESTIMATE; MODELLING; DISTRIBUTION; CONSERVATION; SURVEY–AERIAL; SURVEY–VESSEL; ATLANTIC OCEAN; HABITAT; NORTH ATLANTIC RIGHT WHALE; HUMPBACK WHALE; MINKE WHALE; FIN WHALE; BOTTLENOSE DOLPHIN; COMMON DOLPHIN; HARBOUR PORPOISE; HARBOUR SEAL

INTRODUCTION

Marine mammals are important marine resources in New Jersey's nearshore waters which are prime areas targeted for offshore renewable energy development, particularly wind power development, on the United States (US) Atlantic Outer Continental Shelf (OCS). In 2010, Geo-Marine, Inc. (GMI) successfully completed the US's first Ecological Baseline Study (EBS) specific to offshore wind planning for the New Jersey Department of Environmental Protection (NJDEP) (GMI, 2010). The EBS is a precursor to the initiation of the State of New Jersey's test project to obtain practical knowledge of the benefits and impacts of offshore wind turbine facilities off the coast of New Jersey. This study was conducted in accordance with the New Jersey Blue Ribbon Panel on Development of Wind Turbine Facilities in Coastal Waters formed by New Jersey State Executive Order 12. The EBS provided critical information on the marine resources that may be impacted by the construction and operation of these facilities. This paper describes the results of the marine mammal surveys which were an important component of the NJDEP EBS. The data collected from these baseline surveys were used to conduct an assessment of potential environmental impacts and to assist in the siting of offshore wind power facilities in nearshore waters off New Jersey.

The National Marine Fisheries Service (NMFS) and other organisations have been conducting marine mammal surveys along the US east coast for many years. Although several of these surveys have included waters surveyed during the EBS (e.g. mid-Atlantic *Tursiops* aerial surveys, *Delaware II* 97–05 shipboard survey, Cetacean and Turtle Assessment Program [CETAP] aerial and shipboard surveys), none has concentrated efforts specifically in New Jersey's nearshore waters with the exception of a photo-identification survey conducted by NMFS' Southeast Fisheries Science Center and the Rutgers University Marine Field Station in coastal waters off southern New Jersey from May through October in 2003, 2004 and 2005 (Blaylock, 1995; CETAP, 1982; Garrison and Yeung, 2001; NMFS-NEFSC, 1997; Toth Brown, 2007). In addition, no year-round survey efforts have been conducted in this region. The NJDEP EBS includes the first year-round systematic survey effort for marine mammals in this region.

MATERIALS AND METHODS

Field methods

Study area

The study area encompassed 5,259km^2 of nearshore waters from the shoreline to approximately 37km offshore between Wildwood Crest and northern Barnegat Bay, New Jersey (Fig. 1). The offshore boundary of the study area roughly followed the 30m isobath which is the maximum installation depth of the turbines that are planned for this region.

Aerial surveys

Aerial surveys were conducted once a month from February through May 2008 and twice a month (when possible) from January through June 2009. The surveys followed standard line-transect methods (see Buckland, 2001). In 2008, they were conducted from a twin-engine, high-winged Cessna *Skymaste*r 337 with bubble windows on each side of the

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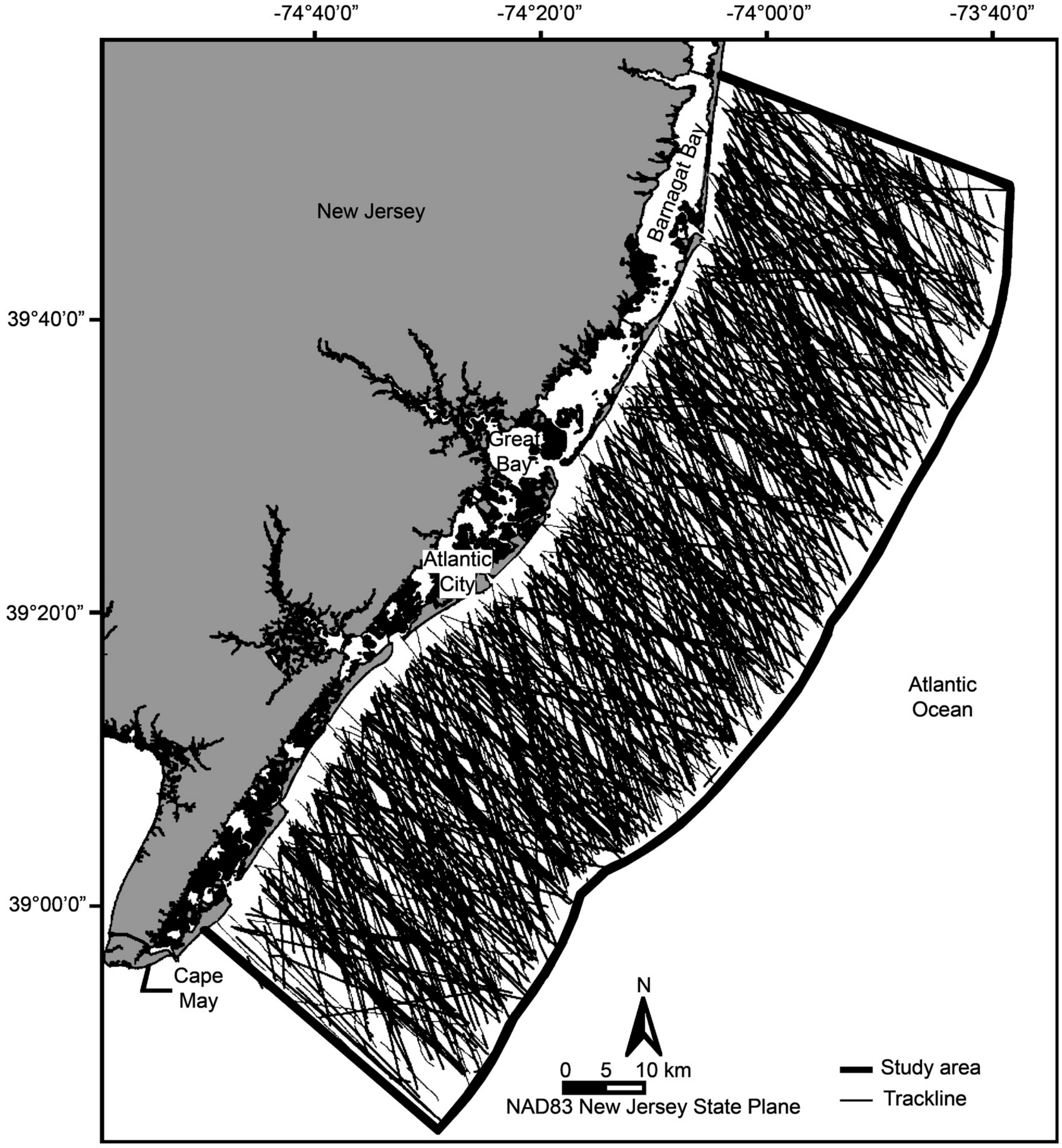

Fig. 1. Tracklines covered during the aerial and shipboard surveys.

aircraft to allow unobstructed views of the transect lines directly beneath the plane. During the 2009 surveys, a Cessna *Skymaster* without bubble windows was used, resulting in limited visibility below the aircraft. Surveys were flown at ~229m altitude and a speed of ~220km per hour (km/h) during daylight hours when there was at least 3.7km visibility and a Beaufort Sea State (BSS) less than 6.

For the February 2008 survey, randomly-generated transect lines (tracklines) were spaced 3.7km apart and orientated perpendicular to the coastline. Survey design was changed to a double saw-tooth pattern for the rest of the surveys to provide comparable spatial and temporal coverage of the entire study area and allow the entire study area to be surveyed in one day, thereby minimising the temporal variation. Tracklines were randomly generated in a double saw-tooth pattern for each survey using the program *Distance 5.0* (Buckland *et al.*, 2004; Thomas *et al.*, 2010).

Visual observations were recorded by a team of three people during the 2008 surveys. Two experienced observers searched for animals at the surface from directly beneath the aircraft out to a perpendicular distance of approximately 1,500m. The third person served as the data recorder and was stationed in the co-pilot seat. During the 2009 surveys, flight protocols followed those stated above with some modifications; a co-pilot was added so there was no room in the plane for a dedicated data recorder. Therefore, the two experienced observers positioned in the rear seats were responsible for observations and recording data. One observer recorded the time and position of each sighting on a laptop while the second observer recorded the sighting information on a digital tape recorder.

The aircraft's position along the trackline (in addition to all other survey information) was collected every 10s on a computer interfaced with the aircraft's global positioning system (GPS) *via* a custom data acquisition program. Environmental conditions (e.g. BSS, solar glare, water colour and transparency), which may affect the ability to detect animals, were recorded prior to the start of each trackline and updated as needed while on effort. All sightings data, including time, position, declination angle, group size, species and behaviour were recorded. Animals were identified to the lowest possible taxonomic group.

During the 2008 surveys, when an animal was sighted perpendicular to the aircraft along the trackline, the angle to the sighting (≤60°) was determined either using a digital inclinometer or 10° intervals (bins) marked on the aircraft windows for calculation of perpendicular sighting distances. During the 2009 surveys, the perpendicular sighting distances were calculated based on GPS locations.

During both the 2008 and 2009 surveys, the observers went into off-effort mode at the time of a sighting to verify species identification and estimate group sizes. The species identification, best estimate of group size, behaviour, time, position and associated animals were also recorded. A circle-back procedure was used if necessary to verify species identification and estimate group sizes.

Shipboard surveys

Shipboard surveys were conducted monthly from January 2008 through December 2009 on the University of Delaware's R/V *Hugh R. Sharp* using a single platform and following standard line-transect methods (Buckland *et al.*, 2001). The surveys were conducted at 18.5km/h along randomly-generated tracklines in a double saw-tooth pattern which crossed the bathymetry gradient and maximised uniform coverage of the study area. The starting point and time of each cruise was chosen based on the timing of high tide and weather conditions due to the docking criteria of the R/V *Hugh R. Sharp*. Tracklines were altered only if sea state, glare, or weather inhibited survey efforts.

Visual observations were recorded from the flying bridge (10m above water) during daylight hours when weather permitted at least 2km of visibility and BSS was 5 or less. The marine mammal observer team consisted of six individuals; three observers were actively on duty at any one time and rotated positions every 40 min. On-duty observers consisted of one observer searching with 25×150 power *Fujinon* binoculars ('bigeyes') mounted on a pedestal on the port side of the vessel while another observer searched through bigeye binoculars mounted on the starboard side. The third observer served as the data recorder and also searched the water with unaided eyes and 7× hand-held binoculars between the port and starboard bigeye observers. Each observer scanned out to the horizon from abeam (90°) on his/her side of the ship to 10° to the opposite side of the bow (100° in all). The 20° along the ship's trackline thus received overlapping coverage by the two bigeye observers.

Weather conditions (BSS, wind speed, swell height and direction, direction of sun, visibility, etc.), visual effort (on or off), sightings and other survey information were recorded. Weather conditions were recorded every 40 min (when observers rotated positions) and updated when conditions changed. The GPS position of the vessel, as well as the vessel's course and speed, was automatically recorded every 2 min *via* an integrated, stand-alone GPS unit on the flying bridge. The data fields recorded for all sightings included the time, position, initial bearing and distance, group size, species identification (or lowest identifiable taxonomic category) and behaviour. Three estimates of group size (best, maximum and minimum) were recorded for all sightings. Estimates of group size and the percent taxonomic composition were made independently by each observer without discussion to minimise observer bias.

Analytical methods

The following periods were used as seasonal designations in the analyses of sightings data: winter (18 December–09 April), spring (10 April–21 June), summer (22 June–27 September) and fall (28 September–17 December). These seasons were calculated based on three years (2007–2009) of sea surface temperature (SST) data. Winter and summer are the times of year with the lowest and highest temperatures, respectively, while spring and fall represent transitional periods between the two temperature extremes.

Data preparation

Sightings included in the density/abundance analyses met the following criteria: (1) sightings were recorded by on-duty observers while the team was searching in on-effort mode; (2) perpendicular sighting distances were able to be calculated and (3) sightings and effort were recorded in a BSS ≤5 for all species/groups except the harbour porpoise (*Phocoena phocoena*) which was analysed based on sightings and effort recorded in a BSS ≤2 due to the low detectability of this species in higher sea states (Polacheck, 1995).

Density estimation

Aerial and shipboard survey data could not be combined for density/abundance estimation because of the differences in survey techniques and perception bias. Therefore, separate analyses were conducted using the aerial and shipboard sightings data. The Conventional Distance Sampling (CDS) method was used to generate abundance/density estimates for the overall study area using *Distance 6.0*, release 2 (Thomas *et al.*, 2010). Based on line-transect theory (Buckland *et al.*, 2001), density was estimated as a function of (1) encounter rate n/L (where n = number of sightings and L = line-transect length), (2) probability density function at zero perpendicular distance $f(0)$, (3) mean group size $E(s)$ and (4) probability detection function at zero perpendicular distance [$g(0)$].

The estimated density (D) is given by the following equation:

$$D = N/A = n*E(s)*f(0)/2L*g(0)$$

where N = abundance, A = study area and the other parameters are as defined previously.

Density is estimated as the ratio of the number of animals sighted (n) to the survey coverage area (a), where $a = 2wL$, w = strip half-width (truncation distance) and L = transect length. The effective strip half-width (ESW), μ, is defined as the sighting distance such that the number of animals at distances less than μ that were missed by the observer is equal to the number of animals at distances greater than μ that were detected by the observer. The ESW μ is equal to $1/f(0)$.

For those species with sufficient sightings and covariate data, the Multiple Covariate Distance Sampling (MCDS) method was used to model probability of detection as a function of both distance and one or more covariates to increase the precision of density estimates (Marques and Buckland, 2003; Marques *et al.*, 2007). The included covariates were BSS, group size, and visibility which have all been shown to affect perpendicular sighting distances (Barlow *et al.*, 2001). These covariates were all treated as continuous variables.

The error or uncertainty associated with each estimated parameter [*D*, *n/L*, *f*(0), *E(s)*] was quantified by the variance (Var), coefficient of variation (CV) and the 95% confidence interval (CI). The analytical variance of a density or abundance estimate was estimated using the delta method, and the log-normal 95% confidence limits were obtained using equations 3.71–3.74 of Buckland *et al*. (2001) except that t-based limits were calculated using degrees of freedom calculated using the Satterthwaite method given in formula 3.75. The nonparametric bootstrap method was used to estimate variance when group size was included as a covariate in the MCDS.

A discussion of factors affecting animal detectability and methods of accounting for detection bias are discussed in Thomsen *et al.* (2005). A *g*(0) of 1 was assumed because estimates of *g*(0) could not be calculated due to the limitations of the single platform observer configuration for both the ship and aerial surveys. During attempts to consistently implement the Hiby circle-back method (Hiby, 1999) during the aerial surveys, the additional data recording requirements of the team and the circle-back protocol resulted in unconfirmed or loss of sightings due to the multi-tasking of observers. In addition, the method of conducting simultaneous ship and aerial surveys to estimate *g*(0) (Palka *et al.*, 2005) was not practical for this study due to the relatively low encounter rates in the study area. Previously estimated *g*(0) values from similar surveys were not used in the current study since detection probability has been shown to vary substantially among observers, platforms, weather conditions, etc. (Borchers, 2005). Therefore, the density and abundance estimates calculated for this study are considered relative estimates and are not absolute and may be underestimated due to both perception and availability biases.

To account for group-size bias, an expected mean group size was estimated using a regression method in which the logarithm of group size of observation was regressed against the estimated detection probability. Mean group size in the population was estimated from the predicted mean size of detected groups in the region where the detection probability was 1 (at zero perpendicular distance from the trackline). This regression method corrected for size-biased detections and for the underestimation of size of detected groups (Buckland *et al.*, 2001). A statistical hypothesis test was applied to the regression of group size on distance, and the expected mean group size was only used in the analysis if it was significantly ($P<0.15$) smaller than the arithmetic mean group size.

The decrease in detection probability as a function of increasing perpendicular distance from the trackline was modelled using the uniform, half-normal, and hazard-rate key functions along with polynomial or cosine series expansion terms as required, except for the MCDS models which do not allow for the uniform key function. In most cases, the optimal model was chosen as that model which yielded the smallest value of the Akaike's Information Criterion (AIC) index (Buckland, 2001; 2004). In some cases where the behavioural observations indicated a problem with avoidance or attraction to the survey platform, the optimal model was subjectively chosen. For example, when a spike near the trackline was thought to be caused by the attraction of the animals to the platform, the optimal model chosen was the one that did not fit the detection function to the whole spike since fitting the spike near the trackline results in inflated abundance/density estimates.

This model optimisation analysis was conducted for each species/group in which there were around 20 sightings that met the criteria listed above. A sample size of at least 60 sightings is typically recommended for estimating a detection function (Buckland, 2001), and 15 sightings may be the absolute minimum number of sightings that can be used to fit a detection function (Barlow *et al.*, 2006). The sightings recorded during 2008 and 2009 were combined to maximise the number of sightings for each species/group for analysis. Species with fewer than 20 sightings were pooled into taxonomic groups with species of similar sighting characteristics, when possible, to model a group detection function. The data were then stratified by species to estimate abundance/density of individual species using the pooled detection function. For some species and groups, sufficient sightings data were recorded such that density/abundance estimates could be generated for different seasons while others were limited to annual analyses.

Histograms of the perpendicular distance data and selected various cutpoints were plotted to identify suitable truncation points for removal of spurious data and outliers. Right truncations were based on specific distances from the trackline which were determined on a case-by-case basis for the different species/groups. In some cases, spurious data can cause spikes of detections near the trackline. These spikes often arise when animals are attracted to the survey vessel and detections were not made before any responsive movement occurred (Thomas *et al.*, 2010). For the shipboard survey analyses, the spiked data were not removed with a left truncation so that data with a near-100% detection probability at short distances were not eliminated. A left truncation was used for the aerial survey data collected in 2009 not because of a spike near the trackline but because of the limited visibility of the trackline due to the lack of bubble and belly windows on the survey plane. In this case, a left truncation position was chosen where detection was certain.

RESULTS

Survey effort

The aerial surveys covered 12,222km of on-effort trackline between February 2008 and June 2009 (Fig. 1). The total amount of aerial survey effort that met the criteria (i.e. BSS 0 to 5) for the abundance/density analyses for all species/groups except the harbour porpoise was as follows: winter (6,188km), spring (4,084km) and summer (1,950km). No aerial surveys were conducted during the fall. The shipboard surveys covered 12,893km of on-effort trackline between January 2008 and December 2009 (Fig. 1). The total amount of shipboard survey effort that met the criteria (i.e. BSS 0 to 5) for the abundance/density analyses for all species or groups except the harbour porpoise was as follows: winter (3,696km), spring (2,704km), summer (3,830km) and fall (2,663km). The total survey effort included in the harbour porpoise analysis (BSS 0 to 2) for winter abundance/density was 1,150km. There were insufficient sightings data to model the abundance/density of this species during the other seasons or from the aerial surveys.

Distribution and abundance

Eight species of marine mammals were sighted in the study area during the study period: North Atlantic right whale (*Eubalaena glacialis*), humpback whale (*Megaptera novaeangliae*), minke whale (*Balaenoptera acutorostrata*), fin whale (*B. physalus*), bottlenose dolphin (*Tursiops truncatus*), common dolphin (*Delphinus delphis*), harbour porpoise and harbour seal (*Phoca vitulina*). During the aerial and shipboard surveys, a total of 512 sightings (396 of which were on effort) were recorded (Figs 2–4). The sighting information and abundance/density estimates for each species are discussed below. Table 1 provides a summary of the sightings for each species/group. Both on-effort and off-effort sightings were assessed to describe species distribution in the study area; therefore, all sightings were included in the calculations of mean and range for group size, water depth, distance from shore, and SSTs for each species (Table 1). Given the relatively low number of sightings and associated variables, CDS was used to analyse the data for most species/groups. MCDS was attempted for the bottlenose dolphin analyses due to the larger number of sightings and associated covariates. Results of the analyses, including density/abundance estimates with corresponding 95% CIs and CVs, are summarised in Tables 2 and 3. Detection functions were also plotted versus perpendicular sighting distance in the form of histograms of the collected data overlaid by a curve describing the fit of the optimal model to the sightings data (Fig. 5).

Endangered marine mammals

North Atlantic right, humpback, and fin whales are all designated as endangered marine mammals under the US Endangered Species Act (ESA). These species were pooled to fit a detection function since they have similar sighting characteristics due to their large body sizes and distinct blows and because there were not enough sightings recorded for humpback or North Atlantic right whales to fit separate

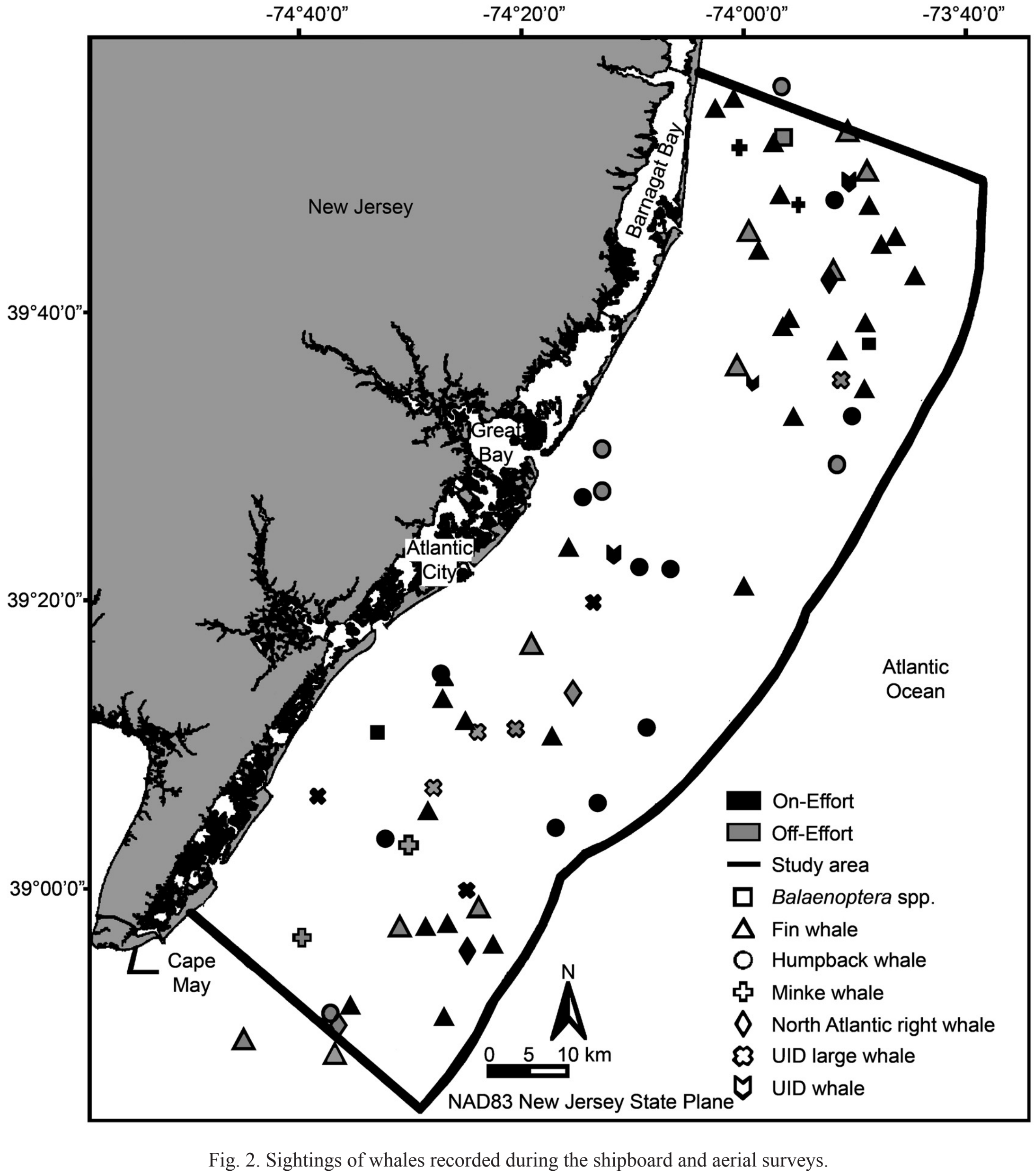

Fig. 2. Sightings of whales recorded during the shipboard and aerial surveys.

detection functions for these species. Sightings of this group were recorded throughout the year. Due to the overall low number of sightings of this group, abundance/density estimates were generated for the entire year and not for any specific seasons using the shipboard survey data. The distance data were truncated at 5,000m which left 33 sightings to be analysed; only one sighting was removed from the analysis based on the chosen truncation distance. A half-normal key function with no adjustments was chosen as the best model based on the lowest AIC value and the fit of the detection function (Fig. 5). The year-round abundance of endangered baleen whales was estimated to be three individuals (95% CI = 2–5; %CV = 29.49; Table 3). Therefore, at any given day of the year, three endangered baleen whales may be in the study area.

NORTH ATLANTIC RIGHT WHALE

Four sightings of North Atlantic right whales were recorded during the study period (Fig. 2, Table 1). Only two of these sightings were on effort; therefore, no estimates of abundance could be generated for this species. These sightings and the results of passive acoustic monitoring for right whales in the study area are discussed in detail in Whitt *et al*. (2013). North Atlantic right whales were sighted during winter, spring and fall and were acoustically detected year round (Whitt *et al.*, 2013). Three of the sightings were recorded during November, December and January when right whales are known to be on calving grounds off Georgia/Florida (Winn *et al.*, 1986) or in the Gulf of Maine (Cole *et al.*, 2013). In 2008, a cow-calf pair was sighted offshore Atlantic City in May and subsequently sighted in the Bay of Fundy in August (Whitt *et al.*, 2013). Photos of each right whale sighted were matched to the North Atlantic Right Whale Catalog maintained by researchers at the New England Aquarium (Whitt *et al.*, 2013).

