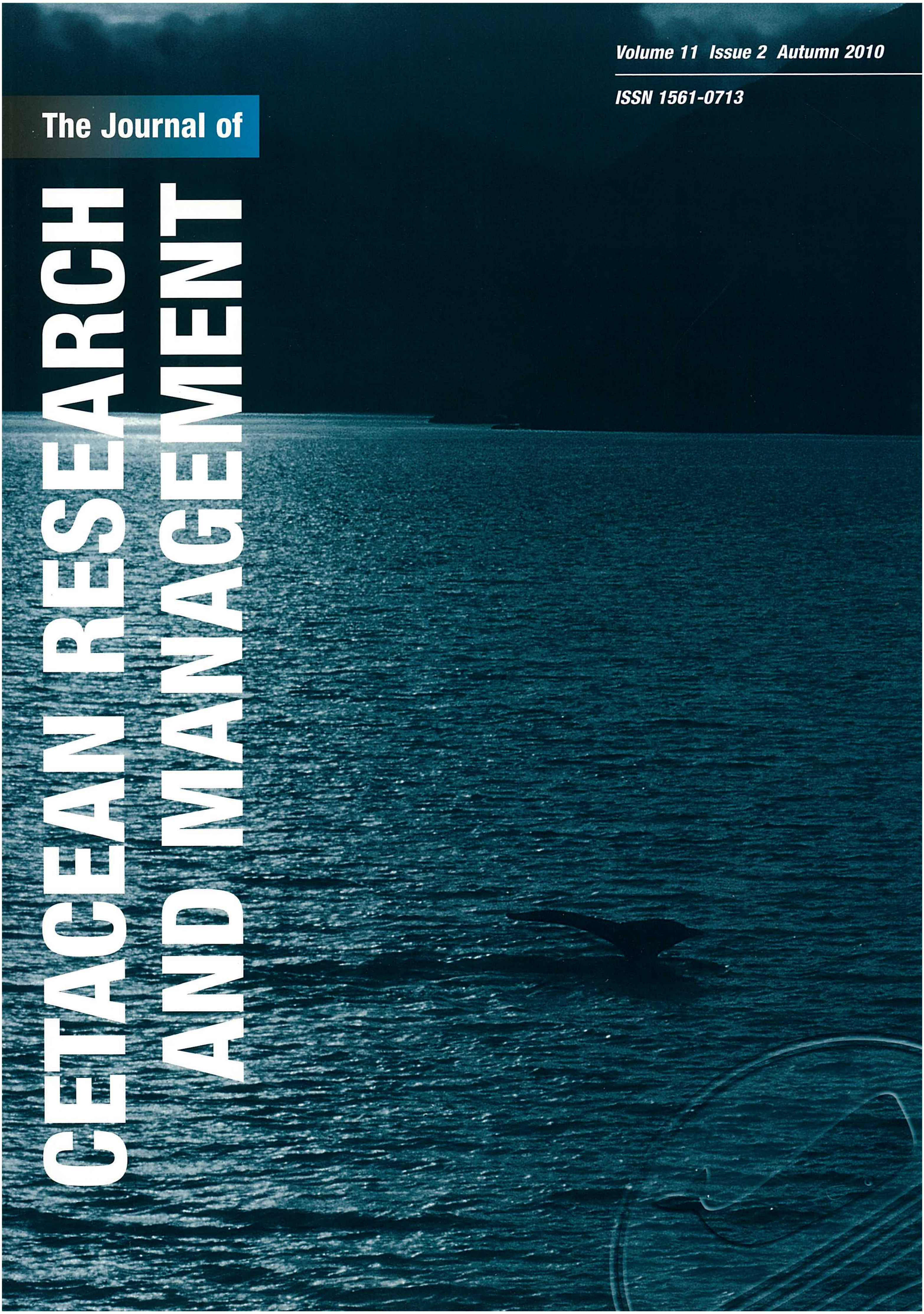

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The Journal of CETACEAN RESEARCH AND MANAGEMENT

Contents

Editorial

Welcome to this the second issue of the eleventh volume of the *Journal of Cetacean Research and Management*. Unfortunately, the problems with our printers referred to in the last issue continued with the new company but we have now begun to work with Cambridge University Press. We hope that, despite the present economic climate, this will form a lasting and stable partnership.