HUMPBACK WHALE

Seventeen sightings of humpback whales were recorded throughout the study area; seven of these were off effort and 10 were on effort (Fig. 2, Table 1). Humpback whales were sighted during all seasons; the majority of sightings (nine) were recorded during winter. In mid-September 2008, a mixed species aggregation of a fin and humpback whale was recorded south of Atlantic City. The humpback whale was observed lunge feeding in the vicinity of the fin whale in water depths of 15m. A cow-calf pair was recorded in February 2008 just north of the study area boundary in 20m of water. This was the only sighting of a humpback calf during the study period. Breaching behaviour was observed during two sightings: one in May 2009 and the other in October 2009. Photographs were compared to the College of the Atlantic's North Atlantic Humpback Whale Catalog. One individual sighted in the August 2009 was matched to the catalog and had previously been observed in the Gulf of Maine in 2008 (M. Weinrich pers. comm.). The endangered marine mammal data were stratified by species so that an individual year-round abundance estimate could be generated for the humpback whale using the pooled detection function. Based on this analysis, one humpback whale may be in the study area on any given day of the year (95% CI = 0–2; %CV = 54.64; Table 3).

FIN WHALE

Fin whales were the most frequently sighted large whale species during the survey period with a total of 37 sightings recorded (27 were on effort) (Fig. 2). This species was sighted throughout the year. One mixed-species aggregation of a fin and humpback whale was observed in September 2008. While the humpback whale was lunge feeding, the fin whale surfaced multi-directionally but did not appear to be feeding. One calf was observed with an adult fin whale in August 2008. Photographs were compared to the North

Table 1

Summary of sightings data (combined aerial and shipboard survey data) by species/group.

	Sightings (no. of groups)			Group size (no. of animals)		Water depth (m)		Distance from shore (km)		SST* (°C)	
Common name	On effort	Off effort	Total	Mean	Range	Mean	Range	Mean	Range	Mean	Range
North Atlantic right whale	2	2	4**	1.5	1–2	22.5	17–26	23.7	19.9–31.9	10.0	5.5–12.2
Humpback whale	10	7	17	1.2	1–2	20.5	12–29	18.4	4.8–33.2	10.1	4.7–19.5
Minke whale	2	2	4	1.0	1	18.0	11–24	13.1	6.7–18.5	8.3	5.4–11.5
Fin whale	27	10	37	1.5	1–4	21.5	12–29	20.0	3.1–33.9	9.6	4.2–19.7
Bottlenose dolphin	257	62	319	15.3	1–112	16.6	1–34	11.3	0.4–37.7	16.3	4.8–20.3
Common dolphin	23	9	32	12.8	1–65	23.2	10–31	23.5	3.0–37.5	7.1	4.7–12.4
Harbour porpoise	42	9	51	1.7	1–4	21.5	12–30	19.5	1.5–36.6	5.8	4.5–18.7
Harbour seal	1	0	1	1.0	1	18.0	18	9.9	9.9	11.4	11.4
Unidentified cetacean	0	1	1	3.0	3	28.0	28	22.0	22.0	5.2	5.2
Unidentified small cetacean	3	0	3	1.0	1	21.0	14–25	19.5	9.3–32.3	5.3	4.5–6.0
Unidentified dolphin	13	8	21	5.0	1–20	22.2	12–32	19.4	5.0–37.6	11.2	5.3–19.6
Unidentified small delphinid	5	0	5	2.0	1–4	22.6	10–29	19.6	3.2–35.3	5.6	5.1–6.4
Balaenoptera spp.	2	1	3	1.0	1	20.3	17–23	16.2	8.6–27.7	9.6	4.4–18.9
Unidentified whale	3	0	3	1.0	1	22.0	17–25	17.0	12.7–21.1	13.9	11.3–18.9
Unidentified large whale	3	4	7	1.0	1	19.4	15–28	18.6	5.8–27.6	8.3	4.7–18.9
Unidentified pinniped	3	1	4	1.3	1–2	16.0	8–27	14.4	2.8–30.7	6.4	4.9–10.6

*SST data were remotely sensed. **Two sightings of North Atlantic right whales were recorded close together in both time and space on 12 December 2009. These sightings were originally recorded as two separate sightings and appear as such in GMI (2010). Subsequent photo-identification analyses indicated that these sightings were of the same individual North Atlantic right whale. Therefore, the first sighting of this individual is considered the original sighting, and the second sighting is considered a re-sight of the individual and, thus, is not included in this table.

Atlantic Finback Whale Catalogue managed by Allied Whale for possible matches, but no matches were made.

Enough sightings were recorded to fit an unpooled detection function for this species. A 5,000m truncation was chosen for the year-round analysis which resulted in the removal of only one sighting (Table 2). The remaining 24 sightings were described well by a half-normal model with no adjustments (Fig. 5). Based on the resulting year-round abundance estimate, two fin whales may be present in the study area on any given day of the year (95% CI = 1–4; %CV = 36.48; Table 3).

Minke whale

Four sightings of minke whales were recorded during the survey period (Fig. 2, Table 1). Sightings of minke whales occurred during the winter and spring. The winter sightings were recorded in February in the northern portion of the study area northeast of Barnegat Light. The two spring sightings were recorded in June in the southern portion of the study area southeast of Sea Isle City and northeast of Wildwood. The differing sighting characteristics of this species compared to the other whales sighted during this study prevented any pooling of sightings data to fit a detection function for this species. Therefore, no abundance estimates could be generated for the minke whale.

Delphinids

The common dolphin was the dominant delphinid species sighted during the winter surveys. There were insufficient sightings of this species to model a detection function; therefore, common dolphins were pooled with other delphinid sightings recorded during winter to model a detection function. Fourteen of the sightings included in this delphinids group for winter were common dolphins. The remaining seven sightings were likely common dolphins but were recorded as unidentified dolphins or unidentified small delphinids because species identifications could not be confirmed. A detection function was modeled for the pooled group of common dolphins, unidentified dolphins and unidentified small delphinids for the winter. Detections were truncated at 2,500m which left 18 sightings in the analysis (12 of which were common dolphins) (Table 2). The large spike of detections during the trackline is likely due to the attraction of this species to the ship; common dolphins often approached the ship to bow ride (Fig. 5). The hazard-rate key function had the lowest AIC value but also resulted in very high abundances because this model was fitting the spike of detections near the trackline. The half-normal key function provided a better fit for the data and did not include the entire spike (Fig. 5). The winter abundance estimate for the delphinids group was 92 individuals (95% CI = 38–218; %CV = 46.22; Table 3).

COMMON DOLPHIN

A total of 32 sightings (23 on effort) of this species were recorded during the survey period (Fig. 3, Table 1). The presence of calves was confirmed in 26% of the shipboard sightings. The mean water depth of sightings was 23.2m which is the deepest mean depth for all identified cetacean sightings. This may indicate a preference for deeper waters or may be a construct of the fact that the distribution of sightings of common dolphins during the study period was relatively far from shore (mean = 23.5km). Common dolphins were only sighted during fall and winter (late November through mid-March). The data were stratified by species so that a winter abundance estimate could be

Table 2

Number of sightings meeting the criteria for analysis (before and after truncation), truncation distance, mean group size used in the analysis (expected or observed), fitted detection function model, estimated probability density function evaluated at zero perpendicular sighting distance [*f*(0)] in km^{-1} and the corresponding percentage coefficient of variation (CV), effective strip width (*ESW*) and encounter rate of each species or group in km^{-1} analysed. All analyses, except those designated as 'aerial', were conducted with the shipboard survey data.

Common name or group	Sightings n_{Before}	Sightings n_{After}	Truncation distance *w*(m)	Mean group size***	*f*(0)	%CV *f*(0)	*ESW* (m)	Encounter rate (*n/L*)
Endangered marine mammals								
Year-round	34	33	5,000	1.303 (*e*)	0.000334	13.45	2991.9	0.002554
Humpback whale*								
Year-round	7	7	5,000	1.143 (*o*)	0.000418	37.84	2392.5	0.000542
Fin whale								
Year-round	25	24	5,000	1.381 (*e*)	0.000307	15.78	3253.8	0.001857
Delphinids								
Winter	21	18	2,500	9.000 (*o*)	0.000797	16.37	1254.9	0.004854
Common dolphin*								
Winter	14	12	2,500	12.333 (*o*)	0.000797	16.37	1254.9	0.003236
Bottlenose dolphin								
Spring	69	68	3,500	19.853 (*o*)	0.000582	9.45	1719.2	0.025074
Summer	98	97	3,500	10.448 (*e*)	0.000521	7.59	1919.9	0.025338
Summer (aerial)	72	40	10**	18.350 (*o*)	0.001554	12.61	643.63	0.020508
Harbour porpoise								
Winter	30	27	2,200	1.889 (*o*)	0.000848	16.10	1179.9	0.023254

*Species were pooled with others of similar detectability to model detection functions due to the limited number of sightings of the individual species. **Left truncation was chosen within 10m of the trackline due to the limited visibility of the trackline directly below the survey plane. ***(*e* = expected; *o* = observed).

Table 3

Estimates of abundance and density (individuals/km^2) and the corresponding 95% confidence intervals (CI) and percentage coefficient of variation (CV) for each species and group analysed. All estimates, except those designated as 'aerial', were generated from the shipboard survey data.

Common name or group	Abundance (*N*)	95% CI(*N*)	Density (*D*) per 1km^2	95% CI(*D*)	%CV
Endangered marine mammals					
Year-round	3	2–5	0.000560	0.000317–0.000988	29.49
Humpback whale					
Year-round	1	0–2	0.000130	0.000045–0.000370	54.64
Fin whale					
Year-round	2	1–4	0.000394	0.000197–0.000790	36.48
Delphinids					
Winter	92	38–218	0.017405	0.007301–0.041493	46.22
Common dolphin					
Winter	84	33–213	0.015901	0.006245–0.040487	50.15
Bottlenose dolphin					
Spring	761	362–1,600	0.144770	0.068903–0.304180	39.10
Summer	363	196–669	0.068942	0.037353–0.127250	31.93
Summer (aerial)	1,537	758–3,119	0.292350	0.144120–0.593050	36.97
Harbour porpoise					
Winter	98	35–272	0.018612	0.006704–0.051676	55.27

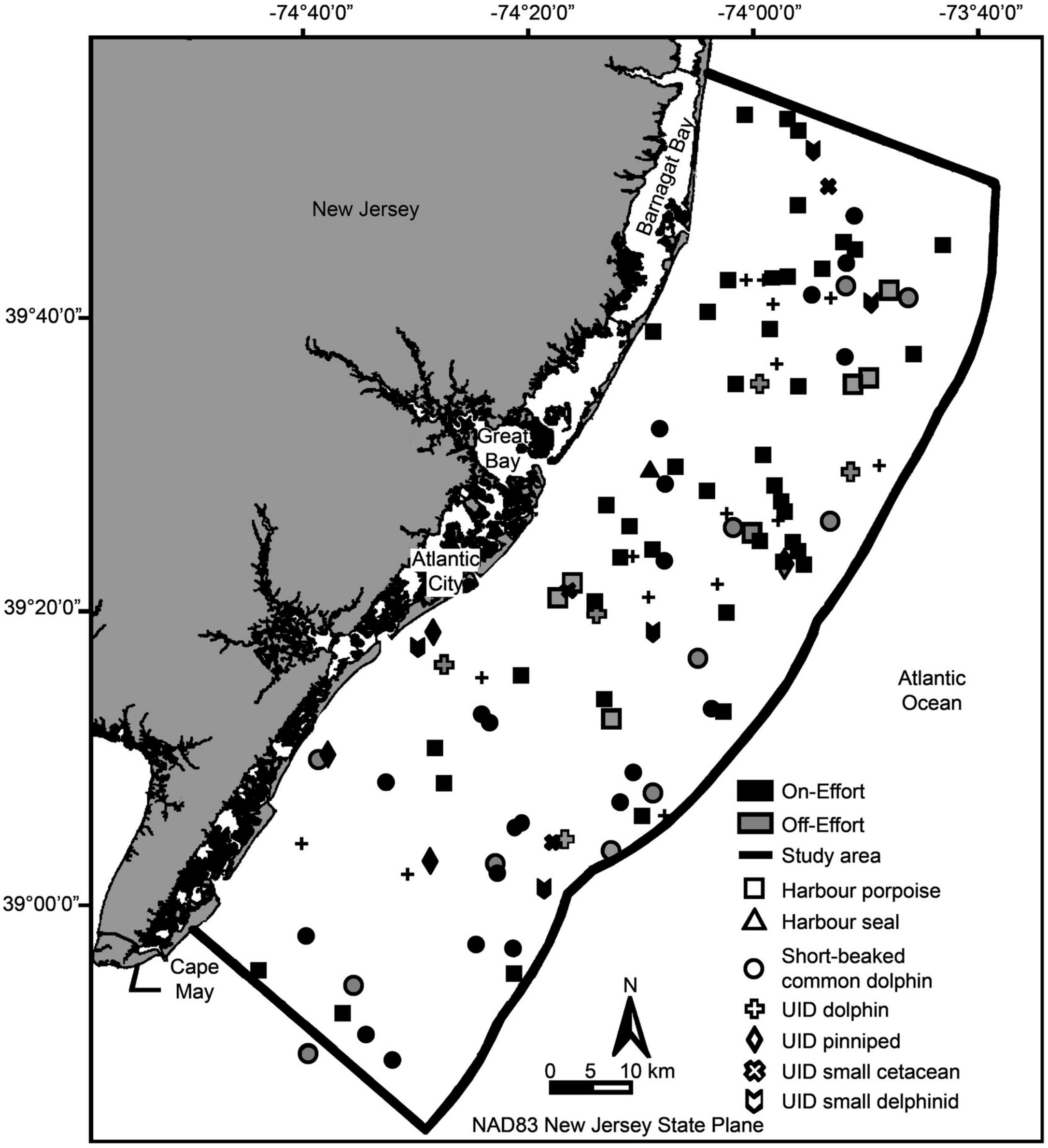

Fig. 3. Sightings of small cetaceans and pinnipeds recorded during the shipboard and aerial surveys.

generated for this species. This abundance estimate was 84 individuals (95% CI = 33–213; %CV = 50.15; Table 3). There were not enough sightings of this species to generate fall abundance/density estimates.

BOTTLENOSE DOLPHIN

Bottlenose dolphins were the most frequently sighted species during this study. A total of 319 sightings were recorded; most of these (257) were on effort (Fig. 4, Table 1). The presence of calves was confirmed in 24% of all sightings. This species was sighted during all seasons. Occurrence was documented as early as the beginning of March and as late as mid-October, but the vast majority of sightings were during the spring and summer. There were not enough sightings of this species to generate abundance/density estimates for the fall or winter seasons; therefore, only spring and summer analyses were conducted. The spring analysis using the shipboard survey data included a right truncation at 3,500m which resulted in 68 sightings left for analysis (Table 2). The half-normal key function was used although the hazard-rate actually resulted in a lower AIC value. A high number of detections of bottlenose dolphins within 250m of the trackline resulted in a spike near zero (Fig. 5); the hazard-rate key function fitted the detection function to this spike which resulted in a higher estimate of abundance. This spike was likely caused by the attraction of this species to the ship and the failure of observers to detect the animals before any responsive movement occurred. To minimise the influence of this spike, the half-normal key function with no adjustments was used to fit the detection function and resulted in a model with a flatter 'shoulder' to the detection function (Fig. 5). The spring abundance of bottlenose dolphins using the half-normal model was estimated to be 761 individuals (95% CI = 362–1,600; %CV = 39.10; Table 3).

The analysis of bottlenose dolphin sightings recorded from the shipboard surveys during the summer was based on a right truncation at 3,500m which resulted in 97 sightings left for analysis (Table 2; Fig. 5). The best model included BSS as a covariate and used a half-normal key function with no adjustments. This MCDS model provided a reasonable fit

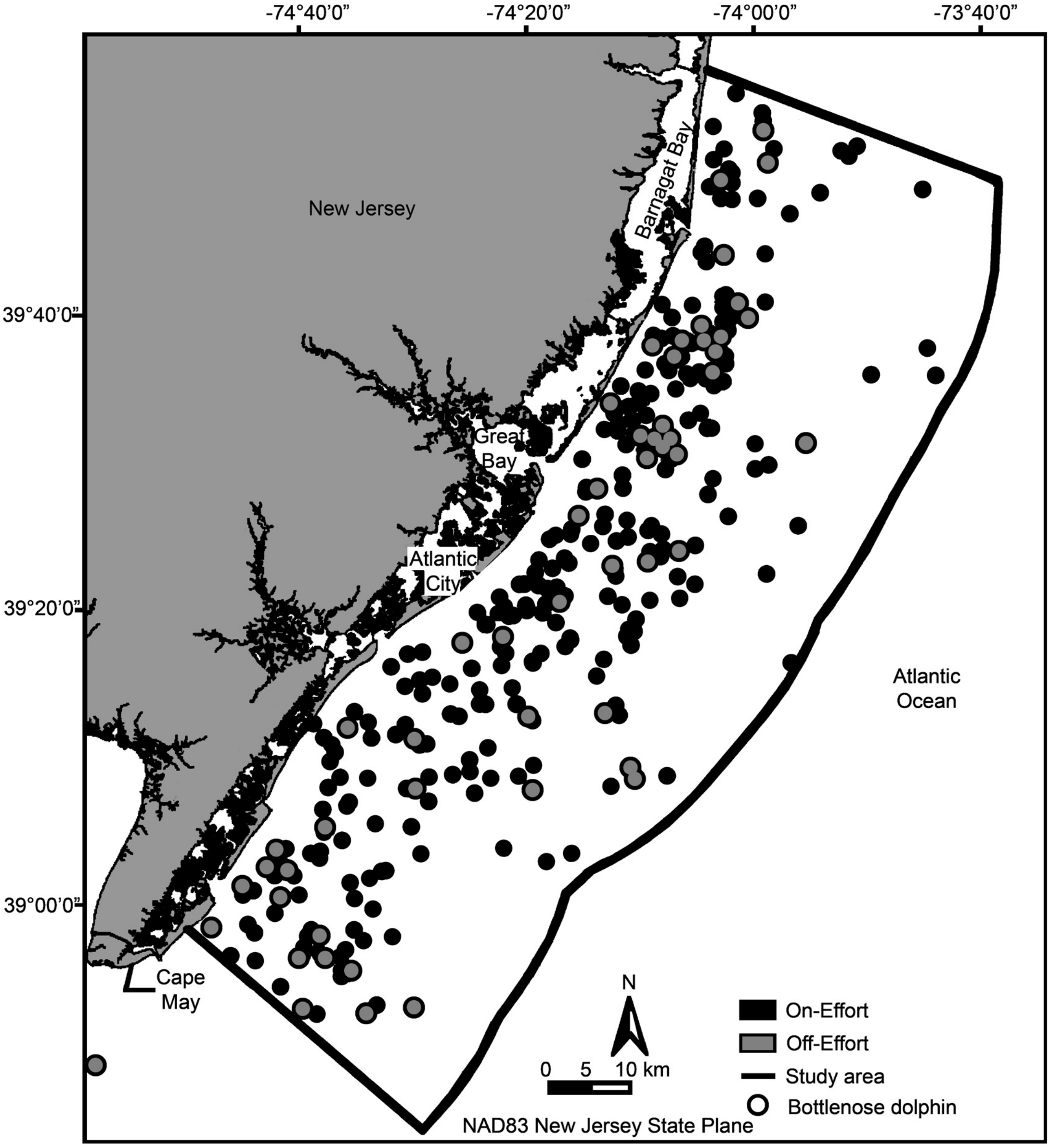

Fig. 4. Sightings of bottlenose dolphins recorded during the shipboard and aerial surveys.

to the data and provided a low AIC value. Note that we chose a model that did not fit the spike of detections near the trackline to minimise the influence of the likely attraction of bottlenose dolphins to the ship. The summer abundance estimated from this model was 363 individuals (95% CI = 196–669; %CV = 31.93; Table 3). The analysis of bottlenose dolphin sightings recorded from the aerial surveys during the summer was based on a left truncation at 10m (Table 2). Summer aerial surveys were only conducted in 2009 during which the survey plane did not include bubble or belly windows. Therefore, visibility below the aircraft directly on the trackline and within 10m on either side of the trackline was limited, violating the assumption that all animals on the trackline were detected. Therefore, the left truncation position was chosen to include only the portion of the trackline where detection of animals was certain. After the left truncation at 10m, 40 sightings were left for the analysis. A MCDS model with BSS as a covariate and the half-normal key function with no adjustments provided the best fit for the data (Fig. 5). The summer abundance estimated from these aerial survey data was 1,537 individuals (95%CI = 758–3,119; %CV = 36.97; Table 3).

Harbour porpoise

The harbour porpoise was the second most frequently sighted cetacean after the bottlenose dolphin. A total of 51 sightings were recorded (42 on effort) (Fig. 3, Table 1). Over 90% of harbour porpoise sightings were recorded during winter (mainly February and March). Three sightings occurred during spring (April and May), and one sighting was recorded during summer (July). The mean SST (5.8°C) for harbour porpoise sightings was the lowest value for all identified cetacean species. There were insufficient sightings of this species to conduct a fall, spring or summer analysis. A right truncation of 2,200m was chosen for the winter analysis to maximise the sample size. This truncation distance only removed three sightings; therefore, 27 sightings remained for the analysis (Table 2). A very small spike of detections was evident within 250m from the trackline which might suggest responsive movements to the presence of the vessel. No apparent attraction behaviour was documented for this species during the survey period; this species is known to move away from vessels (Barlow, 1988; Palka and Hammond, 2001; Polacheck and Thorpe, 1990). A half-normal key function with no adjustments was chosen as the best model based on the fit and the low AIC value (Fig. 5). The winter abundance of harbour porpoises in the study area was estimated to be 98 individuals (95% CI = 35–272; %CV = 55.27; Table 3).

Harbour seal

Only one harbour seal was recorded during the survey period; therefore, no abundance estimate could be generated for this species. This individual seal was observed in shallow

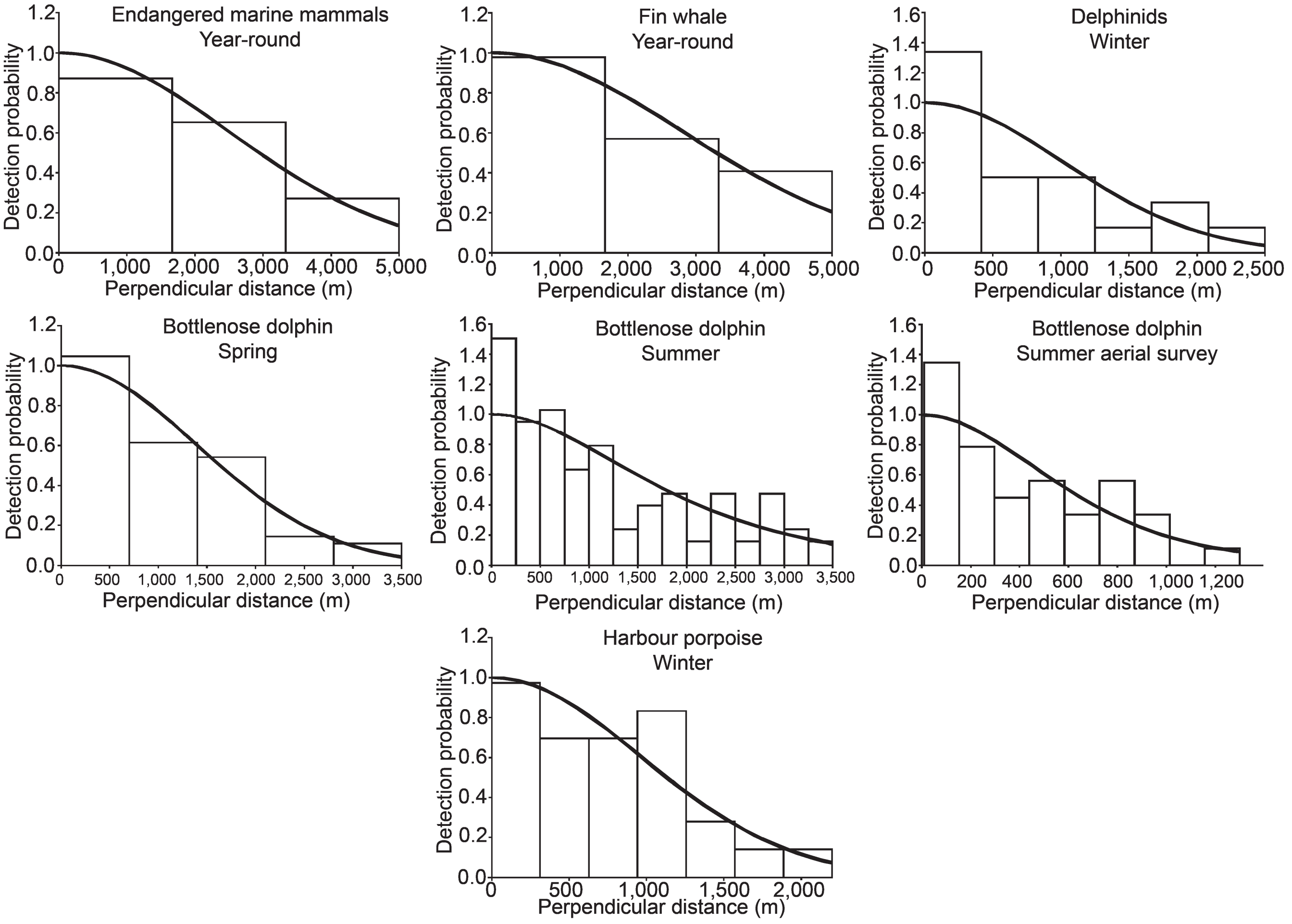

Fig. 5. Histograms of observed distances and fitted detection functions for the species and groups analysed.

waters (18m) 9.9km east of Little Egg Inlet in June 2008 (Fig. 3, Table 1). The three unidentified pinnipeds recorded in the study area were probably harbour seals but species identification could not be confirmed.

DISCUSSION

Baleen whales

Endangered baleen whales

The year-round detections of North Atlantic right, fin and humpback whales confirm the occurrence of these species in this portion of the Mid-Atlantic outside of 'typical' migratory periods (i.e. summers spent at high-latitude feeding grounds and winters spent at low-latitude breeding grounds) (Corkeron and Connor, 1999). The year-round presence of fin and humpback whales was visually confirmed. Although right whales were visually detected in all seasons except summer, they were acoustically detected during the summer months, which also confirms the year-round presence of this species (Whitt *et al.*, 2013). Humpback whales are known to migrate between summer feeding grounds from south of New England to northern Norway (Kenney and Winn, 1986; Stevick *et al.*, 2003b; Weinrich *et al.*, 1997; Whitehead, 1982) and winter calving grounds in the West Indies region (Smith *et al.*, 1999; Stevick *et al.*, 2003a; Whitehead and Moore, 1982). Similarly, North Atlantic right whales undertake a well-defined, strongly seasonal migration between their feeding grounds off the northeastern US and Canada and their calving grounds off the southeastern US (Kenney, 2001; Winn *et al.*, 1986). Fin whales are believed to follow the typical baleen whale migratory pattern consisting of movement between northern summer feeding grounds and southern winter calving grounds (Aguilar, 2009; Clark, 1995). However, not all humpback, right or fin whales in the western North Atlantic undergo these seasonal migrations (e.g. Aguilar, 2009; Charif *et al.*, 2001; Clapham, 2009; Clapham *et al.*, 1993; Dawbin, 1966; Kraus *et al.*, 1986; Swingle *et al.*, 1993). Although the abundance estimates for these whales were relatively low, the presence of even one humpback, right or fin whale in nearshore New Jersey waters is enough to trigger monitoring and mitigation measures given their endangered status.

The detections of these species in the study area, particularly during times of the year when individuals are known to be in other areas, demonstrate the potential year-round importance of this region as more than habitat for seasonal migrants. Based on the sightings and behavioural observations from the current study, the nearshore waters off New Jersey may provide important nursery and feeding habitat for endangered baleen whales. A right whale cow-calf pair sighted in the study area in May was presumably en route to the Bay of Fundy (Whitt *et al.*, 2013). During the encounter of a fin whale cow-calf pair in August, the calf circled our ship while the cow appeared to be making foraging dives several hundred meters from the calf. One of the humpback whales sighted exhibited lunge feeding behaviour, and the two juvenile right whales sighted together appeared to be skim feeding (Whitt *et al.*, 2013). The main feeding grounds for both species are north of the study area (Cole *et al.*, 2013; Nichols *et al.*, 2008; Weinrich *et al.*, 1997). Although feeding could not be confirmed for any of these whales, the observations of feeding behaviour suggest that New Jersey's nearshore waters may serve as additional feeding areas for these endangered species.

Minke whale

Minke whales are widespread throughout US waters but are most likely to occur in US Mid-Atlantic waters during winter. Sightings of this species in the study area during winter (February) are consistent with the known movement of minke whales southward from New England waters from November through March (Mellinger *et al.*, 2000; Mitchell, 1991). Occurrence of minke whales in New England waters increases during the spring and summer and peaks from July through September (Murphy, 1995; Risch *et al.*, 2013; Waring *et al.*, 2013). The June sightings recorded during the study period may have been of individuals moving back to New England waters for the summer.

Delphinids and harbour porpoise

The occurrence of delphinids and porpoises was largely seasonal. Although bottlenose dolphins were present during all seasons, abundance was highest in the spring and summer which coincides with the known movement of the Northern Migratory Coastal stock into the northern portion of their range (Waring *et al.*, 2010). Common dolphins and harbour porpoises were frequently seen in the study area during the winter and spring. The high winter abundance of common dolphins in the study area is consistent with their known seasonal movements to mid-Atlantic waters during colder months (Hamazaki, 2002; Payne *et al.*, 1984; Perrin, 2009). High abundances of harbour porpoises also occurred during the winter when the waters off New Jersey and in the New York Bight provide an important habitat for this species (Westgate *et al.*, 1998). The fall season appears to be a transitional period for these seasonal cetacean species. Few sightings of bottlenose dolphins and common dolphins were recorded during the fall despite the large amount of shipboard survey effort. It is likely that most bottlenose dolphins have already moved south of the study area, and most common dolphins and harbour porpoises are farther north during this time of year.

Bottlenose dolphin

The bottlenose dolphin was the most abundant and most frequently sighted species found in the study area. High abundances of bottlenose dolphins off New Jersey have been documented since the 19th century (True, 1885). New Jersey and Long Island, New York represent the northernmost range of coastal bottlenose dolphins in US waters (Waring *et al.*, 2010) with the exception of extralimital sightings in Cape Cod Bay (Wiley *et al.*, 1994). The bottlenose dolphins found in coastal waters off New Jersey are thought to belong to the Western North Atlantic Northern Migratory Coastal stock which occupies a small range between New York and North Carolina. This stock moves between the mouth of Chesapeake Bay and Long Island during summer (July–September) and between Cape Lookout, North Carolina and the North Carolina/Virginia border during winter (January–March) (Waring *et al.*, 2010). During our study, bottlenose dolphins were sighted during all seasons but were most abundant during the spring and summer months, particularly May through August, which coincides with the known movement of the coastal stock into the northern portion of their range. The sightings data also confirmed the presence of this species in New Jersey waters as early as March and as late as mid-October. Although no bottlenose dolphins were recorded in the study area between November and February, previous sightings have been recorded in December and January (CETAP, 1982). In addition, a group travelled into the Shrewsbury and Navesink Rivers in northern New Jersey in the summer of 2008 and remained there into the winter months[5]. In February 2010, a group of 8 to 15 animals, most likely bottlenose dolphins, was spotted in the Hackensack River far inland in northern New Jersey[6].

The seasonal occurrence of bottlenose dolphins off New Jersey is thought to be due to the presence of preferred prey species (sciaenid fishes) which occur off New Jersey during June through August (Able and Fahay, 1998; Gannon and Waples, 2004). Seasonal movements off New Jersey may also be indirectly influenced by water temperatures which affect the distribution of these sciaenid fishes (Toth *et al.*, 2011). Previous bottlenose dolphin surveys off New Jersey recorded average temperatures of the first and last sightings of the migration season between 14 and 16.3°C (Toth *et al.*, 2011). During the current study, bottlenose dolphins were recorded in SSTs ranging between 4.8 and 20.3°C (mean SST was 16.3°C) (Table 1), indicating that bottlenose dolphins off New Jersey can regularly withstand a wide range of temperatures, particularly low temperatures. They are also known to withstand water temperatures as low as 0.7°C based on the sightings of bottlenose dolphins that overwintered in the New Jersey rivers in January 2009 (A. Gorgone, pers. comm.). However, these sightings may represent extraordinary circumstances since coastal bottlenose dolphins do not typically overwinter this far north.

Bottlenose dolphins off New Jersey are known to prefer coastal habitat over estuarine habitat although they are found in Delaware Bay off the southern end of New Jersey (Toth *et al.*, 2011). Previous coastal studies focused on fine-scale distributions within 6km from shore (Toth Brown, 2007; Toth *et al.*, 2011). Toth Brown (2007) documented a significant break in the habitat usage of bottlenose dolphins in this range of New Jersey's nearshore waters, with one group using the waters within 2km of the shore and the other occupying waters outside of 2km of shore with very little overlap between the two groups. Toth *et al.* (2011) noted a 'core area' used by bottlenose dolphins, particularly cows and their calves between Brigantine and Little Beach. The current study covered a wide longitudinal range of the coast and resulted in sightings extending approximately 38km offshore with a mean distance of 11.3km from shore (Table 1). Sightings were scattered within this range along the coastline with slight concentrations detected north of Little Beach/Great Bay and between Great Bay and Atlantic City (Fig. 4).

Results indicate that the preferred coastal habitat for this migratory stock may extend offshore to approximately 38km off New Jersey. However, the bottlenose dolphins sighted during the current study could not be confirmed as belonging to the coastal stock or the Western North Atlantic Offshore stock, which is recognised seaward of 34km from the US coastline (Waring *et al.*, 2008). North of Cape Lookout, these two stocks are thought to be separated by bottom depth; the coastal form occurs in nearshore waters (<20m deep) while the offshore form is in deeper waters (>40m deep) (Garrison *et al.*, 2003). In addition, no offshore bottlenose dolphins have been detected within 40km from shore in this region (Garrison *et al.*, 2003). Because the bottlenose dolphin sightings were all within 38km from shore and in waters less than 35m deep, it is assumed that all of these sightings were of individuals from the coastal stock. Additional surveys and genetic sampling are required to confirm the current distribution patterns and any mixing or segregation of these stocks off New Jersey.

Common dolphin

Although common dolphins were confirmed in the study area during the fall and winter (November through March), they may occur year round. Previous sightings have been recorded in May and July just east and north of the study area (Canadian Wildlife Service, 2006; CETAP, 1982), and sightings farther offshore near the shelf break are common during the summer months (Jefferson *et al.*, 2009). Strandings have also been recorded along the New Jersey coastline during all seasons (NMFS Northeast Region Marine Mammal Stranding Network, unpublished data). Common dolphins primarily occur offshore in waters 200 to 2,000m in depth (Canadian Wildlife Service, 2006; CETAP, 1982; Jefferson *et al.*, 2009; Ulmer, 1981); however, they are known to occur in shallower waters in the Mid-Atlantic (Hamazaki, 2002; Payne *et al.*, 1984). During the current study, this species was sighted throughout the study area in waters 3 to 37km from shore and 10 to 31m in depth. Therefore, sightings support the occurrence of this species in shallow, coastal waters in this region.

Harbour porpoise

Harbour porpoises were most common in the study area in February and March, which is the time of year when New Jersey waters are known to be an important habitat for this species (Westgate *et al.*, 1998). However, harbour porpoises were also recorded in the study area in April, May and July, indicating that this species utilises this region during other times of the year. Strandings have also been recorded in the study area during winter, spring and summer (NMFS-NEFSC, 1997). No harbour porpoise sightings were recorded during the fall; however, weather conditions were often above a BSS 2 which makes sighting this species very difficult. The densest concentrations of harbour porpoises are thought to occur from New Jersey to Maine from October through December (NMFS-NEFSC, 2001). Therefore, harbour porpoises are likely to occur in the study area throughout the fall. Harbour porpoises are known to occur most frequently over the continental shelf and are most often found in waters cooler than 17°C (Read, 1999). Sightings data from the current study are consistent with these known habitat associations; harbour porpoises were recorded between 1.5 and 37km from shore in waters ranging from 12 to 30m in depth and 4.5 to 18.7°C.

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[5] Information available at *http://www.nefsc.noaa.gov/njdolphins* and *http://usatoday30.usatoday.com/news/nation/2008-12-27-dolphins_N.htm*. Accessed 15 August 2013.

[6] Information available at *http://www.northjersey.com/news/021710_Dolphins_seen_in_Hackensack_River.html*. Accessed 15 August 2013.

Pinnipeds

Harbour seals may be found in the study area during any time of year and are known to make seasonal movements in New Jersey waters during the winter, specifically from late October to early May (Slocum, 2009). Only one harbour seal was recorded in the study area during the study period. This seal was sighted in shallow waters east of Little Egg Inlet in June. Other unidentified pinnipeds recorded near Ocean City in April were likely also harbour seals but could not be confirmed. Harbour seals regularly haul out inshore of the study area at three major sites: Great Bay, Barnegat Inlet, and Sandy Hook (Slocum, 2009). The harbour seal observed in June was likely from one of these sites.

Biases

The relative abundance/density estimates presented in this paper are most likely underestimates because they are not fully corrected for perception or availability biases. Perception bias results when an observer fails to detect an animal on the trackline when the animal is actually at the surface on the trackline. Factors that can influence perception bias include viewing conditions (e.g. BSS, glare, swell height, visibility), observer condition (e.g. experience, fatigue) and platform characteristics (e.g. pitch, roll, yaw, altitude). Perception bias was minimised by using experienced observers, allowing sufficient observer breaks to minimise fatigue, and conducting surveys during optimal sea conditions. However, because the goal was to record any marine mammal species in the study area, survey effort was not limited to near perfect detection conditions (e.g. BSS 0–2). Instead, survey effort was limited to the maximum sea conditions at which large blows could be detected (i.e. BSS 0–5).

Availability bias results when an animal is submerged or otherwise hidden from view while on the trackline and, hence, is unable to be detected. Factors that can affect availability bias include species-specific behaviour, group size, blow and dive characteristics and dive intervals. Availability bias was not fully accounted for, but inflated abundance/density estimates were minimised by not fitting detection functions to spikes in detections resulting from possible attractive animal movements toward the survey platform prior to detection. The factors tested in the MCDS models for bottlenose dolphins included BSS, visibility, and group size; BSS was the only factor chosen in the best MCDS models for bottlenose dolphins during the summer shipboard and aerial surveys. Further correction for perception and availability biases would provide absolute estimates of abundance/density which would be useful for determining the overall status of species, populations or stocks in the Mid-Atlantic but are not necessary for the purposes of the current study which was to generate relative baseline estimates which can be used for future trend and impact analyses.

Management implications

This study provides the first year-round abundance and density estimates for marine mammal species in nearshore waters off New Jersey. These relative estimates and the distribution and habitat utilisation information obtained from this study are critical for assessing the potential impacts of anthropogenic activities in this portion of the Mid-Atlantic Bight which is a prime region of future offshore renewable energy development on the OCS. These baseline data will provide the industry and regulators with the necessary details to inform the permitting and licensing of offshore renewable energy technologies and to determine potential monitoring and mitigation strategies for minimising impacts on marine mammals. The distribution and abundance information for the endangered North Atlantic right, fin and humpback whales will be particularly important for future construction and post-construction impact studies. Assuming the levels of bias remain constant for future surveys (e.g. use of similar protocols, platforms, observers, etc.), these relative abundance/density estimates provide a baseline that can be compared to estimates obtained during pre-construction, construction and post-construction activities to assess impacts and changes over time. The baseline estimates can also be used to determine site-specific take estimates for incidental take authorisations and may be used to inform the timing of construction activities to minimise potential impacts during known periods of marine mammal occurrence.

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Estimating gray whale abundance from shore-based counts using a multilevel Bayesian model

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ABSTRACT

Counts of southbound migrating whales off California form the basis of abundance estimation for the eastern North Pacific stock of gray whales (*Eschrichtius robustus*). Previous assessments (1967–2007) have estimated detection probability (p) from the detection-non detection of pods by two independent observers. However, tracking distinct pods in the field can be difficult for single observers; resulting in biased estimates of pod sizes that needed correcting, and matching observations of the same pod by both observers involved key assumptions. Due to these limitations, a new observation approach has been adopted wherein a paired team of observers work together and use a computerised mapping application to better track and enumerate distinct pods and tally the number of whales passing during watch periods. This approach has produced consistent counts over four recently monitored migrations (2006/7, 2007/8, 2009/10 and 2010/11), with an apparent increase in p compared to the previous method. To evaluate p and estimate abundance in these four years, counts from two independent stations of paired observers operating simultaneously were compared using a hierarchical Bayesian '*N*-mixture' model to jointly estimate p and abundance without the challenge of matching pods between stations. The baseline detectability p_o was estimated as 0.80 (95% Highest Posterior Density Interval [HPDI] = 0.75–0.85), which varied with observation conditions, observer effects and changes in whale abundance during the migration. Abundance changes were described using Bayesian model selection between a parametric model for a normally distributed common migration trend and a semi-parametric model that estimated the time trends independently for each year; the resultant migration curve was a weighted compromise between models, allowing for key departures from the common trend. The summed estimates of migration abundance ranged from 17,820 (95% HPDI = 16,150–19,920) in 2007/08 to 21,210 (95% HPDI = 19,420–23,230) in 2009/10, consistent with previous estimates and indicative of a stable population.

KEYWORDS: ABUNDANCE ESTIMATE; MIGRATION; MODELLING; GRAY WHALE; SURVEY – SHORE BASED; PACIFIC OCEAN; NORTHERN HEMISPHERE

INTRODUCTION

The eastern North Pacific stock of gray whales migrates annually along the west coast of North America from high latitude feeding grounds to winter breeding grounds in the lagoons and adjacent ocean areas off Baja California, Mexico (Rugh *et al.*, 2001). This nearshore migration pattern has enabled repeated abundance estimates from shore-based counts off Granite Canyon, central California. In 23 years, between 1967 and 2007, counts of the number of observed pods travelling southbound have been rescaled using estimates of pods undetected during watch periods, pods passing outside watch periods, and night travel rate (Buckland and Breiwick, 2002; Buckland *et al.*, 1993; Hobbs *et al.*, 2004; Laake *et al.*, 2012; Laake *et al.*, 1994; Rugh *et al.*, 2005). Population models based on these estimates indicate that gray whales have increased substantially in population size, recovering from whaling operations in the 19th and 20th centuries, and are now close to carrying capacity and likely pre-exploitation levels (Punt and Wade, 2012). The most recent population estimate from abundance counts in 2006/07 was approximately 19,000 whales (Laake *et al.*, 2012).

To facilitate continued population monitoring, the abundance estimation approach has seen continual evolution throughout this time series to more realistically estimate detection probability (p) to link observed counts to true abundance; this paper describes the latest modification. Notably, previous assessments have estimated p from the detection and non-detection of pods by independent observers using an analytical mark-recapture approach. However, tracking distinct pods in the field is difficult (Rugh *et al*. 2008), particularly for a single observer using just hand-recorded entries onto a paper data form. As a result, matching observations of the same pod by both observers involved key (and untestable) assumptions and limited observations of a given pod required corrections for bias in pod size estimation (Rugh *et al*. 2008; Laake *et al*., 2012). Due to these limitations, a new observation approach has been developed wherein a paired team of observers work together and use a computerised mapping application to help better track distinct pods and tally the number of whales passing during watch periods (Durban *et al*., 2010). This approach has a number of advantages, including open communication between observers, enabling observers to search for whales continually without the distraction of looking down to record data, and easier separation and tracking of distinct pods due to the precise computerised data recording and visualisation. As a result, this approach enables more repeated observations of each pod, leading to larger (and presumably less biased) estimates of pod size (Durban *et al*., 2010) and has produced consistent counts over four recently monitored migrations (2006/07, 2007/08, 2009/10 and 2010/11), with an apparent increase in p compared to the previous method (Durban *et al*., 2011).

To evaluate p for this new approach, watch period counts from two independent stations of paired observers operating simultaneously were compared during two of the four years (2009/10 and 2010/11), using a hierarchical Bayesian '*N*-mixture' model (Royle, 2004) to jointly estimate the probability of detection and abundance in all four years, without the challenge of matching pods between stations.

This '*N*-mixture' approach has been successfully used to estimate abundance and detectability from replicate count data for a range of wildlife species where it has not been possible to match repeat sightings of individuals (e.g. Chelgren *et al.*, 2011; Joseph *et al.*, 2009; Kery *et al.*, 2005). The untility of this approach to extend the time series of abundance estimates for eastern North Pacific gray whales is demonstrated in this paper.

METHODS

Data samples

Counts of gray whales were conducted from shore-based watch stations at Granite Canyon, California, during the 2006/07, 2007/08, 2009/10 and 2010/11 southbound migrations (see Table 1). Counts were made by rotating teams of observer pairs using naked eye aided by 7×50 binoculars; the primary observer in the pair kept continual visual watch while the secondary observer served as a data recorder but also kept watch and assisted with tracking already identified pods whenever possible. Each observer had one 90 minute shift as primary observer, followed by a second 90 minute shift as secondary observer and then a 90 minute break. Sightings were entered into a real-time data logging PC program, which had a mapping screen to help track repeated sightings of the same pod. The map projected the likely movement tracks (and error ellipses) of the pods using predicted swimming speeds (1.44–1.95 ms^{-1}), allowing re-sightings and new sightings to be queried. Up to six lots of 1.5 hour watch periods were used to cover daylight hours from 07:30 to 16:30 local time, during which the observers recorded passing whales and environmental conditions, specifically visibility (subjectively categorised from 1–6 for excellent to unusable) and sea state (Beaufort scale). To control for weather conditions and for consistency with previous abundance estimations, only counts during watch periods with acceptable weather conditions throughout their entire duration were used, specifically visibility code <5 (excellent to fair) and Beaufort Scale <5.

Estimating detection probability

The '*N*-mixture' approach was used (Royle, 2004) to simultaneously estimate detection probability p_{ijt} and abundance N_{jt} for each watch period *j* in each year *t*, based on the total aggregated counts n_{ijt} of passing whales recorded by each of $i = 1{:}2$ watch stations in each period. The observed counts n_{ijt} were modelled as a binomial outcome conditional on the unknown true number of whales passing N_{jt} and the detection probability p_{ijt} with hierarchical models assumed to describe variability in both *N* and *p* (e.g. Chelgren *et al.*, 2011). The power to estimate detectability was achieved by comparing gray whale counts from two independent stations of paired observers operating simultaneously during two years (2009/10 and 2010/11) from watch stations that were positioned 35m apart at the same elevation (22.5m) above sea level. In 2009/10 counts were compared from the two watch stations operating simultaneously during 70 lots of 1.5 hour watch periods with acceptable weather conditions, covering 20 different days of the migration; in 2010/11 simultaneous counts were available from 94 watch periods over 24 different days (see Table 1). However, detectability was extrapolated for all monitored watch periods in each of the four years based on the fitted model for detectability. In order to accomplish this, the counts for the south watch station were treated as zero-inflated binomial outcomes, with the binomial probability specified as a function $u_{ijt}\, p_{ijt}$ where $u = 1$ or 0 to indicate whether or not count data were actually collected from that station, thus ensuring that structural zero counts from periods without a second watch did not contribute to the likelihood for estimation of *p* or *N*.

Consistent with Laake *et al.* (2012), the model for detectability incorporated fixed effects β for visibility (VS) and Beaufort Scale (BF), as well as random effects associated with each observer *o* in 1:OB observers. These were modelled as additive effects on a general intercept so that the direction and magnitude of the estimated effects away from zero (no effect) could be assessed. The selection for the inclusion of these effects using Bayesian model selection with stochastic binary indicator variables *g* to switch each of the three possible effects either in or out of the model depending on their relevance to the observed data (Kuo and Mallick, 1998):

$$\mathrm{logit}\,(p_{ijt}) = \mathrm{logit}(p_{\mathrm{o}}) + g^{bf}\beta^{bf}\,\mathrm{BF}_{jt} + g^{vs}\beta^{vs}\,\mathrm{VS}_{\mathrm{jt}} + g^{ob}\boldsymbol{\beta}^{\boldsymbol{ob}}_{\boldsymbol{ijt=o}}$$

where the intercept p_{o} was the base detection probability in the absence of covariate effects, assigned a Uniform(0,1) prior distribution, and $\mathrm{logit}(p_{\mathrm{o}}) = \ln(p_{\mathrm{o}}/1{-}p_{\mathrm{o}})$. Centred around this base detectability, each of the fixed effects β^{bf} and β^{vs} was assigned a Normal prior distribution with mean zero and large standard deviation of 10; this prior value was smaller than the corresponding posterior estimates of standard deviation, and as such this was vague prior distribution that allowed any non-zero effects to emerge if supported. The random effect for each observer was drawn from a Normal distribution with mean zero and standard deviation σ^{ob}~Uniform(0,10). Each of the binary indicator variables, *g*, was assigned a Bernoulli(0.5) distribution to specify equal probability of inclusion or not of the effect in the model.

Table 1

The number of whales recorded during the southbound gray whale surveys from 2006/07 to 2010/11. Data are the total counts, hours and distinct days for watches during acceptable observation conditions.

	North Station			South Station		
Migration	Dates	Whales	Hours (days)	Dates	Whales	Hours (days)
2006/07	02/01–03/02	2,691	204 (34)	–	–	–
2007/08	02/01–09/02	2,079	202.5 (34)	–	–	–
2009/10	30/12–19/02	2,034	246 (43)	11/01–06/02	1,551	105 (20)
2010/11	03/01–18/02	2,885	265 (45)	10/01–04/02	1,754	141 (24)

Fitting migration curves

The *N*-mixture approach also accounted for variation in *p* relative to changes in *N* (latent watch period abundances) during the migration. So, some power to estimate detectability was achieved by assuming a model for changes in watch period abundance over the course of the migration. A Poisson distribution $N_{jt} \sim \text{Poisson}(\lambda_{jt})$ was adopted as a hierarchical prior for the distribution of abundances, and a model was specified for the Poisson mean λ in terms of the number of whales passing each day (*d*), with an offset for the effort duration of each watch period, E_{jt} in decimal days (e.g. Laake *et al.*, 2012):

$$\log(\lambda_{jt}) = \log(\mathrm{E}_{jt}) + \mathrm{model}_{\mathrm{d}(j)t}$$

$$\mathrm{model}_{dt} = \mathrm{z}_{dt}\mathrm{Common}_{dt} + (1-\mathrm{z}_{dt})\ \mathrm{Specific}_{dt}$$

Days were specified as $d = 0$ to D_t. In all four years *t* we used $D_t = 90$, where days were counted from 12:00am on 1 December, and we added an abundance of 0 whales passing for day 0 and D_t to anchor the fitted model when we assumed whales did not pass (following Buckland *et al.,* 1993). Estimates from the remaining days were derived from a mixture (or compromise) of two competing models ('Common' and 'Specific', e.g. Li *et al.*, 2012) describing changes in abundance across each annual migration. The model contributing each daily estimate was indicated using stochastic binary indicator variables z_{dt}, each assigned a non-informative Bernoulli(0.5) prior distribution. As such, each z_{dt} indicated the probability of a daily estimate conforming to the common trend, allowing flexibility for departures from this trend that may only exist on certain days in certain years to be identified and modelled (rather than assuming all counts from an entire year conform to or depart from a common trend, which would be represented by z_t). The total number of whales passing during each migration was then estimated by summing the expected value from the model-averaged number of whales passing each day from time 0 to D_t (e.g. Laake *et al.*, 2012). These estimates were then rescaled to account for the differential passage rate at night (Perryman *et al.*, 1999), based on the nine hour day multiplicative correction factor of Rugh *et al.* (2005). Specifically, we applied a constant night time correction factor that was assumed to be a Normally distributed fixed effect with mean of 1.0875 and standard deviation of 0.037.