This issue includes 11 papers covering a range of issues from those related to aboriginal subsistence whaling through ship strikes to whalewatching.

A key component of determining safe, sustainable catch limits for subsistence whaling is the estimation of reliable estimates of abundance. This volume includes new estimates of abundance from aerial surveys of common minke whales from West Greenland in 2007 (22,952, 95% CI 7,815–67,403) and fin whales (4,468, 95% CI 1,343–14,871) in papers by Heide-Jørgensen and colleagues, and a new mark-recapture estimate (from photo-identification studies) for 2004 of 12,631 (95% bootstrap percentile CI 7,900–19,700) for the Bering-Chukchi-Beaufort Seas stock of bowhead whales in a paper by Koski and colleagues.

Knowledge of current abundance is important for determining the status of all populations and assessing the need for conservation measures, not just those subject to direct exploitation; in this issue, Speakman and colleagues present mark-recapture estimates of seasonal abundance and survivorship of bottlenose dolphins off South Carolina.

Beekmans and colleagues highlight the impact of the environment on minke whale density in the Southern Ocean with regard to population modelling.

Another key component of effective conservation and management strategies is an understanding of population structure. Genetic data play an important role in this but, as Archer and colleagues illustrate, the standard null models of panmixia are based on a number of assumptions that can, and probably are, violated. Using the available information from the Bering-Chukchi-Beaufort Seas stock of bowhead whales, the authors develop an individual-based model of whale dynamics, genetics and whaling. They demonstrate that by failing to account for the unique features of particular situations, use of standard methods may lead to misleading results.

A good understanding of catch history is also an important component of assessing the status of a population against conservation objectives. For those species where the primary exploitation occurred long in the past, before reliable records were kept, this is particularly difficult. Fortunately, many historical records remain (e.g. logbooks, production records) that allow a reconstruction of past removals (both catches and animals struck-and-lost). In his paper, Higdon develops a catch history (and explains the inevitable uncertainties in the record) for the commercial and subsistence harvests of bowhead whales in eastern Canada and West Greenland. Commercial whaling began around 1530AD while subsistence whaling has an even longer history dating back at least to 1200AD. He estimates that during the main period of commercial whaling (1530–1915), whalers took around 61,500 animals, resulting in overexploitation that negatively impacted on subsistence harvests.

As noted in the last issue, there is an increasing awareness that ship strikes can be a problem for both cetaceans and humans. Two papers, one by Carrillo and Ritter and one by Ritter, address this issue for the Canary Islands where there have been increasing numbers of reported collisions and where there has also been a rapid expansion of fast ferry traffic. Both papers highlight the need for mitigation measures to be developed and implemented.

Information on ship strikes and other causes of death often come from the examination of stranded carcases. In this issue, Danil and colleagues summarise an extremely long series (1851–2008) of strandings data for San Diego County, California. Whilst recognising the limitations of such data, the authors show that they can provide valuable information on distribution, mortality (natural and due to anthropogenic causes) and other biological information such as calving seasons.

The potential of apparently benevolent activities such as whalewatching to negatively affect populations has been gaining increasing attention. In this issue, Schaffar and colleagues examine the exposure of humpback whales to unregulated whalewatching activities in a reproductive area in New Caledonia, where unregulated growth in whalewatching has occurred since 1995. In particular, the authors raise concern over the cumulative exposure of mothers and calves to whalewatching vessels and suggest that management measures should be introduced for whalewatching on this small population.