For the 'Common model', we assumed a typical trend in abundance throughout each annual migration (e.g. Buckland *et al.*, 1993), with abundance changes assumed Normally distributed around a migration mid-point, with a Normal distribution specified as a quadratic function of days, on the log scale:

$$\mathrm{Common}_{dt} = \mathrm{a}_t + \mathrm{b}_t d_t + \mathrm{c}_t d_t^2$$

where the mid-point of the migration curve for each year *t* was derived by $-b_t/2a_t$. This assumed common migration curve allowed information to be 'borrowed' across years when needed, specifying association across years to strengthen inference about migration curves in years with relatively sparse counts. However, we specified each of the curve parameters a_t, b_t and c_t to be drawn from hierarchical Normal distributions with means μ^a, μ^b, $\mu^c \sim \mathrm{N}(0, 10)$ and standard deviations σ^a, σ^b, σ^c ~Uniform(0,10); hyper-parameters that were common across years, rather than assuming that the parameters themselves were constant. This random effects formulation allowed the timing, level and extent of the Normal migration curve to vary annually around the general pattern, if supported by the data.

Although it is likely that there is a typical pattern to the migration, it was acknowledged that abrupt departures may occur at any time in any particular year. To incorporate unusual patterns, the selection of an alternative 'Specific' migration model was allowed; a semi-parametric model that estimated the time trends independently for each year (e.g. Laake *et al.*, 2012). A method in which the shape of the relationship of abundance across days was determined by the data was adopted without making any prior assumptions about its form, by using penalised splines (Ruppert, 2002). Following Crainiceanu *et al.* (2005) a linear (on the log scale) penalised spline was used to describe this relationship:

$$\mathrm{Specific}_{dt} = S_{0t} + S_{1t} d_t + \Sigma_{k=1}^{m} \lambda_{kt}\,(d_t - \kappa_{kt})$$

Where S_{0t}, S_{1t}, ${}_{1t},\ldots,{}_{kt}$ were regression coefficients to be estimated separately for each year and $\kappa_{1t} < \kappa_{2t} < \ldots < \kappa_{kt}$ were fixed knots. We used $m = 15$ knots, a relatively large number to ensure the desired flexibility, and let κ_{kt} be the sample quantile of 's corresponding to probability $k/(m + 1)$. To avoid overfitting, the λ's were penalised by assuming that these coefficients were Normally distributed random variables with mean 0 and standard deviation ~Uniform(0,10). The parameters S_{0t}, S_{1t} were modeled as fixed effects with Normal(0, 10) prior distributions.

Bayesian inference using MCMC

The multi-level model was fit using Markov Chain Monte Carlo (MCMC) sampling using the WinBUGS software (Lunn *et al.*, 2000). Inference was based on 15,000 repeated draws from the posterior distribution of each model parameter conditional on the observed data, following 5,000 iterations that were discarded as burn-in. Convergence of parameters within these initial 5,000 iterations was determined based on Gelman-Rubin statistics below 1.05 (Brooks and Gelman, 1998) calculated from three independent chains begun from over-dispersed starting values. To gauge the adequacy of the model for each annual set of count data, Bayesian P-values were computed (Gelman *et al.*, 1996) by using the same MCMC sampler to predict a distribution for each watch-period count from the posterior estimates of model parameters and comparing the total predicted and observed counts. For each year, there was good agreement between the model predictions and observed counts, with Bayesian P-values ranging from 0.45 to 0.53; values close to 0.5 would indicate that the data was consistent with replications under the model, with the distribution of the predicted count symmetrically overlapping the observed count (Gelman *et al.*, 1996).

The MCMC sampling approach allowed uncertainty to be propagated across levels of the model. Notably, estimates of parameter values across MCMC iterations were used to estimate the probability of inclusion of covariate effects in the model for detectability, given by the posterior probability $p(g = 1)$ of each indicator variable *g*. Fitting and selection of the two competing migration models was achieved within the same MCMC run using the 'cut' function in WinBUGS to ensure that estimation of the two models was not affected by the selection of the model indicator (e.g. Li *et al.*, 2012). The posterior probability of conforming to the common trend model was then calculated by the relative frequency that each model was selected by the indicator z_{dt} in the overarching mixture model, and inference about abundance on each day was based on a weighted compromise between the competing models by sampling across the posterior distribution of z_{dt}.

RESULTS

The base detectability was estimated as p_o = 0.80 (95% Highest Posterior Density Interval [HPDI] = 0.75–0.85), which was modified by observation conditions and observer effects (see Table 2). The posterior distribution for the effect of sea state β^{bf}, measured using the Beaufort scale*,* largely overlapped with zero and there was therefore low support for including this effect in the model with $p(g^{bf} = 1) = 0.004$. In contrast, there was a relatively strong negative effect of visibility on detectability (higher visibility code = lower visibility = lower detectability), with the entire distribution for β^{vs} falling below zero [$p(g^{vs} = 1) = 1$]. There was also support for inclusion of observer effects [$p(g^{bs} = 1) = 1$], with both positive and negative effects reflecting relatively high and low counts by different observers. A total of 35 different observers were used over 4 years between North and South stations; 15/35 counted in multiple years (2 years = 7, 3 years = 4, 4 years = 4). The Posterior medians for observers' effects ranged from –0.59 to 0.80, but only five observer effects (all positive) had posterior distributions that did not include zero.

Detectability also varied with changes in whale abundance during the migration, as shown by the extent of extrapolation from the daily summed counts (effort adjusted) to the estimated daily abundances (Fig. 1). Detectability declined with increasing abundance, with a greater proportion of whales estimated to be missed as more whales passed during busy watch periods. In general, changes in abundance during the migrations were adequately described by a Normal curve over time, but there was greater uncertainty in the tails of the distribution resulting from generally sparse coverage. The Normal trend was useful for comparing migration timing: the median of the curve midpoints was 53.5 days since December 01 (23–24 January), ranging between 49–57 days. However, there were some notable deviations from the Normal trend, with estimates from the year-specific non-parametric trend model being favoured for some days in each of the four years. In particular, there was a high probability in favour of the Specific model [$p(z = 0) > 0.75$] on 9 days in 2006/07, 9 days in 2007/08, 16 days in 2009/10 and 11 days in 2010/11, representing key departures from the Normal migration trend. The summed (model-averaged) estimates of migration abundance ranged from a posterior median of 17,820 (95% HPD = 16,150–19,920) in 2007/08 to 21,210 (95% HPDI = 19,420–23,230) in 2009/10, consistent with previous estimates (Fig. 2). These new estimates were also relatively precise with coefficients of variation (CV = Posterior Standard Deviation/Posterior Median) ranging from 0.04 to 0.06 (median = 0.05), but nonetheless the 95% HDPI's of all four estimates overlapped.

DISCUSSION

The new counting method adopted here was intended to reduce reliance on the ability of single observers acting independently to record and track distinct whale groups. By adopting teams of paired observers working together, with the benefit of a real-time computerised tracking and

Table 2

Parameters of models for detectability, *p*. All estimates are presented as the 2.5%, 50%, 97.5% highest density posterior probability intervals, plus the probability of inclusion in a model (if tested), given by the posterior probability $p(g = 1)$ of each indicator variable *g*. Observers are arbitrarily numbered, differently for each year.

Detection model	2006/07	2007/08	2009/10	2010/11
p_o	0.75, **0.80**, 0.85	0.75, **0.80**,0.85	0.75, **0.80**,0.85	0.75, **0.80**,0.85
β^{bf} [$p(g^{bf} = 1)$]	–19.34, **–0.003**, 19.98 [0.004]	–19.34, **–0.003**, 19.98 [0.004]	–19.34, **–0.003**, 19.98 [0.004]	–19.34, **–0.003**, 19.98 [0.004]
β^{vs} [$p(g^{vs} = 1)$]	–0.38, **–0.30**, –0.20 [1]	–0.38, **–0.30**, –0.20 [1]	–0.38, **–0.30**, –0.20 [1]	–0.38, **–0.30**, –0.20 [1]
σ^{ob} [$p(g^{bs} = 1)$]	0.26, **0.37**, 0.54 [1]	0.26, **0.37**, 0.54 [1]	0.26, **0.37**, 0.54 [1]	0.26, **0.37**, 0.54 [1]
Observer 1	–0.36, **0.02**, 0.49	0.03, **0.37**, 0.81	–0.42,**–0.24**, 0.06	–0.13, **0.08**, 0.30
Observer 2	0.03, **0.37**, 0.81	–0.78, **–0.03**, 0.70	–0.09, **0.30**, 0.81	–0.36, **0.02**, 0.46
Observer 3	–0.24, **–0.07**, 0.11	–0.24, **–0.07**, 0.11	0.03, **0.37**, 0.81	–0.42, **–0.24**, 0.06
Observer 4	–0.42, **–0.01**, 0.49	–0.42, **–0.24**, 0.06	–0.13, **0.08**, 0.30	–0.25, **0.01**, 0.29
Observer 5	–0.04, **0.14**, 0.35	–0.13, **0.08**, 0.30	–0.24, –**0.07**, 0.11	0.16, **0.43**, 0.73
Observer 6	0.06, **0.42**, 0.83	–0.04, **0.14**, 0.35	–0.27, **–0.06**, 0.18	–0.04, **0.14**, 0.35
Observer 7	–0.17, **0.11**, 0.46	–0.18, **0.19**, 0.61	–0.04, **0.14**, 0.35	–0.50, **–0.13**, 0.26
Observer 8	–0.39, **–0.16**, 0.07	–0.17, **0.11**, 0.46	0.12, **0.33**, 0.59	–0.39, **–0.16**, 0.07
Observer 9	0.12, **0.33**, 0.59	0.12, **0.33**, 0.59	–0.25, **0.01**, 0.29	–0.09, **0.23**, 0.60
Observer 10	–	–0.39, **–0.16**, 0.07	–0.08, 0.26, 0.64	–0.27, **–0.06**, 0.18
Observer 11	–	–	–0.71, **–0.43**, 0.13	0.31, **0.80**, 1.46
Observer 12	–	–	–0.66, **–0.37**, 0.07	–0.54, **–0.29**, 0.04
Observer 13	–	–	–0.42, **0.00**, 0.49	–0.75, **–0.22**, 0.33
Observer 14	–	–	–0.63, **–0.13**, 0.40	0.12, **0.33**, 0.59
Observer 15	–	–	0.31, **0.80**, 1.46	–0.73, **–0.29**, 0.14
Observer 16	–	–	–0.18, 0.19, 0.61	–0.18, **0.19**, 0.61
Observer 17	–	–	0.16, **0.43**,0.72	–0.70, **0.02**, 0.76
Observer 18	–	–	–0.39, **–0.16**, 0.07	–0.63, **–0.13**, 0.40
Observer 19	–	–	–0.22, **0.22**, 0.72	–0.83, **–0.59**, 0.36
Observer 20	–	–	–0.28, **0.14**, 0.59	–0.24, **–0.07**, 0.11
Observer 21	–	–	–0.18, **0.28**, 0.83	–0.21, **0.11**, 0.47
Observer 22	–	–	–	–1.05, **–0.49**, 0.06

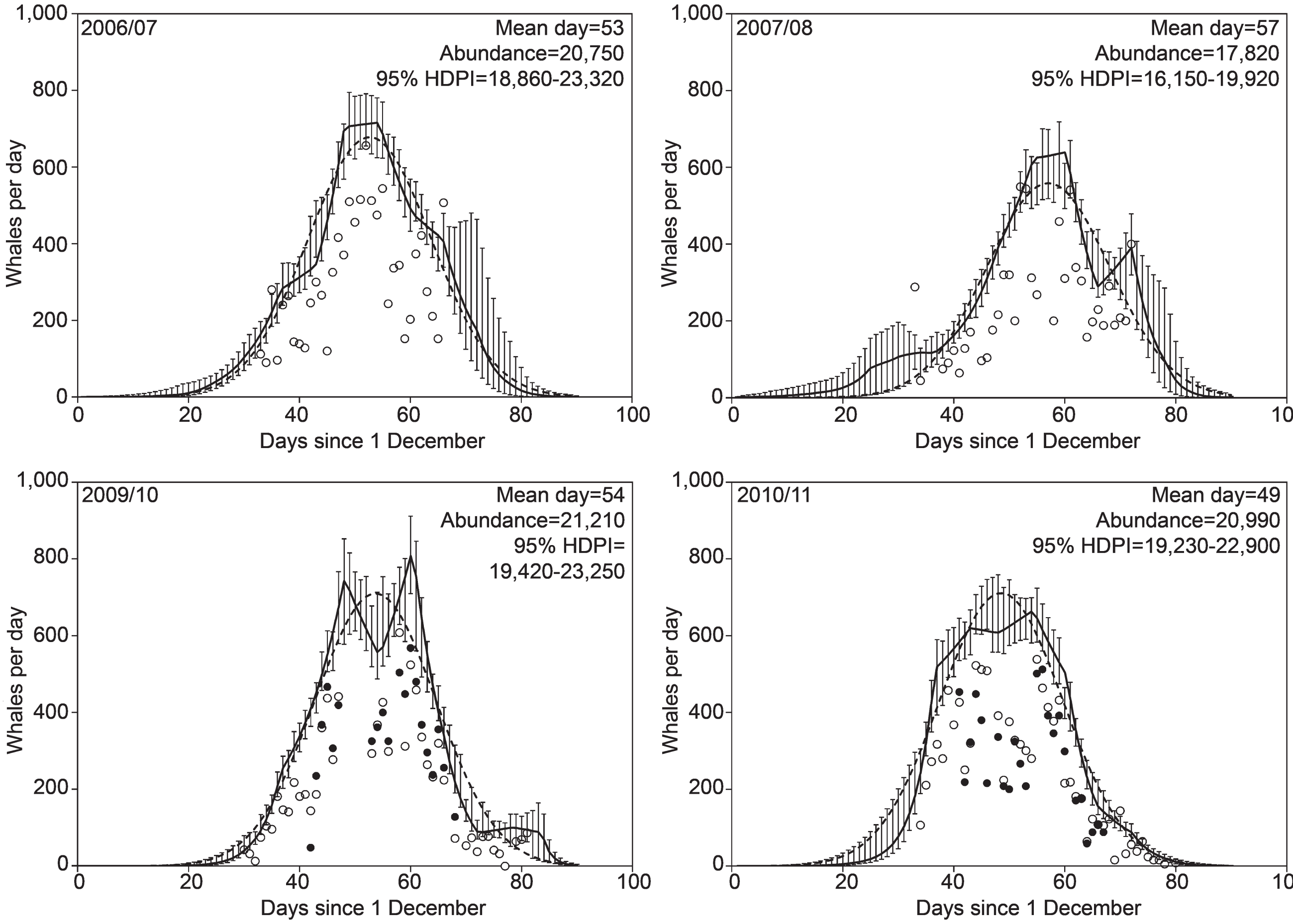

Fig. 1. Observed whale passage rates expressed as total counts per day/ proportion of day observed (circles) and fitted migrations models (lines) for the four southbound gray whale migration counts from 2006/07 to 2010/11. Solid circles represent counts from a second watch station, when operating. The broken line represents the median estimates from a hierarchical Normal model for migration and the solid line represents a semi-parametric model of penalised splines; the abundance estimate for each day (95% highest posterior density interval shown by vertical lines) is a model averaged compromise between the migration models, and these were summed to estimate the overall abundance for the migrations.

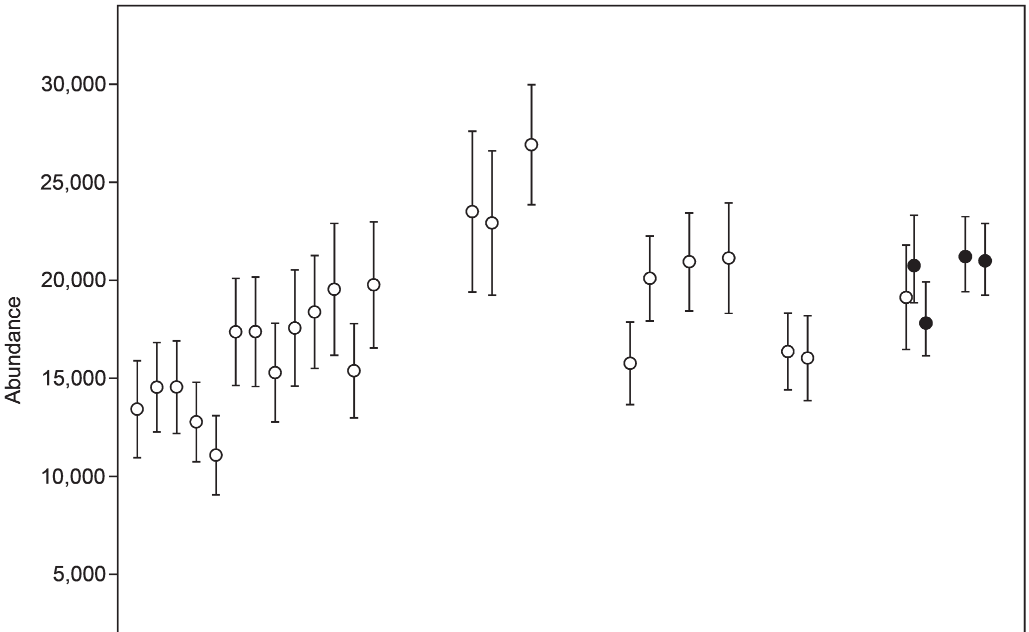

Fig. 2. Gray whale abundance estimates for each of 23 southbound migrations with an end year between 1967 and 2007 (open circles, with 95% confidence intervals; from Laake *et al.,* 2012) together with the four recent migrations reported here (closed circles show posterior medians, lines are 95% highest posterior density intervals).

visualisation tool, this approach has proved successful in increasing detection probability (Durban *et al.*, 2011) and also reducing variability in detections due to observer effects. Although still present, the magnitude of observer effects estimated from the new counts (see Table 2) was generally not as great as those apparent with the traditional counting approach (see Laake *et al.*, 2012, table 7).

Furthermore, our method for estimating detectability departed from the mark-recapture approach of matching detections and non-detections of specific pods by independent observers. Instead, inference was based on total watch period counts that were not sensitive to differential lumping and splitting of pods by observers, and avoided the assumptions required to match observed pods between pairs of observers. As an alternative to the mark-recapture analytic approach, we have shown how tallied watch period counts from two observer pairs counting simultaneously can lead to similar inference when analysed using with the *N*-mixture approach (Royle, 2004).

The *N*-mixture approach is conceptually simple: multiple observations of watch period counts, *n*, from the different observer teams represented different samples from an unknown binomial distribution with total population size *N* and detection probability *p*. A binomial likelihood function could then be easily used to estimate *N* and *p* from the sample of *n*'s. Although there were only a maximum of two samples of *N* during any specific watch period, a large sample of *n*'s was built up across many watch periods, allowing the estimation of the parameters. Layered on top of this core estimation process were both a trend model for true daily abundance through time based on the migration pattern and a model for how detection varied according to environmental conditions and different observers. Specifically, a hierarchical model fit to the replicate count samples allowed us to link detectability to key covariates, as in previous gray whale assessments (e.g. Laake *et al.*, 2012), and also extrapolate detectability based on these covariate relationships for watch periods without replicate counts. Similarly, by assuming a common underlying model for the migration pattern, this approach notably accounted for variation in *p* relative to changes in abundance *N* during the migration. Furthermore, this joint modelling of data from multiple years allowed the borrowing of strength across years to better parameterise the migration during years with sparse data.

Previously, two contrasting approaches have been used to model changes in abundance over the course of the annual gray whale migration: either by assuming a parametric model to determine the shape of the migration curve (Buckland *et al.*, 1993) or by fitting a non-parametric smoother to allow the data to determine the trend in abundance over time (Laake *et al.*, 2012). Here we drew on elements of both these approaches in a flexible framework using Bayesian model selection between a parametric model for a common migration trend and a semi-parametric model that estimated the time trends independently for each year; the resultant migration curve was a weighted compromise between models, allowing for key departures from the common trend.

The abundance estimates produced for 2006/07, 2007/08, 2009/10 and 2010/11 were internally consistent, consistent with previous estimates and indicative of a stable population (Fig. 2). The 95% HDPI's of all four estimates overlapped, and there was substantial overlap between the 95% HDPI from the 2006/7 estimate with the 95% confidence intervals of the estimate for the same migration produced using the previous counting and estimation approach (Laake *et al.* 2012). Further, our estimates are very similar to the predictions of Punt and Wade (2012) based on assessment models for the full time series; their baseline model prediction for 2009/10 had 90% posterior density intervals ranging from 17,726 to 23,247; the posterior distribution for our 2009/10 estimate was centered within these intervals at 21,210 (95% HPDI = 19,420–23,250). It is noteworthy that the estimates produced using our approach were relatively precise with CVs ranging from 0.04 to 0.06 (median = 0.05) in contrast to CVs ranging from 0.06 to 0.09 (median = 0.08) for the 23 previous estimates.

This consistency provides a level of confidence in our approach and resultant estimates, but nonetheless there are limitations to address. Our approach makes a number of important modelling assumptions, both in terms of distributional forms and model structure. It was assumed that the detectability relationships described by modelling repeated counts during two years were also applicable in the remaining two years with no replicate counts. We also assumed observer effects remained constant, although in reality this may change with experience. Additionally, the definition of what constituted the common migration trend was dependent on the joint modelling of just four years of data, and precise inference about the shape of the migration curve relies on count data being collected from throughout the migration time span. During at least 3/4 of the years reported here, count data were sparse (or non-existent) during the tails of the migration, resulting in uncertainty over the shape of the abundance curve. While this uncertainty was propagated into inference about overall abundance in our Bayesian inference using MCMC sampling, the resulting imprecision will ultimately constrain power to detect between-year changes in migration patterns and abundance. Data collected during further migrations will be incorporated into this hierarchical model and therefore used to refine parameter estimates; this will benefit from replicate counting experiments, repeated when possible. As the time series grows, specific goodness-of-fit tests should be adopted to investigate aspects of model structure and suggested changes as necessary.

There are also practical considerations as well as modelling assumptions. Previous work has shown that the new counting approach produces estimates of pod size that are typically larger (and presumably less biased) than the traditional counting approach (Durban *et al.*, 2010), likely because the computerised tracking software facilitates more repeated observations of the same groups. In fact, it has been assumed that estimates of pod size using this observation approach are effectively unbiased and have not been rescaled to tally watch period counts. This is an assumption that remains to be tested, but suitable calibration experiments are difficult to design and implement, particularly due to the inherently subjective differences between observers in lumping and splitting whales to define groups. Similarly, although observer effects have been accommodated in the model for detectability, it is clear that too many observers

(35 in total) counted too infrequently to allow precise parameterisation of their relative effects on detectability in many cases. This will have resulted in further imprecision.

Although there may be field protocols that could be adapted to address these limitations within the current approach, further modernisation of the observation process is recommended. Specifically, more accurate information could be gleaned from observations recorded with high-definition video files to allow subsequent review and re-review, rather than relying on instantaneous assessment by visual observers. The use of infra-red sensors would further allow for 24 hour monitoring (e.g. Perryman *et al*., 1999) and provide greater coverage of the entire migration during acceptable weather conditions; automated blow detectors (e.g. Santhaseelan *et al*., 2012) can be developed to eliminate observer effects and standardise detectability to provide counts with minimal (and quantifiable) bias. These extensions would further serve to build a more robust and automated observation model to combine with the flexible abundance model for the migration process described in this paper.

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Spatial and temporal dynamics of whalewatching in Península Valdés, Patagonia, Argentina

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ABSTRACT

Península Valdés (Patagonia, Argentina) is considered one of the best places in the world to watch southern right whales (*Eubalaena australis*) due to the large number of animals as well as to their predictability and proximity to the coast. The present study describes the spatial and temporal dynamics of whalewatching, and the different groups of whales that were the focus of this activity in Península Valdés during six reproductive seasons (from 2005 to 2008 and from 2012 to 2013). The aim was to generate useful tools to improve whalewatching activity in this area. Data were recorded from 1,816 whalewatching trips operated from Puerto Pirámides. Every trip had several stopovers to watch whales, defined as 'sightings'. At the beginning of the season, most sightings occurred near Puerto Pirámides port, while at the end of the season, sightings were farther from the port. During the first half of the whale season, trips tended to be coastal and shorter but the groups of whales sighted were more varied, including solitary animals, mating groups and mothers with their recently born calves. In the second half of the season, trips tended to be further from the coast and longer, but the whales sighted were mainly mother-calf pairs, the last group of whales to leave the area. This difference in the characteristics of the sightings as the whale season progressed could be the basis to generate different recreational experience opportunities. Whalewatching has a major impact on the regional economy and whalewatching regulations, if correctly applied, could improve the quality of a conservation plan, considering that both gulfs of Península Valdés (San José and Nuevo) are the main calving areas for this species in the South Atlantic Ocean.

KEYWORDS: WHALEWATCHING; REGULATIONS; DISTRIBUTION; BREEDING GROUNDS; SHORT-TERM CHANGE; SOUTHERN RIGHT WHALE; SOUTH AMERICA; SOUTHERN HEMISPHERE

INTRODUCTION

The Patagonian coast, particularly Península Valdés (Chubut, Argentina), is one of the most important places in the world for the reproduction of the southern right whale (*Eubalaena australis*) in the Southwest Atlantic (Bastida and Lichtschein, 1984; Bastida *et al.*, 2007; Payne *et al.*, 1990). This whale has a current annual population growth rate of about 4–6% (Crespo *et al.*, 2014) and a breeding population estimated around 4,000 whales (Cooke, 2013). Southern right whale adults arrive in Península Valdés between April and May each year and increase in number (by reproduction) until September, reaching more than 1,000 individuals (Crespo *et al.*, 2014) in only 4,000km^2. The whales prefer near-shore areas (between 10 and 100m from the shore; Rivarola *et al.*, 2001) and shallow waters (around 5m depth), especially mothers with calves (Bastida *et al.*, 2007), which stay long periods of time on the surface (Fazio, 2013). The first births take place in mid-June and the last ones at the end of October. Females remain in the area with their calves for two or three months after birth (Best and Rüther, 1992; Cooke *et al.*, 2001).

Due to the large number of whales as well as to their predictability and proximity to the coast, Península Valdés is considered one of the best places in the world to watch right whales (Argüelles and Bertellotti, 2008; Rivarola *et al.*, 2001). Tourist numbers at this site peak at the end of September or early October (Rowntree *et al.*, 2001), coinciding with the peak in whale abundance (Crespo *et al.*, 2014). Although wildlife tourism is a relatively recent phenomenon, it is growing rapidly (Cisneros-Montemayor *et al.*, 2010; Hoyt, 2001; Hoyt and Hvenegaard, 2002; Orams, 2002) and has become a global business worth over U$S two billion a year worldwide (Bailey, 2012; Chen, 2011; O'Connor *et al.*, 2009). Like other wildlife tourism destinations, Península Valdés has also experienced a rapid growth: between 1991 and 2004 the number of tourists who took part in a boat-based whalewatching activity increased from 17,446 to 96,436 (Losano and Ruíz Díaz, 2009). However, since 2005 differences in the number of tourists between years have been small, with a total of around 100,000 tourists per year (see Table 1) (Losano, 2008; Secretaría de Turismo y Áreas Protegidas, pers. comm; Secretaría de Turismo y Áreas Protegidas, 2011).

Ecological tourism, including whalewatching and tours to see penguins, sea lions and elephant seals, is the main tourist attraction of Chubut (Campagna *et al.*, 1995; Crespo and Dans, 2012) and is today one of the fastest growing sources of income and employment after oil exploitation and fisheries (Argüelles and Bertellotti, 2008). In 1985, there were only two companies working with three boats, but since the early 1990s, 12 boats have been operating simultaneously (Tagliorette *et al.*, 2008). As in other countries in the world (Heckel *et al.*, 2003), this increasing activity needed adequate local regulation, as recognised initially by the owners and captains of the whalewatching companies. In the 1990s, the government of Chubut Province granted whalewatching licenses to only six companies, allowing no more than two boats per company to be in the water at the same time.

The rapid development of whale tourism has undoubted economic and public-consciousness benefits but has also raised concern about potentially negative effects on the animals. Chubut Province is at the forefront of protecting

Table 1

Evolution of the number of tourists who took part in a whalewatching tour from boats that operated from Puerto Pirámides (Chubut, Argentina); months, number of trips and sightings done in each year studied; duration of each whalewatching trip and sighting. Means are followed by their standard deviation (SD). Time was measured in minutes.

Year	Number of tourists	Months	Number of trips	Number of sightings	Mean time of a trip ± SD	Median time of a trip (range)	Mean time of a sighting ± SD	Median time of a sighting (range)
2005	92,514[a]	Jul. to Dec.	363	1,011	85.77 ± 22.19	84 (34–228)	15.16 ± 11.36	12 (1–59)
2006	107,731[a]	Jun. to Dec.	552	2,304	81.65 ± 15.96	79 (42–171)	11.17 ± 8.89	9 (1–71)
2007	113,148[a]	Jun. to Dec.	552	2,045	73.90 ± 13.51	72 (41–211)	11.35 ± 8.50	9 (1–62)
2008	101,743[a]	Jul. to Nov.	92	343	96.46 ± 11.35	94 (79–146)	14.07 ± 15.13	10 (1–185)
2009	107,103[a]	–	–	–	–	–	–	–
2010	114,628[a]	–	–	–	–	–	–	–
2011	91,424[a]	–	–	–	–	–	–	–
2012	100,823[b]	Aug. to Nov.	138	467	90.24 ± 17.02	90 (33–159)	14.17 ± 15.36	10 (1–185)
2013	94,843[b]	Jun. to Nov.	119	355	91.03 ± 10.86	89 (61–131)	12.44 ± 12.80	11 (1–129)
Total	–	–	–	–	82.14 ± 17.63	81 (33–228)	12.30 ± 6.52	15 (2–75)

[a]Secretaría de Turismo y Áreas Protegidas, 2011. [b]Secretaría de Turismo y Áreas Protegidas, pers. comm.

its wildlife resources. It has specific legislation and the appropriate enforcement authorities to control the development of the whalewatching activities (Coscarella, 2005). In 2008, the Government Office of Tourism of Chubut Province implemented a new whalewatching Law Nº 5714 and Decree 167, which establishes that whalewatching trips must be done in a limited area of around 160km^2, between Punta Piaggio and Punta Cormoranes (Fig. 1), from the lowest mean tide line to three nautical miles away from the coast, and that boats (only one per company at the same time) can only operate from Puerto Pirámides. The law also approves the 'Patagonian Technique for Whale Watching', which includes a code of conduct for whalewatching. The main goal of the 'Patagonian Technique for Whale Watching', as for most whalewatching regulations worldwide (Carlson, 2010; Kessler and Harcourt, 2013), is to establish the technical aspects expressly permitted and prohibited for disposal of marine transportation of persons for whalewatching tourism purposes. It is founded on a sustainable basis to adapt the whalewatching manoeuvres of service permittees to conservation guidelines.

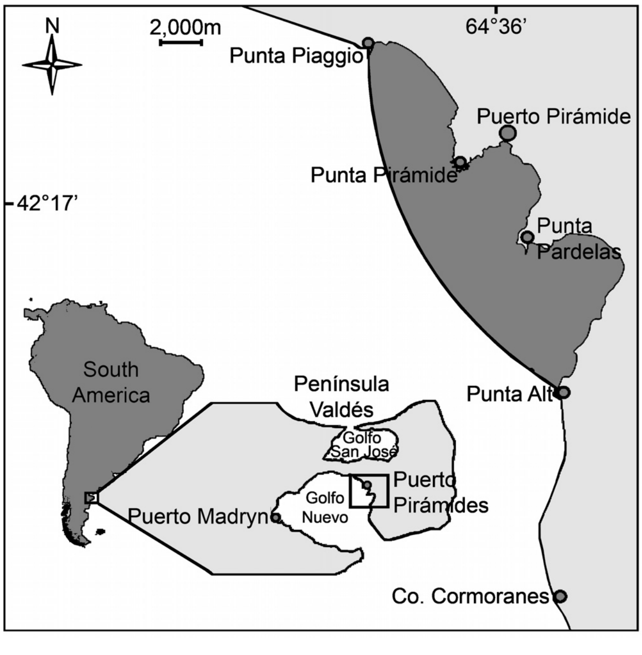

Fig. 1. Main study area (dark grey) in Golfo Nuevo, Península Valdés.

The present study describes the spatial and temporal dynamics of whalewatching in Península Valdés and the different groups of whales sighted during this activity along six whale breeding seasons (from 2005 to 2008 and from 2012 to 2013). This data could also be useful to define different recreational experience opportunities in whalewatching in the area.

MATERIALS AND METHODS

This study was carried out during the whale breeding seasons (June to December) from 2005 to 2008 and from 2012 to 2013 (Table 1). One or two observers recorded data from 1,816 whalewatching boat trips, obtaining more than 1,338 hours of direct observation during 2,486 hours on board. All boats of the six companies that operated in those years set sail from Puerto Pirámides (42º34'S, 64º16'W) (Fig. 1). The different types of boats (around 15 boats in the whalewatching fleet) included inflatable boats, single hull ships and a catamaran, and the number of passengers each could carry ranged from 19 to 70, according to the size of the boat. Large boats usually had more than one outboard engine, while small boats had only one, and these engines ranged from 150 to 300HP each. Trips normally took place between Punta Piaggio (42º32'S, 64º21.5'W) and Punta Alt (42º41'S, 64º15.1'W) (Fig. 1).

Table 2

Data recorded in each sighting.

Data recorded	Details
Duration	Starting when the boat was approx. 50m away from the focal whale, and finishing when the boat was more than 50m away from the whale.
Location	GPS used: Garmin eTrex Legend.
Wind intensity	0 = no wind; 1 = low intensity (1–8kn); 2 = mid intensity (9–15kn); 3 = strong wind (16–22kn); 4 = very rough wind (>22kn). Anemometer used: SKYWATCH Xplorer.
Douglas (Dg)	0 (no waves)–4 (large waves)
Number of whales	Maximum value observed: 16, always nearer than 50m from the boat.
Type of focal whale	Mother-calf: one or more pairs of a mother and a calf born in the current season (less than one year old). Mating group: one female and several males performing a peculiar mating behaviour. Other: solitary animals that could be grouped by chance but not in a mating behaviour.

On every trip, the date, type of boat, duration and weather condition were recorded (with southerly winds of more than 20 kn, marine authorities closed the port and prohibited all navigation). During each trip, boats often stopped several times to observe a whale or groups of whales. Each stopover was considered as a 'sighting', defined as the observation that took place when the boat stopped or stayed for at least one minute at a distance of around 50m from one or more whales. The number of trips and sightings in each year are shown in Table 1. On each sighting, several variables, such as duration, location, wind intensity, Douglas scale and number and type of focal whales were recorded (Table 2).

The years studied were gathered together in most analyses because they had similar patterns. All statistical analyses

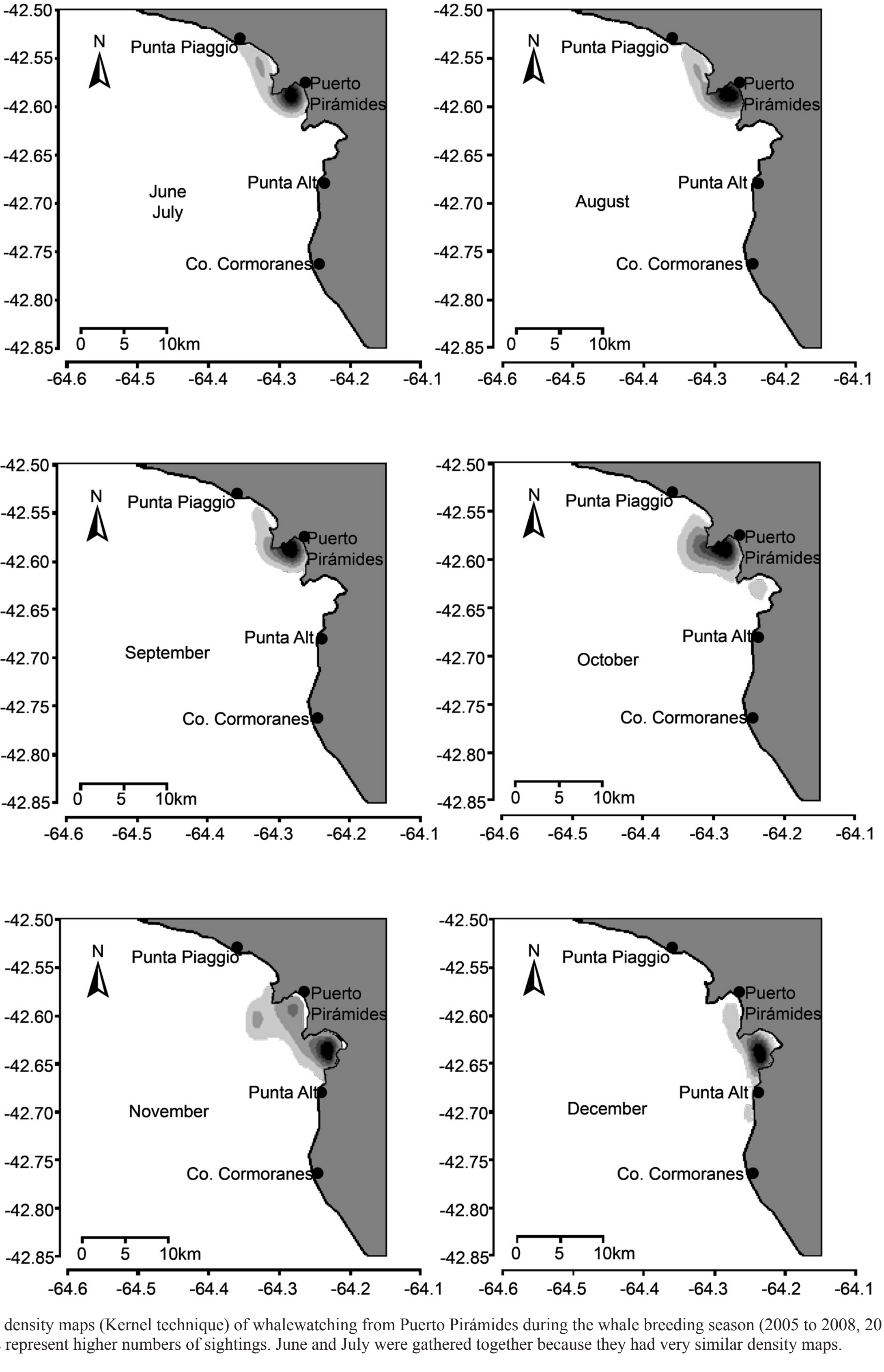

Fig. 2. Sighting density maps (Kernel technique) of whalewatching from Puerto Pirámides during the whale breeding season (2005 to 2008, 2012 and 2013). Darker zones represent higher numbers of sightings. June and July were gathered together because they had very similar density maps.

were performed using SPSS 15.0.1 for *Windows* (data analysis software system, 2006). The variance homogeneity of the data sets was assessed using the Levene test to determine the use of parametric or non-parametric analyses. Spatial distribution analyses were performed using R 2.13.0 (R Development Core Team, 2011), the word editor Tinn-R (Faria, 2009) and sp libraries rgdal, PBSmapping, maptools, gpclib, maptools, spatstat and fields (Baddeley and Turner, 2005; Bivand *et al.*, 2008; Furrer *et al.*, 2010; Keitt *et al.*, 2010; Lewin-Koh *et al.*, 2011; Pebesma and Bivand, 2005; Peng *et al.*, 2010; Schnute *et al.*, 2010) developed by R.

RESULTS

As the season progressed, sightings were carried out in different areas (Fig. 2). In the first half of the season (June to September), the median distances of sightings to Puerto Pirámides were shorter (Kruskal-Wallis: = 1382.15, $p < 0.001$, all T3-Dunnett: $p < 0.001$; Fig. 3), with 61.7% of the sightings (n = 3,247) at less than 1,000m from the coast.

Data from all the years studied together, except 2005 (due to insufficient data), showed that 60.2% of the sightings were of mother-calf pairs, 11.4% of mating groups and 28.4% of others. There were significant differences in the percentages of each category of whale sighted as the season progressed ($G_{6;\,0.95} = 1633.4$, $p < 0.001$). In earlier months (June to August), it was more frequent to watch a mating group or other type of group in a sighting, while in later months (September to December), mother-calf pairs were the most frequent group to watch (Fig. 4). In earlier months, mother-calf pairs were sighted only at less than 2,000m from the coast, while in later months, mother-calf pairs were spread thoughout the total range of distances to the coast; mating groups and others had different or even opposite distribution patterns (Fig. 5). These spatial distributions for each group were neither homogeneous in earlier months ($G_{3;\,0.95}$: 103.0, $p < 0.001$) nor in later months ($G_{3;\,0.95} = 142.3$, $p < 0.001$).

The weather conditions affected whalewatching activity. Most trips were made with northerly winds (39.3%), followed by westerly (29.7%) and southerly winds (20%). When the sea conditions were bad (higher Douglas, Dg, values), trips tended to be shorter (ANOVA: $F_6 = 5.08$, $p < 0.001$; only $D_g = 2.5$ and 3 were significantly different from $D_g = 1$ and 2, Tukey-test: $p < 0.05$; Fig. 6), but sightings tended to be longer (Kruskal-Wallis: $X^2_8 = 33.14$, $p < 0.001$; only $D_g = 0.5$ was significantly different from $D_g = 3.5$, T3-Dunnett: $p < 0.05$; Fig. 7).

The median time of a trip was significantly different between years (Kruskal-Wallis: $\chi^2_5 = 370.92$, $p < 0.001$; T3-Dunnett: years 2006 and 2007 $p < 0.01$ with all other years), decreasing from 2005 to 2007, and increasing in 2008 and

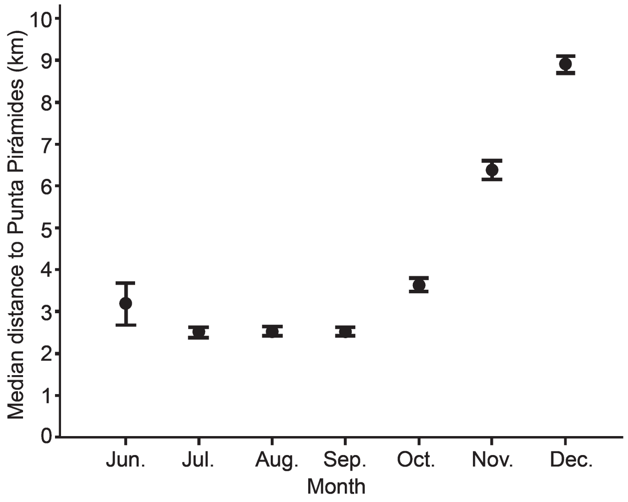

Fig. 3. Median distances of sightings to Puerto Pirámides during the whale breeding season (June to December) of the six years studied. Error bars: 95% CI.

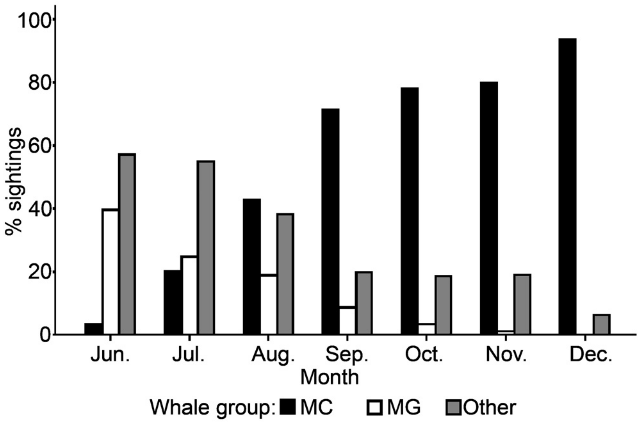

Fig. 4. Percentage of sightings with different types of whale groups during the whale season in the years 2006 to 2008, 2012 and 2013. MC: Mother-Calf pair; MG: Mating Group.

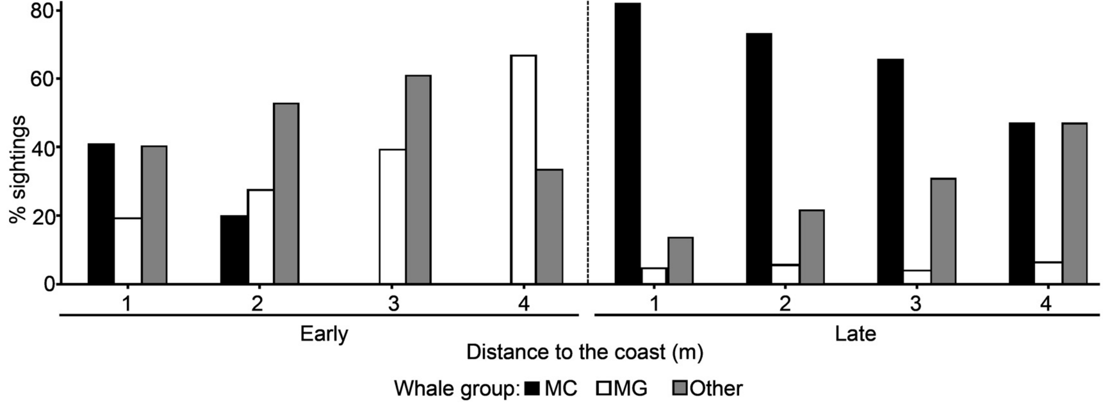

Fig. 5. Percentage of sightings with different types of whale groups according to the distances to the coast in the years 2006 to 2008, 2012 and 2013. Early: from June to August; Late: from September to December. MC: Mother-Calf pair; MG: Mating Group.

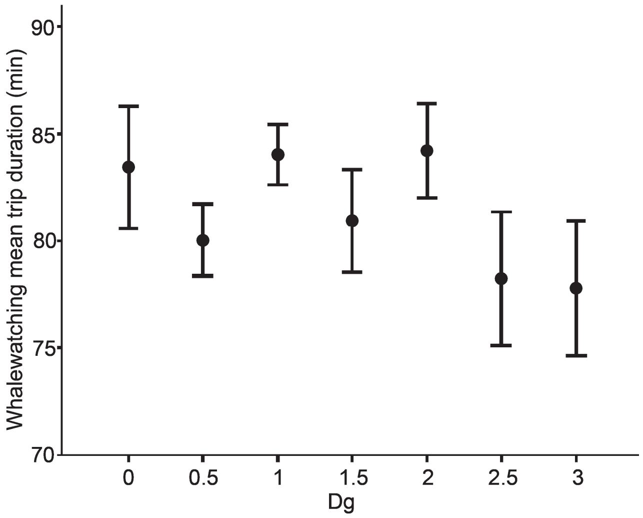

Fig. 6. Whalewatching trip mean duration as a function of Douglas scale (Dg) for the years 2005 to 2008, 2012 and 2013. Error bars: 95% CI.

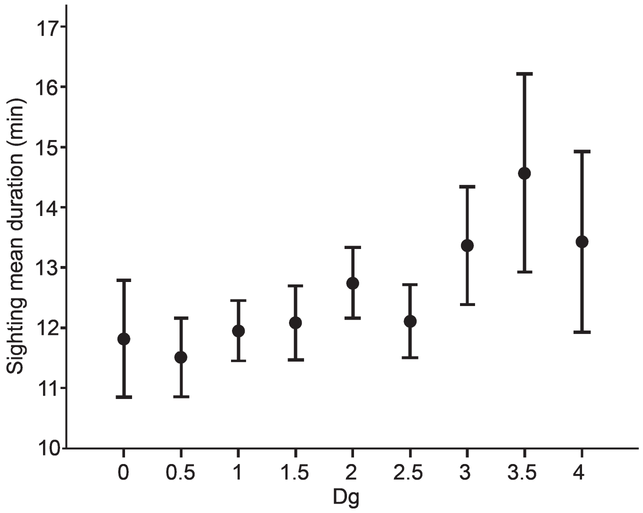

Fig. 7. Sighting mean duration as a function of Douglas scale (Dg) for the years 2005 to 2008, 2012 and 2013. Error bars: 95% CI.

subsequent years (Table 1). Similarly, the median time of a sighting was significantly different between years (Kruskal-Wallis: 155.81, $p < 0.001$; T3-Dunnett: years 2006 and 2007 $p < 0.01$ with all other years, except between each other), with higher durations in 2005, 2008 and succeeding years (Table 1). On the other hand, higher trip durations were recorded towards the end of the season (Kruskal-Wallis: = 40.95, $p < 0.001$; T3-Dunnett: years 2012 and 2013 $p < 0.05$ with all other months; Fig. 8).

DISCUSSION

Whalewatching boats concentrate their activities according to whale aggregation areas. Since southern right whales prefer coastal waters, most sightings took place at less than 1,000m from the coast. Most sighting locations varied across the whale breeding season due to whale movements. During the first half of the season (June to September) most sightings were recorded near Puerto Pirámides port – where large numbers of whales are concentrated – which is a benefit for the companies, which look to optimise their fuel costs. In October, many whales moved into deeper waters, where they perform long dives apparently to feed. Consequently, whalewatching trips at this time took place farther from Puerto Pirámides port and also farther from the coast. Whales have been seen performing feeding behaviours several times (Argüelles, Fazio and Bertellotti, unpublished data), and Hoffmeyer *et al.* (2010) and Vighi *et al.* (2014) demonstrated that the zooplankton patches of Golfo Nuevo in the Southern Hemisphere's spring (September to December) could be dense enough to make feeding worthwhile on this nursery ground. Finally, at the end of the season (November and December), most whales were found farther south and away from Puerto Pirámides, moving outside Golfo Nuevo to southern feeding grounds (Vighi *et al.*, 2014). Despite the micro-scale pattern of whale movements, whalewatching companies always attempted to navigate as close to the port as possible, not only because of economic saving, but also because bad weather conditions occasionally forced them to do so.

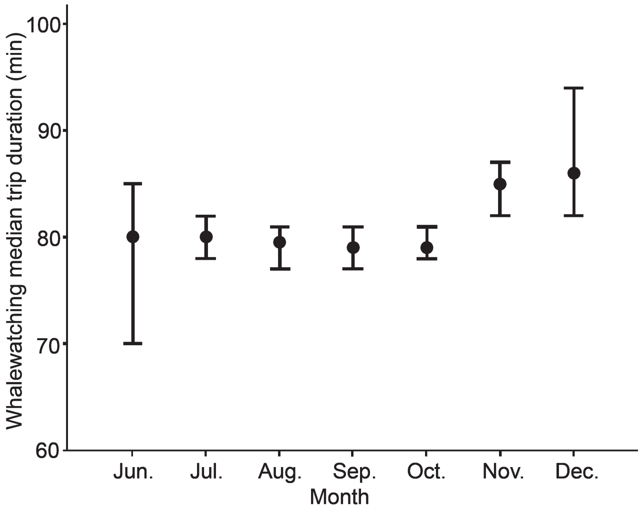

Fig. 8. Median duration of whale watching trips per month (all years gathered together). Error bars: 95% CI.

In the earlier months of the whale season (June to August), most of the sightings were of mating groups or others. In addition, many mothers were still pregnant and it was common to watch them resting alone on the surface. Although births tended to start in July, the new regulation applied from 2008 onwards permitted watching of mother-calf pairs from only 1 September so as not to disturb recently born calves. At mid-season and at the end of the season, sightings were mostly of mother-calf pairs, which is also the last group of whales to leave the area. These results coincided with those reported in 1993 by Rowntree *et al.* (2001). Mother-calf pairs were the most abundant whale group (around 60%) sighted during the season, in agreement with reports by Rivarola *et al.* (2001) and Argüelles (2008), not only because they stayed in the area longer, but also because companies want to show them to tourists at least once per trip. In earlier months, mothers prefer coastal waters because their calves are still very small, whereas in later months, calves are large enough to stay on the surface while mothers remain offshore or swim with them, maybe teaching them to feed. Mother-calf pairs occupy coastal areas at the beginning of the season, whilst mating groups seem to prefer offshore areas, as reported by Crespo *et al.* (2014). Solitary or grouped animals ('others') were distributed along the total range of distances to the coast with no special pattern, except at the end of the season when they shared areas farther from the coast with mother-calf pairs. In general terms, in the first half of the whale season, trips tended to be coastal and shorter (but never less than 90min) but the groups of whales sighted were more varied. In contrast, during the second half of the season trips tended to be further from the coast and longer, but the groups of whales sighted were mainly mothers with their calves. This difference in the characteristics of the sightings throughout the whale season (early or late) could be the basis to generate different recreational experience opportunities, promoting two types of whalewatching boat trips; 'friendly' or 'adventure' (see Fig. 5). A friendly trip would take less time, occur near the coast and have more amenities for tourists. On the other hand, an adventure trip would offer not only whalewatching, but also a more exciting and adventurous navigation.