G. P. Donovan
Editor

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Fully corrected estimates of common minke whale abundance in West Greenland in 2007

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ABSTRACT

A visual aerial line transect survey for common minke whales (*Balaenoptera acutorostrata*) was conducted off West Greenland in August and September 2007. A total of 8,670km of survey effort covered 11 strata in sea states <5 with a total stratum area of 213,807km^2. The 27 sightings of common minke whales were all within a strip width of 300m and the average time from first detection to when the sighting passed abeam was 1.7 sec. Due to the uniform and narrow distribution of the detections, strip census methods were used to analyse the survey. Two methods were deployed to correct the strip census estimates for whales missed by the observers and whales that were submerged during the passage of the plane. Method 1 included all detections of common minke whales (n = 27) and correction for an instantaneous availability that included submergence of whales. Using data from sea states <3 (n = 22) the 'at surface' abundance of common minke whales was 1,866 (CV = 0.30) whales. A correction for whales missed by the observers with a simple mark-recapture estimator resulted in a corrected abundance of 1,904 (CV = 0.30) whales. Adjusting for the availability bias resulted in a fully corrected estimate of 16,609 (95% CI 7,172–38,461) common minke whales. Method 2 used only detections of common minke whales that were observed to break the surface (n = 19). Applying this method to effort data at sea state <3 (n = 14) resulted in an 'at surface' abundance of 1,174 (CV = 0.39) whales. A correction for whales missed by the observers increased the abundance to 1,198 (0.39) whales. Adjusting for the availability bias resulted in a fully corrected estimate of 22,952 (95% CI 7,815–67,403) common minke whales.

KEY WORDS: COMMON MINKE WHALE; ABUNDANCE ESTIMATE; AERIAL SURVEY; SATELLITE TAGGING; WEST GREENLAND

INTRODUCTION

Aerial surveys for common minke whales (*Balaenoptera acutorostrata*) have been conducted at regular intervals in West Greenland since 1984. The first two surveys in 1984 and 1985 were conducted with the intention of obtaining uncorrected line transect estimates of the abundance of common minke whales; however, too few sightings were obtained to generate estimates. After 1985, surveys were conducted as combined cue counting and line transect surveys. Based on surveys conducted in 1987 and 1988, a cue counting estimate of 3,266 (CV = 0.31) common minke whales for both years combined was obtained. A survey in 1989 obtained too few sightings for any meaningful abundance estimate, however a survey in 1993 resulted in a cue counting estimate of 8,371 (CV = 0.43) common minke whales (Larsen, 1995). An estimate of 10,792 (CV = 0.59) common minke whales corrected for perception bias was obtained based on a survey conducted in 2005 (Heide-Jørgensen *et al.*, 2008).

The seven aerial surveys conducted between 1984 and 2005 provided between 9 and 44 primary common minke whale sightings. Most sightings were of single individuals and sightings were widely dispersed on the banks of West Greenland (Heide-Jørgensen and Laidre, 2008). Given the demonstrated difficulties in visually detecting common minke whales it is unlikely that future surveys will obtain significantly more detections.

This study presents the results from the most recent survey for common minke whales in West Greenland conducted in August and September 2007. Furthermore, we explore the options for converting the at-surface abundance of common minke whales to fully corrected total estimates of abundance. This requires the application of correction factors which adjust for whales missed by the observers ('perception bias') and for whales that are not available to be detected at the surface ('availability bias').

MATERIAL AND METHODS

Aerial survey

An aerial line transect survey of large whales in West Greenland was conducted between 25 August and 30 September 2007. The survey platform was a *Twin Otter* plane (Air Greenland, *www.airgreenland.gl*), with long-range fuel tanks and four independent observation platforms each with bubble windows. Sightings and a log of the cruise track (recorded from the aircraft GPS) were recorded on a *Redhen* SDVR (spatial digital video recorder). Declination angle to sightings was measured with *Suunto* inclinometers and the declination angles were converted to the perpendicular distance of the animal to the trackline using an equation to adjust for earth curvature (Buckland *et al.*, 2001). Target altitude and speed was 213m and 167km hr^{-1}, respectively.

Survey conditions were recorded at the start of the transect lines and whenever a change in sea state, horizontal visibility or glare occurred. The survey was designed to systematically cover the area between the coast of West Greenland and offshore (up to 100km) to the shelf break (i.e. the 200m depth contour). Transect lines were placed in an east-west direction except for in south Greenland, where they were placed in a north-south direction (Fig. 1). The surveyed area was divided into 11 strata in addition to several inshore strata. The southern strata were planned to be covered first.