Whalewatching from Puerto Pirámides was frequently restricted by weather conditions. Most days on which the port was closed, it was due to strong southerly or south-westerly winds because of the high waves they caused. This is the reason why most trips were conducted in northerly winds, followed by westerly winds (the most common wind direction in Patagonia) and least frequently in southerly winds (easterly winds are scarce in the region). On days that the sea was very rough, but not rough enough to close the port, trips tended to be shorter and sightings tended to be longer since these sea conditions did not allow captains to find many whales. They stayed longer with each whale. Another interesting detail is that from 2005 until the present, the increase in the number of whalewatching tourists in Puerto Pirámides per year was not as large as the increase that had occurred since its origins, which could indicate that the activity in that town may have reached its carrying capacity. From 2005 to 2007, the number of tourists increased slightly per year, and trips were shortened to maximise passenger numbers per day. Nevertheless, in 2008, probably due to the international economic crisis, there was around a 10% decrease in the number of whalewatchers (101,743) relative to 2007, which reduced the number of trips per day, and trips were also longer. This effect could also be a result of compliance with the current legislation that came into force in 2008. One of the regulations of the 'Patagonian Technique for Whale Watching' states that trips should be at least 90 minutes in length (shorter only in poor weather conditions), to guarantee a high quality tourism service. Longer trips were accompanied by longer sighting-times, which means that the boats stayed longer with the same whales. As expected, at the end of the season, when whales are farther from the port, trips lasted longer. Furthermore, as the 2011 season progressed, the number of tourists decreased markedly, possibly due to the Puyehue volcano eruption that interrupted flights to Patagonia, severely affecting the incoming revenues to the area.

Whalewatching boats follow right whale distribution in a large area of Golfo Nuevo, which makes whalewatching an excellent scientific platform; it also has a strong educational potential and protects right whales against other harmful commercial activities (Chen, 2011; Rivarola *et al.*, 2001). In addition, the spatial and temporal dynamics of the sightings could be a good indicator of the different activities of whales in the area, for example mentioned feeding behaviour. The community involved in whalewatching can help with solving problems with the animals they live and work with. For example, the people of Puerto Pirámides brought about action against the kelp gulls that peck skin and blubber from the backs of southern right whales, causing them serious injuries, a problem that only occurs in Península Valdés and that affects mainly calves (Fazio *et al.*, 2015; 2012).

Governmental guidelines or codes of conduct related to the behaviour of whalewatching operators have greater acceptance when whalewatching operators and tourism organisations are consulted extensively during the drafting of the guidelines. There is top-down remit for the production of new guidelines, but there is bottom-up involvement in their construction (Garrod and Fennell, 2004; Macedo *et al.*, 2013). This is the case for the law on whalewatching implemented in 2008, which was the result of several years of joint work between all those involved in whalewatching, such as agencies of Chubut Province, whalewatching operators, researchers, NGOs, the IWC, and IFAW. Some of this joint work is reflected in the Whale Watching Sustainable Tourism Workshop carried out in Puerto Pirámides in 2004 and the International Workshop on Management and Non-Lethal Use of Cetacean conducted in Puerto Pirámides in 2005.

Most whalewatching regulations issued by Chubut are similar to others that affect this activity in other countries (Kessler and Harcourt, 2013; Secretaría de Turismo y Áreas Protegidas, 2011). Some of these rules, if correctly applied, could improve the quality of a conservation plan, considering that both gulfs of Península Valdés (San José and Nuevo) are the main calving areas for this species in the Southwest Atlantic Ocean. Currently a Conservation Management Plan (CMP) for the Southwest Atlantic Southern Right Whale involving Argentina, Brazil, Chile, Peru and Uruguay is being prepared. One of the main objectives of the CMP is to protect the habitat of the southern right whale and minimise human threats in order to maximise its population recovery.

While the potential negative effects that tourism growth could cause in southern right whalewatching are of great concern, the regulation that currently exists and the management plan that is under development are vital for the conservation of this species in Patagonia and are excellent examples for other countries.

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Substantial decline in energy storage and stomach fullness in Antarctic minke whales (*Balaenoptera bonaerensis*) during the 1990s

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ABSTRACT

A substantial decline in energy storage in the Antarctic minke whale during the 18-year Japanese JARPA research programme (austral summers 1987/88–2004/05) was reported in 2008 (Konishi *et al.,* 2008). The statistical method used in the study was simple multiple linear regression. The results have since been thoroughly discussed by the Scientific Committee of the International Whaling Commission because of the potential importance of the findings. Some had suggested that the sampling heterogeneity in the JARPA data was so substantial that generalised linear models (GLMs) with interaction terms and random-effects terms should be explored. For the present article, five response variables related to energy storage and the variable 'stomach content weight' are systematically analysed using GLMs. For all five energy storage variables, the results show declines in the interval 3% to 9% over the JARPA period, all significantly different from zero at the 5% level, but no later decline. The weight of sieved stomach contents declined by 25% over the same period. The coefficients of the decline and the coefficients for most other independent variables were similar to values obtained by simple linear regression, but in some cases the standard errors were larger. The results indicate that important changes took place in the Antarctic ecosystem during the 1990s. It is hypothesised that the most important cause of the changes was the simultaneous increase in numbers of other krill feeders, especially humpback whales.

KEYWORDS: MINKE WHALES, ENERGY STORAGE, STOMACH FULLNESS, ECOSYSTEM CHANGES, JARPA, INTERSPECIES COMPETITION, ANTARCTIC

INTRODUCTION

Konishi *et al.* (2008) reported a substantial decline in energy storage in Antarctic minke whales sampled during the 18 years (1987/88–2004/05) of the Japanese Whale Research Programme under Special Permit in the Antarctic (JARPA). Sampling took place during the austral summer each year, typically from early December to late March, in the area 35°E to 145°W and south of 58°S. The western and eastern areas, split at 130°E, were surveyed in alternate years so that the entire 180° survey area was covered every two years. Three variables were used as proxies for energy storage: blubber thickness carefully measured at a mid-lateral point at the level of the dorsal fin; the half girth measured at the level of the umbilicus; and the total weight of the fat dissected from the whale (blubber + intestinal fat). Only data from sexually mature males and pregnant females were used in the investigation. Blubber thickness and girth data were available from about 4,700 whales, while fat weight was available only from the first whale caught each day, altogether 740 whales. Details on the sampling and measurement procedures are given in Konishi (2006) and Konishi *et al.* (2008) (see also Fig. 1).

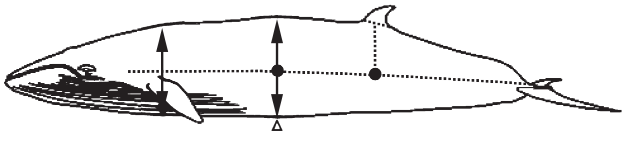

Fig. 1. Position of blubber thickness and half girth measurements. Closed circles = lateral points for blubber thickness measurements; open triangle = position of the umbilicus; arrows: half girth at the levels of the axilla and the umbilicus.

The analyses were carried out using stepwise linear regression (step forward procedure by Wald). The best model was selected using the Bayesian information criterion, BIC (Schwarz, 1978), even when the regression based on *p*-values included more independent variables. The main continuous independent variables were 'year' (1987/88 = year 1), 'body length' (m), 'date' (1 December = day 1), 'longitude' (in degrees east), 'latitude' (degrees) and 'diatom' (scale 1–5). The degree of diatom coverage is believed to be a measure of the time the whale has spent in cold water (Lockyer, 1981). The two sexes were analysed both separately and combined. When they were analysed in combination, 'sex' was used as a categorical variable. The regression analyses showed that blubber thickness, girth and fat weight had been decreasing over the JARPA period. The decrease per year was estimated at 0.02cm for mid-lateral blubber thickness and 17kg for fat weight, corresponding to about 9% for both measurements over the 18-year period. Furthermore, 'date', 'extent of diatom adhesion', 'body length', 'longitude', 'latitude' and 'sex' were identified as partially independent predictors of 'blubber thickness', 'girth' and 'fat weight' (see Konishi *et al.*, 2008).

At the 2011 meeting of the Scientific Committee of the IWC (International Whaling Commission), a paper was presented stating that the particular multiple regression model used by Konishi *et al.* (2008) might have been inappropriate (de la Mare, 2011) and suggesting that mixed-effects models should be fitted to the data to account for various forms of heterogeneity. In response (e.g. see discussions in IWC, 2012; 2013; 2014; 2015a), a large number of mixed-effects models

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were analysed. Two new dependent variables were added to these analyses; (1) 'blubber thickness' at another well-defined lateral point at the level of the umbilicus; and (2) 'half girth' at the level of the axilla.

Konishi *et al.* (2014) hypothesised that the decline in energy storage observed during the JARPA period might indicate that food availability had also declined. To test this hypothesis, the authors used catch data from the 15 years of JARPA during which forestomach contents were weighed and the first five years (2005/06–2009/10) of JARPA II in a linear mixed-effects analysis that showed a 31% decrease in sieved stomach content weight from the research catch of Antarctic minke whales between 1990/91 and 2009/10. Their analyses included 'Local time of day' as an additional explanatory variable because stomach fullness varies with time of day.

At the 2014 IWC Scientific Committee meeting, the model selection procedure used by Konishi *et al.* (2014) was also criticised (IWC, 2015a). The Committee agreed on the model selection procedure described below. These analyses were carried out and subsequently accepted by the Committee as final during the meeting (IWC, 2015b). In the present paper, these analyses have been repeated and extended somewhat. The authors considered this to be an important element of quality assurance for the analyses. However, the main results are unchanged from those presented to the Scientific Committee in 2014.

The energy storage variables have also been analysed for the first six years of JARPA II (2005/06–2010/11) and the results indicate no further decline during these years (Konishi and Walløe, 2014). The data on sieved stomach content weight have therefore also been reanalysed for the JARPA period only for the present paper. For this variable, preliminary analyses showed a small increase in the period 2005/06–2010/11. Thus all analyses described below were of data from the JARPA period only (Fig. 2).

METHODS

In addition to the six continuous response variables and the continuous explanatory variables mentioned above, a number of categorical variables, interaction terms and random-effects terms were used in the analyses. Table 1 contains a list of all response and explanatory variables.

Preliminary model runs with 'DateNum' as a quadratic term always gave a better model fit than the same models run with 'DateNum' as a linear term. Thus in the model runs explored in this article, 'DateNum' has always been used as a quadratic term. For other variables (e.g. 'YearNum', 'Diatom' and 'LtimeNum'), preliminary analyses indicated that linear terms were most appropriate.

The general advice for the exploration of general linear models with possible interaction and random-effects terms is to start from a 'full model' and then add and subtract interaction terms and random-effects terms in a systematic

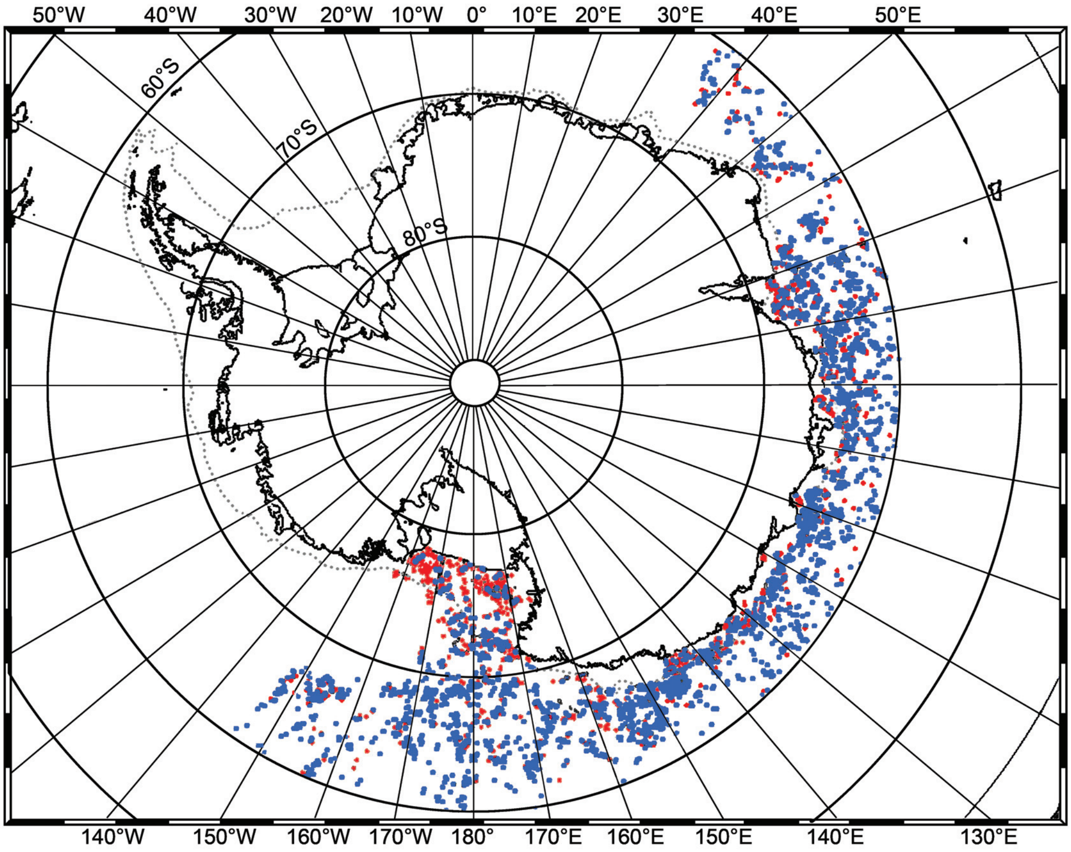

Fig. 2. Map of the Southern Ocean, modified from Konishi *et al.* (2014). The study area for the research programmes is the longitudinal sector between 35°E and 145°W in the Pacific and Indian Ocean sectors of the Southern Ocean. Dots show positions where the Antarctic minke whales used in this study were sampled during JARPA period (1987/88–2004/05) survey seasons (blue male, red female). The grey dotted line shows the 1,000m depth contour, which roughly indicates the edge of the continental shelf. The SCAR Antarctic Digital Database was used for the illustration of Antarctic coastline with extended ice shelves.

Table 1

Names of variables and terms used in the regression analyses.

Response variable (with sample size)	
BT11 (n = 4,727)	Blubber thickness at mid-lateral point on the vertical axis of the dorsal fin (in cm)
BT7 (n = 4,739)	Blubber thickness at a mid-lateral position on the vertical axis of the umbilicus (in cm)
UmbilicusGirth (n = 4,719)	Half girth at the level of the umbilicus (in cm)
AxillaryGirth (n = 3,870)	Half girth at the level of the axilla (in cm)
FatWeight (n = 738)	Weight of subcutaneous fat (blubber) + weight of intestinal fat (in metric tons)
FirstS (n = 3,622)	Sieved stomach content weight from forestomach (in kg)
Explanatory variable (continuous)	
YearNum	Year as a continuous variable (87/88 = year #1)
BLm	Body length (in m)
DateNum	Date number (1 December = day 1)
LongNum	Longitude in degrees E (170°W = 190°E)
LatNum	Latitude in degrees S
Diatom	Degree of diatom coverage (scale 1 to 5)
LtimeNum	Local time of day
Explanatory variable (categorical)	
YearCat	Year as a categorical variable (87/88 = reference level)
LatCat11	Latitude divided into 11 intervals
LongCat11	Longitude divided into 11 sectors
LonSect	Longitude divided into 6 IWC sectors (IIIE = reference level)
Ice	Categorical variable (near ice edge = 1, far from ice edge = 0)
TrackLine	Categorical variable, each straight part of a track line has a different name
Sex	Categorical variable for Sex (female = 0; male = 1)
Interaction and random effects	
YearNum:Sex	Interaction between YearNum and Sex
(1|YearCat)	Random effects of year on the model Intercept
(YearNum | Ice)	Random effects of YearNum partitioned by Ice
(DateNum^2|LonSect)	Random effects of DateNum^2 partitioned by LonSect
(DateNum^2|LatCat11)	Random effects of DateNum^2 partitioned by LatCat11
(DateNum^2|TrackLine)	Random effects of DateNum^2 partitioned by TrackLine

Table 2

Model selection with fat weight as the response variable during the JARPA period.

Model no.	BIC	Models
1	–283	Full.BC<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)
2	–110	Full.BC.re1<–lmer(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LonSect))
3	–102	Full.BC.re2<–lmer(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LatCat11))
4	–135	Full.BC.re3<–lmer(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|TrackLine))
5	–114	Full.BC.re4<–lmer(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(YearNum|Ice))
6	–150	Full.BC.re5<–lmer(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat))
7	–278	Full.BC.1<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11)
8	**–332**	**Full.BC.2<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex)**
9	–290	Full.BC.3<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongCat11+Sex)
10	–290	Full.BC.4<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+LongCat11+Sex)
11	–239	Full.BC.5<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex)
12	–159	Full.BC.6<–lm(FatWeight~YearNum:Sex+BLm+Diatom+LatNum+LongNum+LongCat11+Sex)
13	165	Full.BC.7<–lm(FatWeight~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)
14	–290	Full.BC.8<–lm(FatWeight~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)
15	–326	Full.BC.2.1<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum)
16	–338	Full.BC.2.2<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+Sex)
17	–336	Full.BC.2.3<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+Sex)
18	–291	Full.BC.2.4<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+Sex)
19	–203	Full.BC.2.5<–lm(FatWeight~YearNum:Sex+BLm+Diatom+LatNum+LongNum+Sex)
20	118	Full.BC.2.6<–lm(FatWeight~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+Sex)
21	**–338**	**Full.BC.2.7<–lm(FatWeight~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex)**
22	–302	Full.BC.2.7.1<–lm(FatWeight~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum)
23	**–344**	**Full.BC.2.7.2<–lm(FatWeight~YearNum+BLm+DateNum^2+Diatom+LatNum+Sex)**
24	–343	Full.BC.2.7.3<–lm(FatWeight~YearNum+BLm+DateNum^2+Diatom+LongNum+Sex)
25	–298	Full.BC.2.7.4<–lm(FatWeight~YearNum+BLm+DateNum^2+LatNum+LongNum+Sex)
26	–209	Full.BC.2.7.5<–lm(FatWeight~YearNum+BLm+Diatom+LatNum+LongNum+Sex)
27	112	Full.BC.2.7.6<–lm(FatWeight~YearNum+DateNum^2+Diatom+LatNum+LongNum+Sex)
28	–307	Full.BC.2.7.2.1<–lm(FatWeight~YearNum+BLm+DateNum^2+Diatom+LatNum)
29	**–349**	**Full.BC.2.7.2.2<–lm(FatWeight~YearNum+BLm+DateNum^2+Diatom+Sex)##BESTMODEL**
30	–304	Full.BC.2.7.2.3<–lm(FatWeight~YearNum+BLm+DateNum^2+LatNum+Sex)
31	–214	Full.BC.2.7.2.4<–lm(FatWeight~YearNum+BLm+Diatom+LatNum+Sex)

manner (Zuur *et al.*, 2009). The authors tested a 'full model' with biologically plausible variables, including an interaction term. Five potential random-effects terms were then added, one at a time, including a random effect for year treated as a categorical variable. The random-effects term was included if the model run resulted in a lower BIC value than the 'full model'. Finally, the fixed effects, which did not contribute sufficiently to the model, were deleted based on BIC (IWC, 2015b). This is exactly the same procedure as that recommended by the JARPA II review panel (IWC, 2015a).

At each step the model selected should be the one which gives the lowest BIC value (Schwarz, 1978), formulated as:

$$\mathrm{BIC} = -2 \ln L + \mathrm{K} \log n$$

where L is likelihood and K is the number of parameters. However for complex situations, such as the ones investigated here, even the choice of a 'full model' is difficult and the number of possible interaction terms is extremely large. The choices made were based on experience of the models published previously (Konishi *et al.*, 2014; Konishi *et al.*, 2008) and on discussions in the relevant IWC SC sub-committees during its 2014 meeting. Table 2 illustrates the

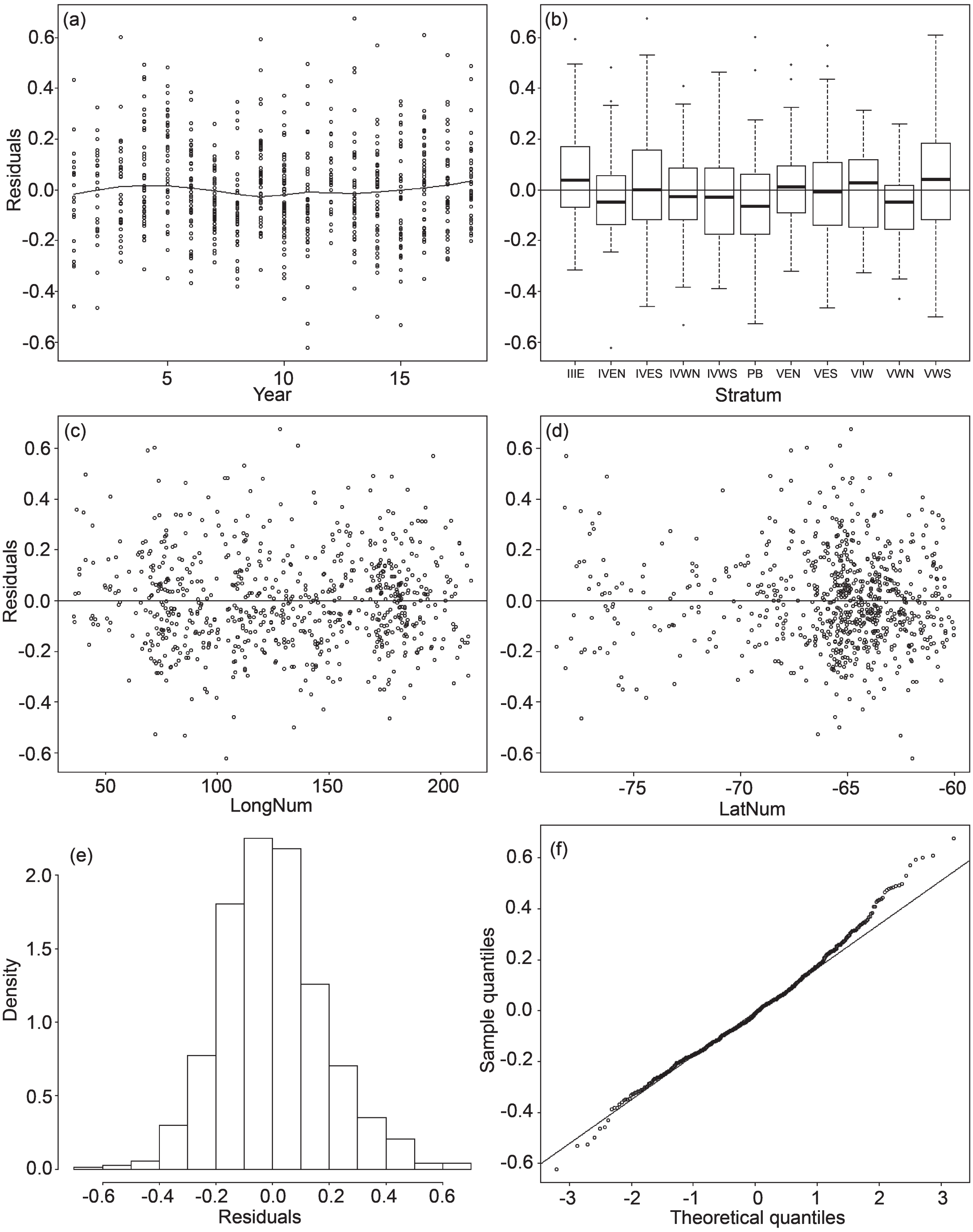

Fig. 3. Diagnostic plots for the best model with FatWeight as the response variable. (a) residual plots against year with spline curve; (b) residual box plots against Stratum from Indian Ocean to Pacific Ocean based on IWC defined areas (Donovan, 1991) with bearing small areas (N, S, E, W); (c) residual plots against longitude (degrees East: LongNum); (d) residual plots against latitude (degrees South: LatNum); (e) distribution of residuals in the best model; and (f) Q-Q plots for the best model.

Table 3

Summary for the best model using FatWeight as the response variable (Full.BC.2.7.2.2 in Table 2).

Coefficients	Estimate	Std. error	*t* value
(Intercept)	–2.1510	0.1494	–14.40
YearNum	–0.0083	0.0014	–5.87
BLm	0.4262	0.0166	25.65
DateNum^2	2.97E–05	2.17E–06	13.69
Diatom	0.0414	0.0058	7.12
Sex	–0.1365	0.0171	–7.99

systematic procedure in the simplest case of the six which were investigated. In this case the best model did not include any interaction terms or random-effects terms. Table 6 illustrates the procedure in one of the more complex of the six cases investigated. In this case, the best model included two random-effects terms.

The use of Maximum Likelihood (ML) or Restricted Maximum Likelihood (REML) can be explained as follows (see also Zuur *et al.*, 2009).

(1) Decide which random effects to include and fit the models using REML.

(2) Systematically try to eliminate some of the fixed effects then fit the models using ML.

(3) When the best model has been identified in step (2), fit it using REML.

The R-programs 3.0.2 (R Development Core Team, 2013) were used for all calculations and package ‘lme4’ version 1.0.4 (Bates *et al.*, 2014) was used for linear mixed-effects models.

RESULTS

Table 2 shows the model selection procedure for the dependent variable ‘FatWeight’. Model 1 shows the basic full model. Models 2–6 show the basic model with five different random-effects terms added one at a time. None of these models resulted in lower BIC values than the basic model. Thus none of these random effects were included in the final model. Models 7–31 show the systematic reduction of explanatory variables from the basic model (No 1). Model 29 gave the lowest BIC value. No further reduction in independent variables gave lower BIC values (not shown in the table). Table 3 presents the statistical parameters of this best model for ‘FatWeight’. It can be seen that the total weight of fat in the whales declined over the 18 JARPA years by 8.3 ± 1.4kg yr^{-1}. The weight of fat was 137 ± 17kg higher in females than in males. The weight of fat also increased with body length, with the date during the feeding season and with extent of diatom adhesion, which is believed to be a measure of the time the animal has spent in cold water. All the regression coefficients are statistically highly significant. Fig. 3 shows six diagnostic plots of the fit of this model.

Table 4 illustrates the model selection for blubber thickness at the mid-lateral point below the dorsal fin (BT11). Again, none of the models with random effects added (Models 2–6) resulted in lower BIC values than the basic model (No. 1). Systematic reduction of independent variables resulted in model 21, which gave the lowest BIC value and thus was considered to be the best fit. Table 5 shows the regression results for this model. The blubber thickness declined by 0.019 ± 0.002cm yr^{-1} over the JARPA period. Blubber thickness, like fat weight, was dependent on body length, extent of diatom adhesion, date during the feeding season and sex. In addition, blubber thickness increased from west to east and decreased from south to north. All coefficients are statistically highly significant. Fig. 4 shows six diagnostic plots for the model fit.

Table 6 illustrates the model selection for blubber thickness at the level of the umbilicus (BT7). When year was added to the basic model as a random categorical variable,

Table 4

Model selection with blubber thickness (BT11) as the response variable during the JARPA period.

Model no.	BIC	Models
1	**10,794**	**Full.BC<–lm(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)**
2	10,948	Full.BC.re1<–lmer(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LonSect))
3	10,920	Full.BC.re2<–lmer(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LatCat11))
4	10,816	Full.BC.re3<–lmer(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|TrackLine))
5	10,948	Full.BC.re4<–lmer(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(YearNum|Ice))
6	10,797	Full.BC.re5<–lmer(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat))
7	10,837	Full.BC.1<–lm(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11)
8	**10,772**	**Full.BC.2<–lm(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex)**
9	10,787	Full.BC.3<–lm(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongCat11+Sex)
10	10,801	Full.BC.4<–lm(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+LongCat11+Sex)
11	11,377	Full.BC.5<–lm(BT11~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex)
12	11,640	Full.BC.6<–lm(BT11~YearNum:Sex+BLm+Diatom+LatNum+LongNum+LongCat11+Sex)
13	10,803	Full.BC.7<–lm(BT11~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)
14	10,787	Full.BC.8<–lm(BT11~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)
15	10,821	Full.BC.2.1<–lm(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum)
16	10,817	Full.BC.2.2<–lm(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+Sex)
17	10,781	Full.BC.2.3<–lm(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+Sex)
18	11,367	Full.BC.2.4<–lm(BT11~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+Sex)
19	11,756	Full.BC.2.5<–lm(BT11~YearNum:Sex+BLm+Diatom+LatNum+LongNum+Sex)
20	10,781	Full.BC.2.6<–lm(BT11~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+Sex)
21	**10,767**	**Full.BC.2.7<–lm(BT11~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex)##BESTMODEL**

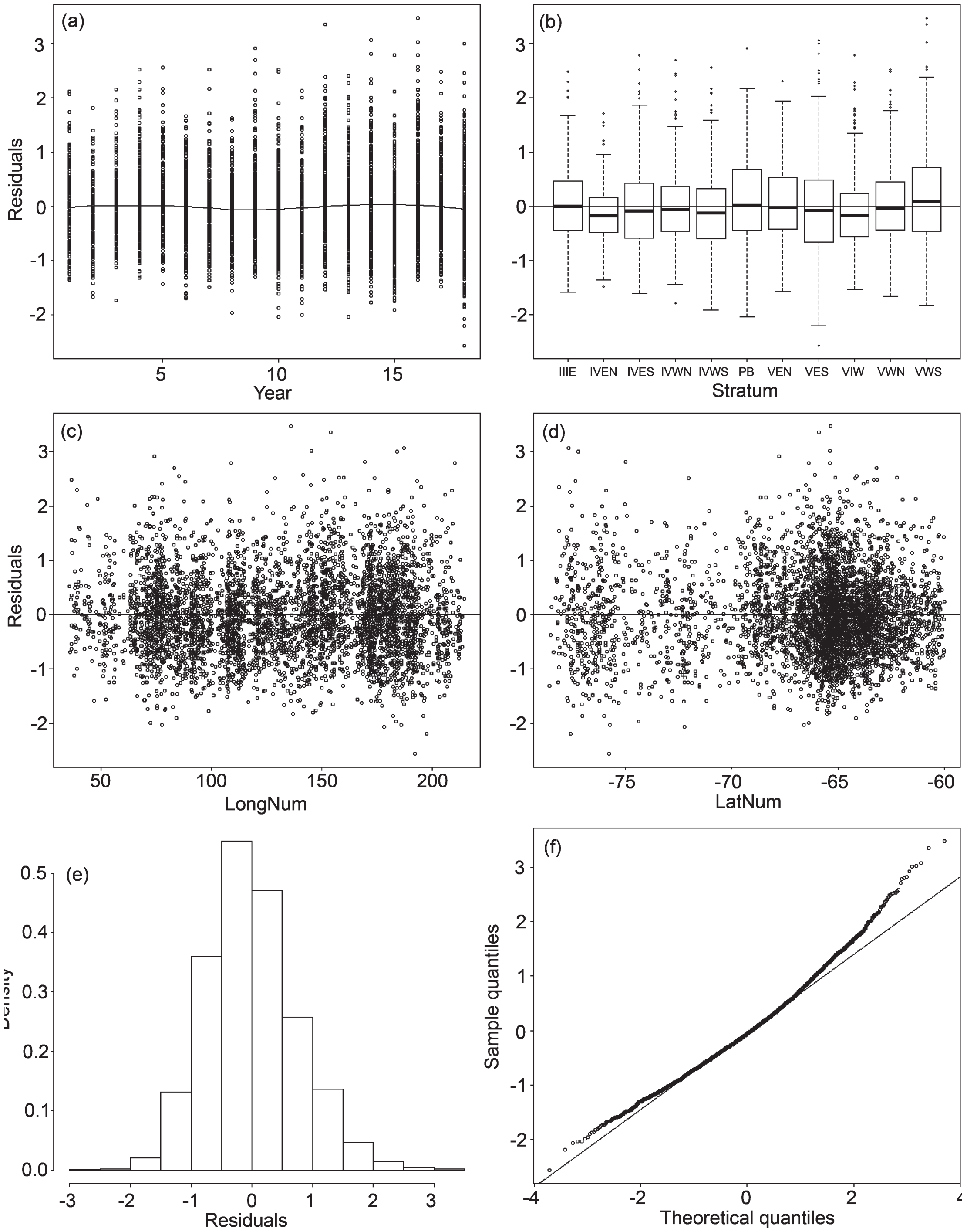

Fig. 4. Diagnostic plots for the best model with blubber thickness (BT11) as the response variable. For further explanation, see the caption for Fig. 3.

Table 5

Summary for the best model using blubber thickness (BT11) as the response variable (Full.BC.2.7 in Table 4).

Coefficients	Estimate	Std. error	*t* value
(Intercept)	0.9766	0.3481	2.81
YearNum	–0.0190	0.0022	–8.65
BLm	0.1142	0.0273	4.19
DateNum^2	0.0001	0.0000	33.19
Diatom	0.2281	0.0092	24.79
LatNum	–0.0151	0.0036	–4.14
LongNum	0.0021	0.0003	7.44
Sex	–0.3329	0.0297	–11.19

the BIC value decreased (Model 6). The next four model runs (7–10) show that another random effect should also be added. Systematic reduction of the linear terms in the basic model showed that model 28 resulted in the lowest BIC value. Table 7 shows the statistical parameters of the random and fixed effects. Blubber thickness at this lateral point declined by 0.015 ± 0.008cm yr^{-1}. This decline is only marginally significant at the 5% level. The other explanatory variables were roughly of the same magnitude as for the other blubber thickness variable, the only exception being that ‘LongNum’ was not included in the best model. All these variables were statistically highly significant. Fig. 5

Table 6

Model selection with blubber thickness (BT7) as the response variable during the JARPA period.

Model no.	BIC	Models
1	9,153	Full.BC<–lm(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)
2	9,317	Full.BC.re1<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LonSect))
3	9,286	Full.BC.re2<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LatCat11))
4	9,222	Full.BC.re3<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|TrackLine))
5	9,316	Full.BC.re4<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(YearNum|Ice))
6	**9,149**	**Full.BC.re5<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat))**
7	9,174	Full.BC.re5.1<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|LonSect))
8	9,173	Full.BC.re5.2<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|LatCat11))
9	**9,135**	**Full.BC.re5.3<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine))**
10	9,174	Full.BC.re5.4<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(YearNum|Ice))
11	9,008	Full.BC.re5.3ML<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
12	9,093	Full.BC.re5.3ML.1<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
13	**8,954**	**Full.BC.re5.3ML.2<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)**
14	9,002	Full.BC.re5.3ML.3<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
15	9,043	Full.BC.re5.3ML.4<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
16	9,559	Full.BC.re5.3ML.5<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
17	9,313	Full.BC.re5.3ML.6<–lmer(BT7~YearNum:Sex+BLm+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
18	9,023	Full.BC.re5.3ML.7<–lmer(BT7~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
19	9,000	Full.BC.re5.3ML.8<–lmer(BT7~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
20	9,045	Full.BC.re5.3ML.2.1<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
21	8,948	Full.BC.re5.3ML.2.2<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
22	8,995	Full.BC.re5.3ML.2.3<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
23	9,508	Full.BC.re5.3ML.2.4<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
24	9,283	Full.BC.re5.3ML.2.5<–lmer(BT7~YearNum:Sex+BLm+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
25	8,968	Full.BC.re5.3ML.2.6<–lmer(BT7~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
26	**8,946**	**Full.BC.re5.3ML.2.7<–lmer(BT7~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)**
27	9,233	Full.BC.re5.3ML.2.7.1<–lmer(BT7~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
28	**8,940**	**Full.BC.re5.3ML.2.7.2<–lmer(BT7~YearNum+BLm+DateNum^2+Diatom+LatNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)##BESTMODEL**
29	8,987	Full.BC.re5.3ML.2.7.3<–lmer(BT7~YearNum+BLm+DateNum^2+Diatom+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
30	9,500	Full.BC.re5.3ML.2.7.4<–lmer(BT7~YearNum+BLm+DateNum^2+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
31	9,274	Full.BC.re5.3ML.2.7.5<–lmer(BT7~YearNum+BLm++Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
32	8,961	Full.BC.re5.3ML.2.7.6<–lmer(BT7~YearNum+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)

shows the six diagnostic plots indicating that the model fit is good.

Table 8 illustrates the model selection for half girth at the level of the umbilicus. As for BT7, two random effects had to be added to the basic model (Model 9). Table 9 shows the regression coefficients for the best model. 'Half girth' declined by 0.406 ± 0.136cm yr^{-1} over the JARPA period, so that total girth declined by 0.81 cm yr^{-1}. The independent variables body length, extent of diatom adhesion, date during the feeding season and sex influenced girth in the same manner as they did the other dependent variables, but girth decreased from west to east. All coefficients were statistically different from zero. Fig. 6 shows the diagnostic plots.

Table 7

Summary for the best model using blubber thickness (BT7) as the response variable (Full.BC.re5.3ML.2.7.2 by REML in Table 6).

Random effects		
Groups	Name	Std. dev.
TrackLine	(Intercept)	9.33E–02
	DateNum^2	1.62E–05
YearCat	(Intercept)	1.59E–01
Residual		6.04E–01

Fixed effects	Estimate	Std. error	*t* value
(Intercept)	0.7281	0.3268	2.23
YearNum	–0.0149	0.0076	–1.96
BLm	0.1049	0.0223	4.70
DateNum^2	0.0001	0.0000	23.83
Diatom	0.1831	0.0076	24.04
LatNum	–0.0277	0.0035	–7.82
Sex	–0.4345	0.0249	–17.45

The model with the lowest BIC value was selected at each step, even if the reduction in BIC was small. However, it may be argued that very small BIC differences have no real significance and that in such cases the simpler of the two models should be selected. The model selection for umbilicus half girth is one such case (Table 8). The introduction of the second random effect term (DateNum^2|TrackLine) in Model 9 results in only a slightly lower BIC value than that for Model 6, but Model 8 is more complex. Therefore, the consequences of using the simpler model as basis for further selection were explored. The coefficients for the fixed effects for the resulting final model were very close to the values listed in Table 9 (difference of less than 1%).

Table 10 illustrates the model selection for axillary half girth. For this model, there was only one random term involving year. Table 11 shows the estimated coefficients from the best model. Total girth declined by 0.90 cm yr^1 or 16cm over the JARPA period. The coefficients for the other explanatory variables had the same sign and were of similar magnitude to the coefficients for girth at the umbilicus. All

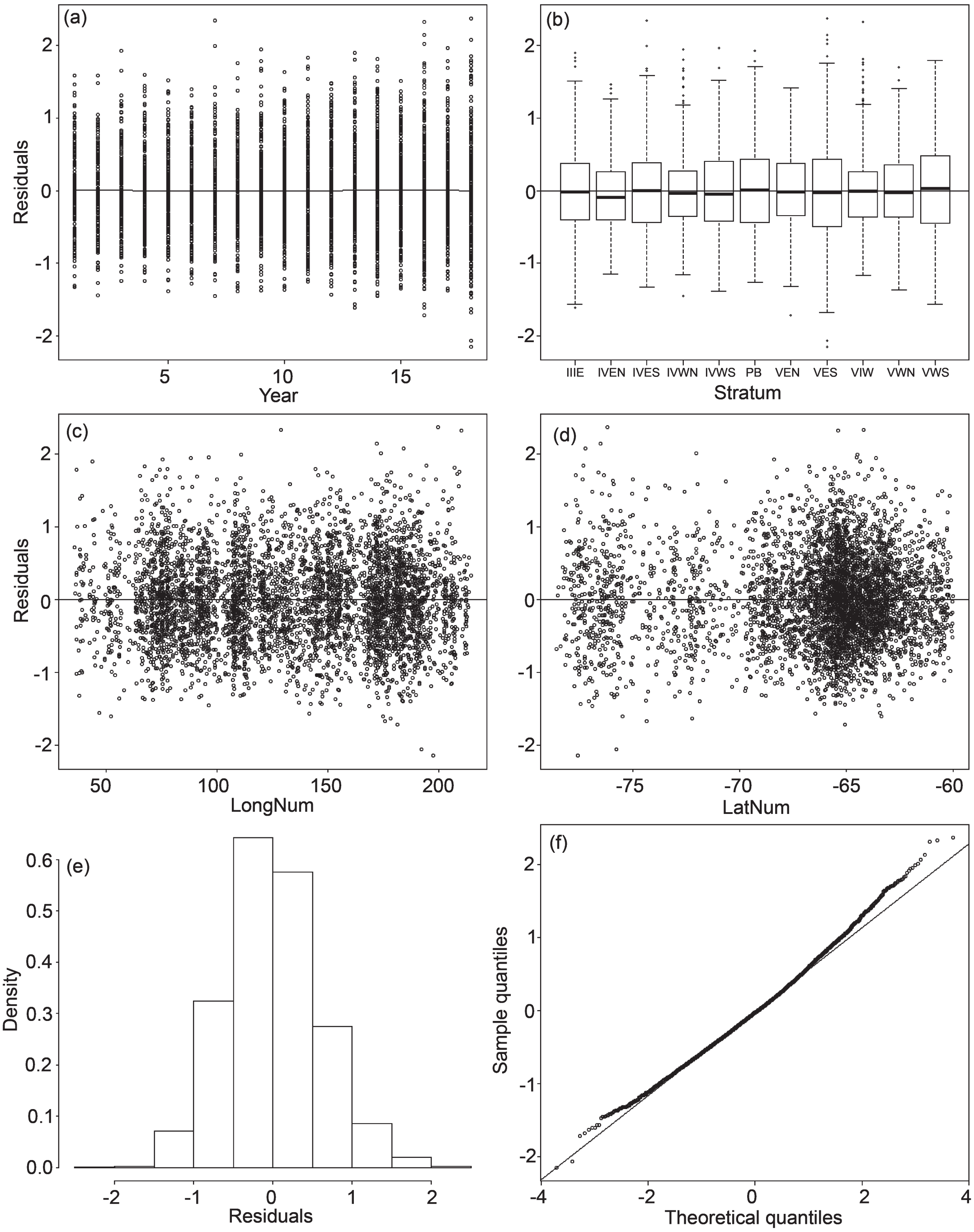

Fig. 5. Diagnostic plots for the best model with blubber thickness (BT7) as the response variable. Descriptions for each plot are same as written in the caption of Fig. 3.

coefficients were statistically different from zero. Fig. 7 shows the diagnostic plots.

Table 12 illustrates the model selection for the log-transformed weight of the sieved contents of the forestomach. Model 25 was the best model; it did not include any interaction terms or random-effects terms. Table 13 shows the regression coefficients for the best model. Stomach content weight decreased by 25% (95%CI 10–37%) over the JARPA period, excluding the first three years when the contents of the forestomach were not weighed. All the listed coefficients are statistically highly significant. Fig. 8 shows the diagnostic plots. Since the distribution of residuals showed a large deviation from a normal distribution, different transformations of the primary data were tested. To examine the effect of the skewness of the distribution of data for the log-transformed stomach content weight, these data were also Box-Cox transformed and model selection was conducted again. The selected best model was same as for log-transformed stomach content weight, showing a significant decline (Table 14 and Fig. 9). The Box-Cox transformed data showed an approximately symmetrical distribution, but with lighter tails than a normal distribution. Thus the real significance probabilities can be assumed to be smaller than the probabilities calculated from normal distributions.

DISCUSSION

The results show that all the five dependent variables related to energy storage declined substantially in Antarctic minke whales in the eastern (Pacific) half of the Antarctic Ocean

Table 8

Model selection with umbilicus half girth as the response variable during the JARPA period.

Model no.	BIC	Models
1	36,745	Full.BC<–lm(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)
2	36,793	Full.BC.re1<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LonSect))
3	36,795	Full.BC.re2<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LatCat11))
4	36,711	Full.BC.re3<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|TrackLine))
5	36,797	Full.BC.re4<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(YearNum|Ice))
6	**36,651**	**Full.BC.re5<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat))**
7	36,665	Full.BC.re5.1<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|LonSect))
8	36,671	Full.BC.re5.2<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|LatCat11))
9	**36,647**	**Full.BC.re5.3<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine))**
10	36,676	Full.BC.re5.4<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(YearNum|Ice))
11	36,631	Full.BC.re5.3ML<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
12	36,641	Full.BC.re5.3ML.1<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
13	**36,575**	**Full.BC.re5.3ML.2<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)**
14	36,623	Full.BC.re5.3ML.3<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
15	36,629	Full.BC.re5.3ML.4<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
16	36,987	Full.BC.re5.3ML.5<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
17	36,846	Full.BC.re5.3ML.6<–lmer(UmbilicusGirth~YearNum:Sex+BLm+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
18	38,018	Full.BC.re5.3ML.7<–lmer(UmbilicusGirth~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
19	36,629	Full.BC.re5.3ML.8<–lmer(UmbilicusGirth~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
20	36,587	Full.BC.re5.3ML.2.1<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
21	36,593	Full.BC.re5.3ML.2.2<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
22	**36,574**	**Full.BC.re5.3ML.2.3<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)**
23	36,931	Full.BC.re5.3ML.2.4<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
24	36,795	Full.BC.re5.3ML.2.5<–lmer(UmbilicusGirth~YearNum:Sex+BLm+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
25	37,961	Full.BC.re5.3ML.2.6<–lmer(UmbilicusGirth~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
26	36,574	Full.BC.re5.3ML.2.7<–lmer(UmbilicusGirth~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
27	36,582	Full.BC.re5.3ML.2.3.1<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
28	36,605	Full.BC.re5.3ML.2.3.2<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
29	36,933	Full.BC.re5.3ML.2.3.3<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
30	36,794	Full.BC.re5.3ML.2.3.4<–lmer(UmbilicusGirth~YearNum:Sex+BLm+Diatom+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
31	37,977	Full.BC.re5.3ML.2.3.5<–lmer(UmbilicusGirth~YearNum:Sex+DateNum^2+Diatom+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
32	**36,573**	**Full.BC.re5.3ML.2.3.6<–lmer(UmbilicusGirth~YearNum+BLm+DateNum^2+Diatom+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)##BESTMODEL**

during the JARPA period (1987/88 to 2004/05). The variable fat weight is perhaps most directly related to energy storage, but was available for about 15% of the whales only. Its value is given by the sum of the weights of the intestinal fat and blubber in the animal. Naturally other parts of the whale body also contain fat, but intestinal fat and subcutaneous fat are the two fat stores which in most mammals increase during fattening and decrease during starvation (Christiansen *et al.*, 2013; Miller *et al.*, 2012; Miller *et al.*, 2011; Williams *et al.*, 2007). The results indicate that these two fat stores decreased by about 9% (95% CI 6%–12%) during the JARPA years. The decreases in this section were calculated as difference of estimated first and last year's value using mean value and the coefficients; see also the example in Konishi *et al.* (2014).

Table 9

Summary for the best model using umbilicus half girth as the response variable (Full.BC.re5.3ML.2.3.6 by REML in Table 8).

Random effects

Groups	Name	Std. dev.
TrackLine	(Intercept)	2.59E+00
	DateNum^2	1.05E–05
YearCat	(Intercept)	2.83E+00
Residual		1.13E+01

Number of obs: 4,711, groups: TrackLine, 720; YearCat, 18

Fixed effects	Estimate	Std. error	*t* value
(Intercept)	75.4200	4.2620	17.69
YearNum	–0.4059	0.1364	–2.98
BLm	17.0500	0.4203	40.57
DateNum^2	0.0012	0.0001	17.41
Diatom	2.4730	0.1430	17.29
LongNum	–0.0559	0.0088	–6.39
Sex	–1.5270	0.4448	–3.43

In most mammals, the thickness of subcutaneous fat in the middle part of the body is another good measure of energy storage. In whales, the girth is mainly a measure of the amount of blubber and intestinal fat, but it also depends on other anatomical factors, e.g. the size of the foetus in female whales. This applies particularly to the girth at the level of the umbilicus. Both blubber thickness measurements and both girth measurements declined during the JARPA period.

One difficulty involved in using all five variables as proxies for measurements of energy storage is that it is known that the fat content of fat tissue can vary. The measurements would have been easier to interpret if the percentage of fat in the tissues had also been measured. Analysis of a limited volume of data from JARPA showed a positive correlation between blubber thickness and lipid content (IWC, 2015a). Even though the fat content of the blubber tissue was not measured, the results for all five variables indicate an important negative trend in energy storage.

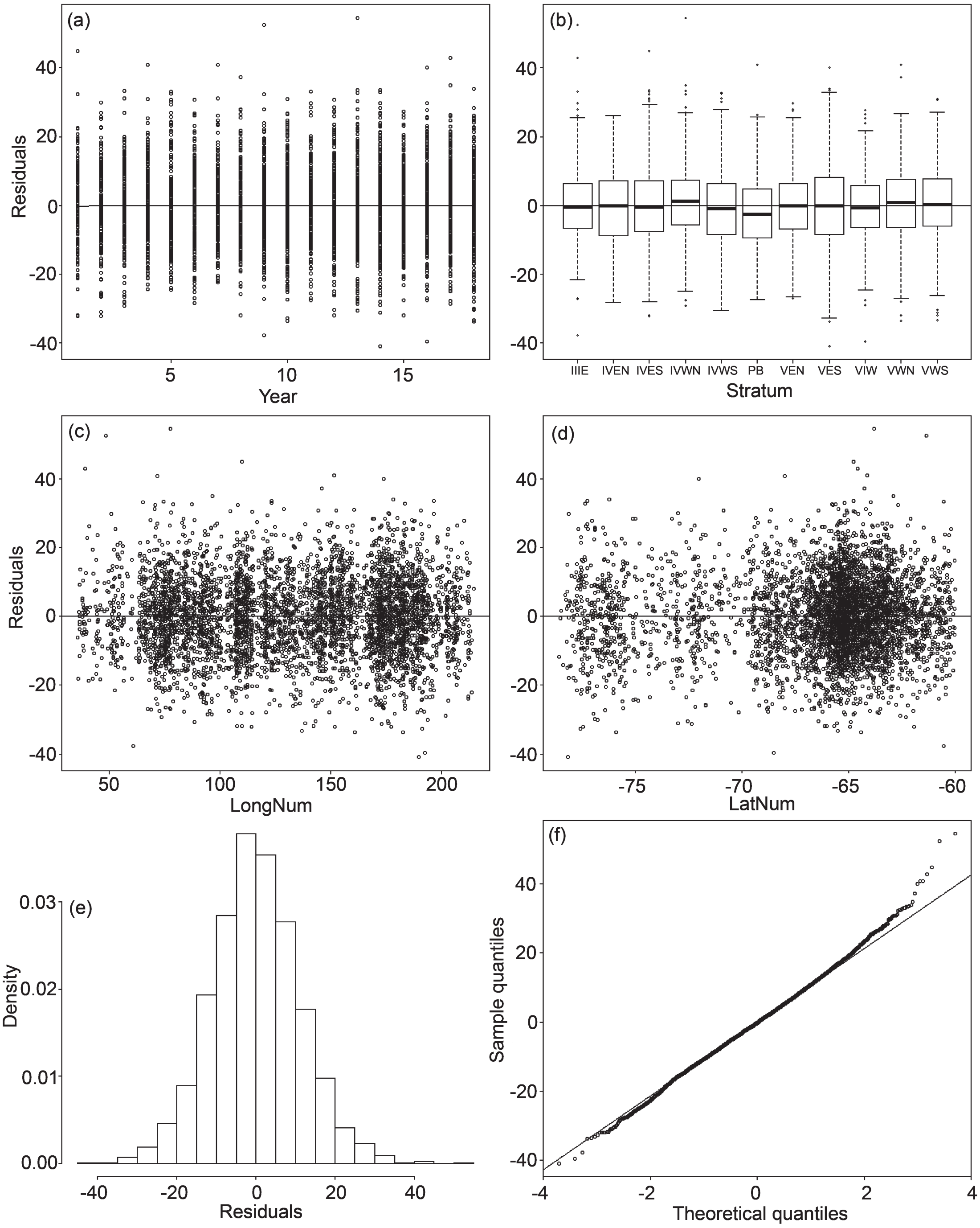

Fig. 6. Diagnostic plots for the best model with umbilicus half girth as the response variable. For further explanation, see the caption for Fig. 3.

The five variables were also significantly related to other independent variables. They all increased with extent of diatom adhesion, which is suggested to be a measure of how long an animal has spent in cold Antarctic waters (Lockyer, 1981). The five variables also increased with time during the feeding season and with body length. The energy stores in females were larger than in males. Other variables, such as longitude and latitude and random-effects variables, were included only in a few of the best models, and did not always have a consistent relationship with the different dependent variables.

The amount of food in the forestomach decreased during the day from the beginning to the end of the sampling period (a linear decrease on the log scale). Sampling started 1 hour after sunrise and ended 1 hour before sunset, but was limited to a maximum of 12 hours per day. On average, the weight of sieved food in the stomach declined during a 12-hour day from 57kg in the morning to 13kg in the evening, a decrease of 77%. An important implication of this finding is that the main feeding period for the Antarctic minke whale must be during the period from evening to early morning. The amount of food in the forestomach decreased substantially during the JARPA period, which indicates that food availability was decreasing and was the reason for the decline in energy storage.

None of five dependent variables showed any further decrease during the JARPA II years (2006/07–2011/12) (Konishi and Walløe, 2014, unpublished results for stomach

Table 10

Model selection with axillary half girth as the response variable during the JARPA period.

Model no.	BIC	Models
1	30,944	Full.BC<-lm(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)
2	30,988	Full.BC.re1<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LonSect))
3	30,987	Full.BC.re2<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LatCat11))
4	30,949	Full.BC.re3<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|TrackLine))
5	30,983	Full.BC.re4<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(YearNum|Ice))
6	**30,907**	**Full.BC.re5<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat))**
11	30,894	Full.BC.re5ML<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat),REML=F)
12	30,913	Full.BC.re5ML.1<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+(1|YearCat),REML=F)
13	**30,830**	**Full.BC.re5ML.2<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat),REML=F)**
14	30,886	Full.BC.re5ML.3<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongCat11+Sex+(1|YearCat),REML=F)
15	30,886	Full.BC.re5ML.4<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+LongCat11+Sex+(1|YearCat),REML=F)
16	30,991	Full.BC.re5ML.5<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+(1|YearCat),REML=F)
17	31,025	Full.BC.re5ML.6<-lmer(AxillaryGirth~YearNum:Sex+BLm+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat),REML=F)
18	32,578	Full.BC.re5ML.7<-lmer(AxillaryGirth~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat),REML=F)
19	30,888	Full.BC.re5ML.8<-lmer(AxillaryGirth~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat),REML=F)
20	30,848	Full.BC.re5ML.2.1<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+(1|YearCat),REML=F)
21	30,825	Full.BC.re5ML.2.2<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+Sex+(1|YearCat),REML=F)
22	**30,823**	**Full.BC.re5ML.2.3<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+Sex+(1|YearCat),REML=F)**
23	30,930	Full.BC.re5ML.2.4<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+Sex+(1|YearCat),REML=F)
24	30,995	Full.BC.re5ML.2.5<-lmer(AxillaryGirth~YearNum:Sex+BLm+Diatom+LatNum+LongNum+Sex+(1|YearCat),REML=F)
25	32,534	Full.BC.re5ML.2.6<-lmer(AxillaryGirth~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat),REML=F)
26	30,824	Full.BC.re5ML.2.7<-lmer(AxillaryGirth~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat),REML=F)
27	30,840	Full.BC.re5ML.2.3.1<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+(1|YearCat),REML=F)
28	30,820	Full.BC.re5ML.2.3.2<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+Sex+(1|YearCat),REML=F)
29	30,922	Full.BC.re5ML.2.3.3<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+LongNum+Sex+(1|YearCat),REML=F)
30	31,001	Full.BC.re5ML.2.3.4<-lmer(AxillaryGirth~YearNum:Sex+BLm+Diatom+LongNum+Sex+(1|YearCat),REML=F)
31	32,542	Full.BC.re5ML.2.3.5<-lmer(AxillaryGirth~YearNum:Sex+DateNum^2+Diatom+LongNum+Sex+(1|YearCat),REML=F)
32	**30,817**	**Full.BC.re5ML.2.3.6<-lmer(AxillaryGirth~YearNum+BLm+DateNum^2+Diatom+LongNum+Sex+(1|YearCat),REML=F)##BESTMODEL**

contents). Fat weight was not measured regularly during JARPA II.

The results of sighting surveys indicate that the abundance of Antarctic minke whales in the Eastern Antarctic Ocean has either been constant or possibly declined somewhat during the JARPA years (Hakamada *et al.*, 2013; IWC, 2012, pp.35–39). The results presented here therefore indicate that major changes took place in the eastern Antarctic ecosystem during the 18 JARPA years that reduced the amount of krill available for Antarctic minke whales. Likely explanations could be either a gradual decrease in krill production due to environmental change (e.g. global warming) or increasing competition from other krill-feeding species. No good estimates of krill abundance are available (IWC, 2015a). Regarding other krill feeders, sighting surveys have shown that the abundance of large baleen whales increased substantially during the JARPA period e.g. blue (*B. musculus*) and southern right (*Eubalaena australis*) whales and especially humpback whales (*Megaptera novaeangliae*) (Branch *et al.*, 2004; Branch and Rademeyer, 2003; Matsuoka *et al.*, 2011). Thus it is possible that our results reflect the reverse of Laws' 'krill surplus hypothesis' (Laws, 1977). Although this hypothesis was not universally accepted, Laws claimed that during the first half of the twentieth century, when the large baleen whales were hunted down to low numbers, krill not eaten by these whales became available to Antarctic minke whales and other krill feeders (seals and birds), allowing their numbers to increase. Law's hypothesis presupposes that large baleen whales such as humpback and blue whales are more efficient krill feeders than Antarctic minke whales. Thus there is no contradiction between the increase in humpback whale abundance during the JARPA period and the simultaneous decline in minke whale energy storage, according to the Law's hypothesis.

When deciding whether an environmental change or interspecies competition is the explanation for the decline in energy storage in Antarctic minke whales during JARPA period, observations on the stomach content weight of animals taken in the Ross Sea appear to be important. The krill species found above the continental shelf of the Ross Sea (*Euphausia crystallorophias*) is different from the species that lives in the rest of the Antarctic Ocean (*E. superba*). Antarctic minke whales enter the Ross Sea and

Table 11

Summary for the best model using axillary half girth as the response variable (Full.BC.re5.3ML.2.3.6 by REML in Table 10).

Random effects

Groups	Name	Std. dev.
YearCat	(Intercept)	2.692
Residual		12.824

Number of obs: 3,868, groups: YearCat, 14

Fixed effects	Estimate	Std. error	*t* value
(Intercept)	35.5500	5.3260	6.68
YearNum	–0.4499	0.1867	–2.41
BLm	24.1200	0.5174	46.62
DateNum^2	0.0009	0.0001	13.76
Diatom	1.6650	0.1732	9.62
LongNum	–0.0207	0.0087	–2.39
Sex	–5.2350	0.5251	–9.97

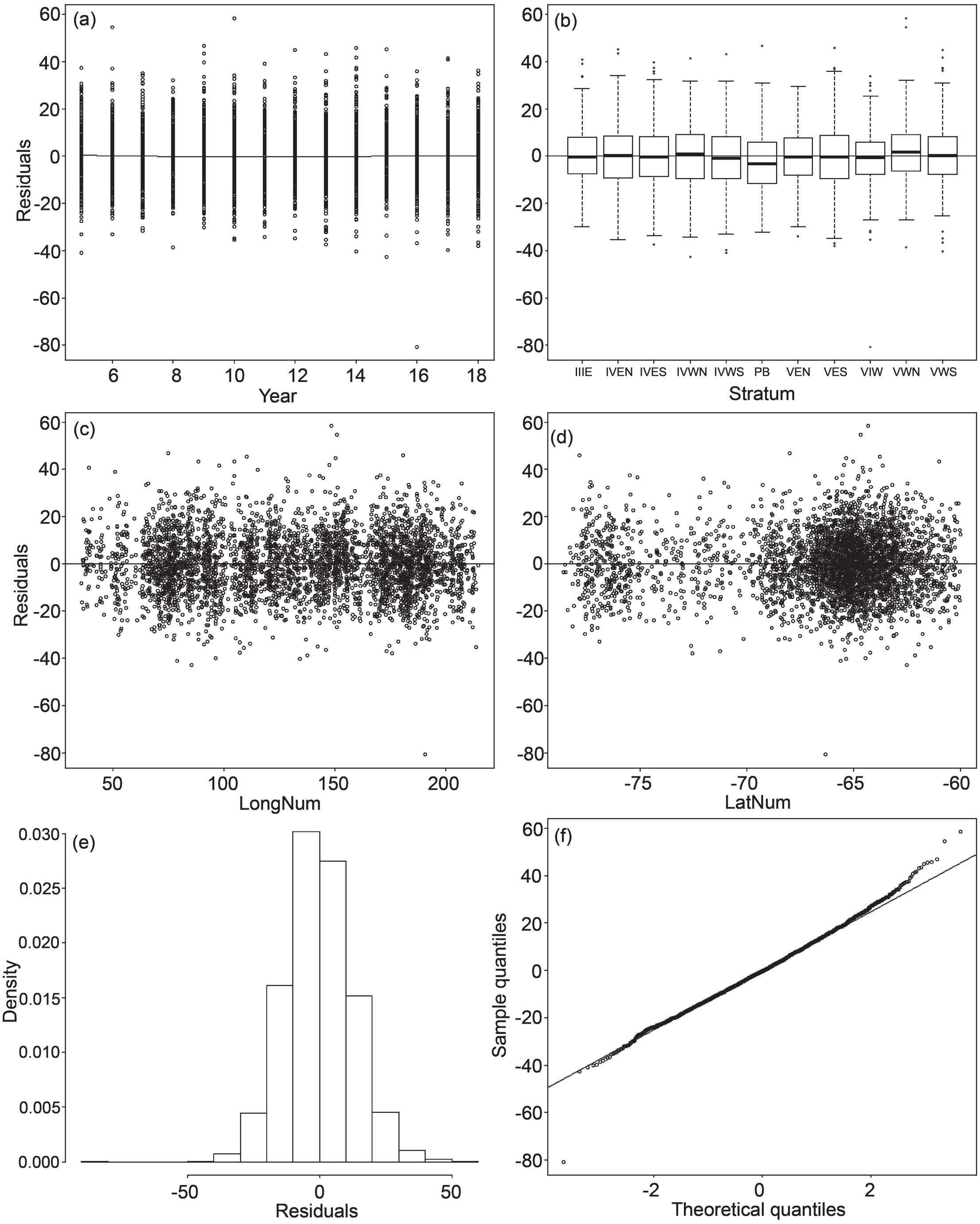

Fig. 7. Diagnostic plots for the best model with axillary half girth as the response variable. For further explanation, see the caption for Fig. 3.

feed on *E. crystallorophias*, whereas humpback whales do not. Thus, there should be no competition between humpback and Antarctic minke whales for *E. crystallorophias* in the Ross Sea. This fits well with the observation that the stomach content weight of whales caught in the Ross Sea did not decline over the JARPA years, in contrast to the decline in the rest of the survey area. For more details on the interpretation of these results, see Konishi *et al.* (2014).

The primary observations for the present investigation were not obtained according to the strict rules laid down originally by Ronald Fisher for experimental design in agricultural research (Fisher, 1935). The deviations are of course explained by the logistics of research vessel movements. Similar logistical limitations are often found in series of observations obtained in environmental and medical epidemiological research, making the exploration of possible models and the corresponding statistical analyses a challenging process. Until quite recently, common practice in such situations was to apply linear regression or analysis of variance, not only to the total available dataset but also to a large number of different subsets of the total material. If all the analyses gave approximately the same results, those results were accepted. The present authors used this approach in the analyses of blubber thickness, girth and fat weight reported in 2008 (Konishi *et al.*, 2008). Today, faster computers and efficient software make it possible to explore a large number of different models, including models with

Table 12

Model selection with sieved stomach content weight as the response variable during the JARPA period.

Model no.	BIC	Models
1	14,041	Full.SCW<–lm(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum) #Fullmodel
2	14,163	Full.SCW.re1<–lmer(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum+(DateNum|LonSect))
3	14,149	Full.SCW.re2<–lmer(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum+(DateNum|LatCat11))
4	14,158	Full.SCW.re3<–lmer(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum+(YearNum|Ice))
5	14,084	Full.SCW.re4<–lmer(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum+(1|Year))
6	14,287	Full.SCW.1<–lm(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex)
7	14,034	Full.SCW.2<–lm(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+LtimeNum)
8	13,985	Full.SCW.3<–lm(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+Sex+LtimeNum)
9	14,033	Full.SCW.4<–lm(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongCat11+Sex+LtimeNum)
10	14,033	Full.SCW.5<–lm(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LongNum+LongCat11+Sex+LtimeNum)
11	14,041	Full.SCW.6<–lm(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum)
12	14,052	Full.SCW.7<–lm(log(FirstS)~YearNum:Sex+BLm+LatNum+LongNum+LongCat11+Sex+LtimeNum)
13	14,164	Full.SCW.8<–lm(log(FirstS)~YearNum:Sex+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum)
14	**14,033**	**Full.SCW.9<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum)**
15	14,279	Full.SCW.9.1<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex)
16	14,040	Full.SCW.9.2<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LatNum+LongNum+LongCat11+LtimeNum)
17	**13,977**	**Full.SCW.9.3<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LatNum+LongNum+Sex+LtimeNum)**
18	14,025	Full.SCW.9.4<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LatNum+LongCat11+Sex+LtimeNum)
19	14,025	Full.SCW.9.5<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LongNum+LongCat11+Sex+LtimeNum)
20	14,044	Full.SCW.9.6<–lm(log(FirstS)~YearNum+BLm+LatNum+LongNum+LongCat11+Sex+LtimeNum)
21	14,156	Full.SCW.9.7<–lm(log(FirstS)~YearNum+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum)
22	14,222	Full.SCW.9.3.1<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LatNum+LongNum+Sex)
23	13,985	Full.SCW.9.3.2<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LatNum+LongNum+LtimeNum)
24	13,999	Full.SCW.9.3.3<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LatNum+Sex+LtimeNum)
25	**13,969**	**Full.SCW.9.3.4<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LongNum+Sex+LtimeNum)##BESTMODEL**
26	13,988	Full.SCW.9.3.5<–lm(log(FirstS)~YearNum+BLm+LatNum+LongNum+Sex+LtimeNum)
27	14,111	Full.SCW.9.3.6<–lm(log(FirstS)~YearNum+DateNum^2+LatNum+LongNum+Sex+LtimeNum)

DateNum was replaced by DateNum^2.

Table 13

Summary for the best model using log-transformed stomach content weight as the response variable (Full.SCW.9.3.4 in Table 12).

Residuals

Min	1Q	Median	3Q	Max
–5.4882	–1.1189	0.3483	1.278	3.6083

Coefficients	Estimate	Std. error	*t* value
(Intercept)	1.3680	0.2690	5.086
YearNum	–0.0203	0.0065	–3.103
BLm	0.3293	0.0271	12.153
DateNum	0.0000	0.0000	4.452
LongNum	–0.0040	0.0006	–6.614
Sex	0.2405	0.0557	4.316
LtimeNum	–0.1239	0.0077	–16.163

Table 14

Summary for the best model using Box-Cox transformed stomach content weight as the response variable.

Residuals

Min	1Q	Median	3Q	Max
–6.3785	–1.9168	0.1629	1.9048	6.7132

Coefficients	Estimate	Std. error	*t* value
(Intercept)	1.7870	0.4030	4.434
YearNum	–0.0317	0.0098	–3.234
BLm	0.5357	0.0406	13.195
DateNum	0.0001	0.0000	4.965
LongNum	–0.0060	0.0009	–6.654
Sex	0.3608	0.0835	4.323
LtimeNum	–0.1998	0.0115	–17.404

Table 15

Comparison of year effects from the simple models and the best models.

	Simple models (from equation below)		Best models (from previous tables)	
Response variable	YearNum	SE	YearNum	SE
Fat weight	–0.0083	0.0014	–0.0083	0.0014
BT11	–0.0161	0.0022	–0.0190	0.0022
BT7	–0.0116	0.0019	–0.0149	0.0076
Half umbilicus girth	–0.4596	0.0348	–0.4059	0.1364
Half axillary girth	–0.4433	0.0532	–0.4499	0.1867
log (FirstS)	–0.0256	0.0066	–0.0203	0.0065

Response variable = YearNum+BLm+DateNum^2+Diatom+Sex.
log(FirstS) = YearNum+BLm+DateNum^2+LTimeNum+Sex.

interaction terms and random-effects terms. De la Mare suggested in 2011 that the sampling heterogeneity in the JARPA data made it impossible to draw any conclusions about time trends. Our extensive modelling exercise has shown beyond doubt that it is in fact possible to draw reliable conclusions, and that all six dependent variables showed a large negative trend during the JARPA period. Even the magnitudes of the regression coefficients are similar to those obtained by multiple linear regression in 2008. The standard errors are larger but the results are still significantly different from zero at the 5% level (see also Tables 3, 5, 7, 9, 11, 13 and 15). Results of this kind are not uncommon in other fields of research. For example, results obtained by multiple linear regressions in medical epidemiology have been

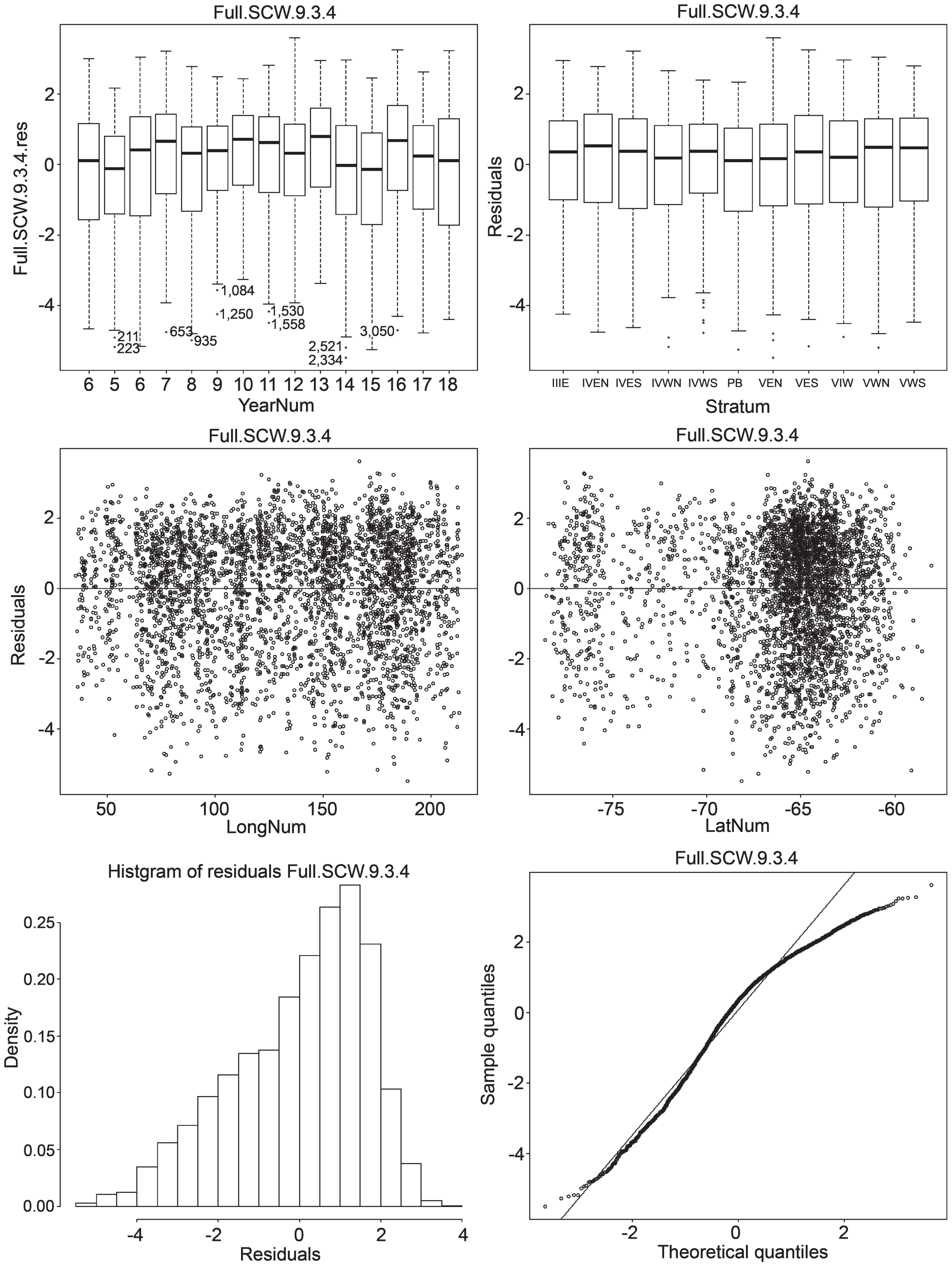

Fig. 8. Diagnostic plots for the best model with log-transformed stomach content weight as the response variable. For further explanation, see the caption for Fig. 3.

confirmed by more sophisticated modern analyses, again usually with somewhat larger standard errors.

For the dependent variable 'Fat weight', the best model was a simple linear regression model without interaction or random-effects terms (Tables 2 and 3). To illustrate the points above, this simple model was run for the other four related dependent variables as well, and a similar simple model was run for stomach fullness. In Table 15, the coefficients for the decline over the JARPA period for these model runs are compared to the coefficients from the best models. This table shows that simple linear regression gives much the same results for point estimates of the decline as the more complex models, but the coefficients from the models with random effects have higher standard errors. Thus the decline in energy storage over the JARPA years seems to be robust to the model selection. Similar results were obtained for all the other independent variables in the simple regression model. In this context it should be remembered that the standard errors found using the more complex models may be artificially low, since the error connected with model selection (based on BIC values) is ignored (Efron, 2014).

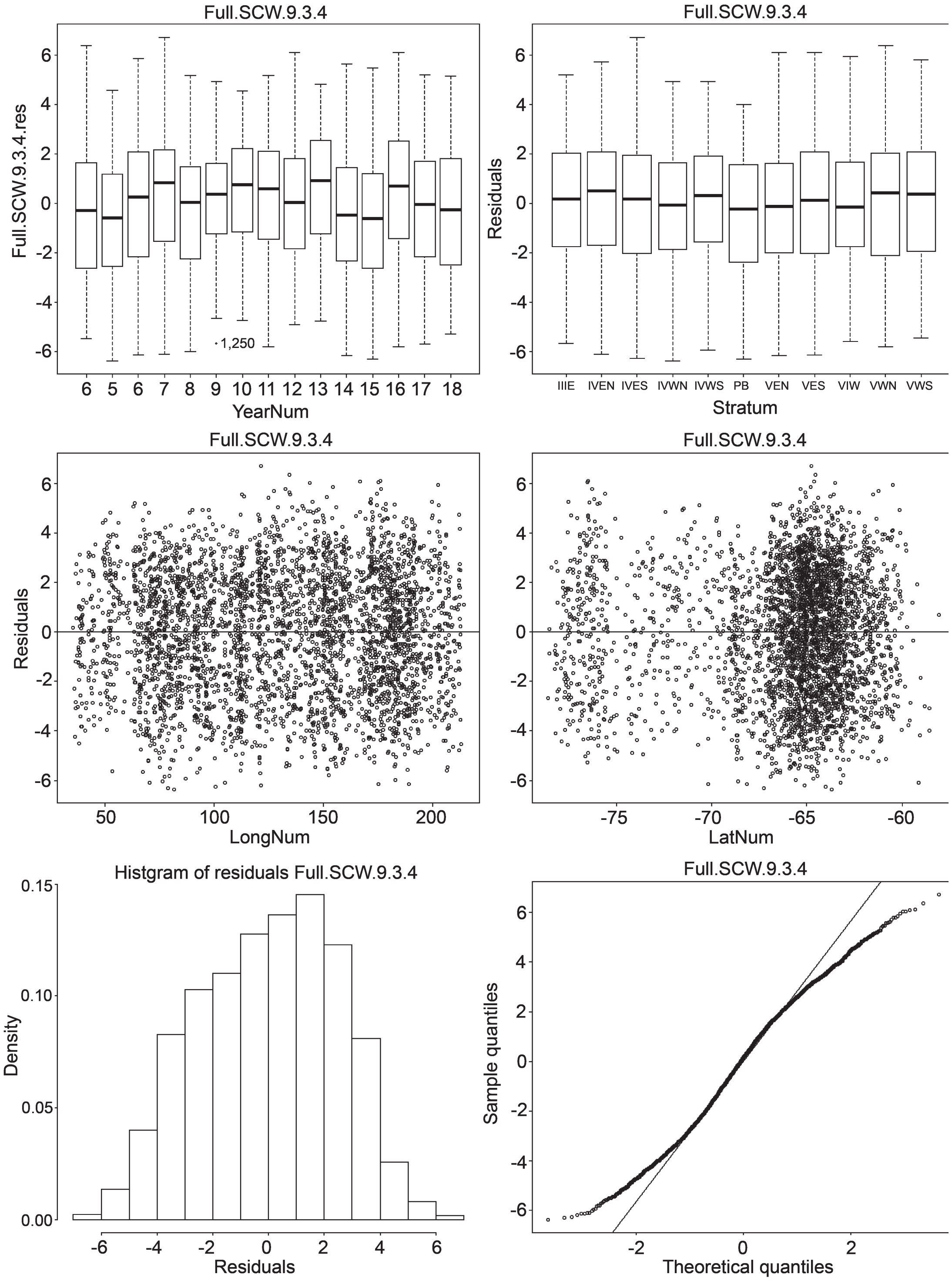

Fig. 9. Diagnostic plots for the best model with Box-Cox transformed stomach content weight as the response variable. For further explanation, see the caption for Fig. 3.

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