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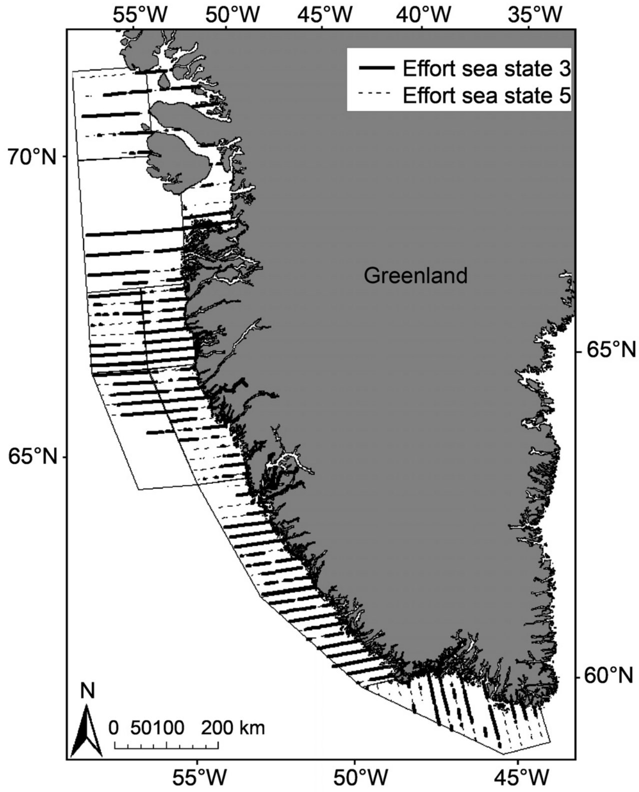

Fig. 1. Effort in sea state <3 and <5 off West Greenland during the aerial survey in 2007.

Availability correction factors

Two methods were utilised to develop correction factors for common minke whales that were submerged during the survey.

Method 1

Common minke whales were photographed from a plane in Faxafloi Bay in Iceland in September 2003. The photo system included two *Hasselblad* cameras with Phase One 10.6-megapixel H10 digital backs, mounted in a sideward horizontal angle of 16 degrees to ensure only marginal sideward overlap. The digital backs were oriented with 3,992 pixels in the vertical direction, and 2,656 pixels in the horizontal direction. Lenses were 40 mm, and combined with a flying altitude of 1,700 feet (about 518m), provided a combined coverage of approximately 480m. The light sensitivity of the H10 backs was set to 400 ASA and the shutter speed to 1/500sec. The average speed of the plane on effort was approximately 95 knots so that a point on the ground was available to be photographed for approximately 10s. On average, images were taken 2.6s apart, and a single point on the ground would generally be found on four sequential images. An average time interval of 2.6s between subsequent images allowed for an approximate estimate of the average availability period of a surfacing common minke whale. The surfacing and diving cycle of a common minke whale was defined into a sequence of 'states' that were used to describe the surfacing behaviour of a single whale (Table 1). Each image in a sequence of images of a surfacing or diving common minke whale was categorised into one of these surfacing or diving states. All states between 'emerging' and 'diving' were assumed to be states where an observer could visually identify a common minke whale. The interval between these states was used to estimate the correction factor for non-visible submerged whales. However, owing to the limited number of images and time that was available for each point on the ground, few full surfacing/diving sequences from 'emerging' to 'diving' were obtained. Therefore, instead of estimating *complete* availability periods, the time periods between consecutive states in the surfacing/diving sequence were estimated. This was accomplished by evenly distributing the time period between two consecutive images of surfacing/diving states. For example, if two images were taken 2.5s apart with the first image of 'surfacing' and the second image of 'back breaking surface' (or the next behaviour category), each state was assigned a time period of 1.25s. The average time periods between subsequent surfacing/diving states was then estimated from all obtained estimates.

Image sequences tended to include either a complete surfacing (from 'emerging' to 'back breaking') or a complete diving sequence (from 'back breaking' to 'diving'), or a surfacing/diving sequence that lacked an estimate for only one surfacing/diving state interval. The average availability period was therefore estimated from an estimate of the average surfacing period and an estimate of the average diving period based on complete surfacing or diving sequences. When a time interval was missing from a surfacing/diving sequence it was estimated to be the average estimate for that interval.

Method 2

Satellite transmitters (ST-15, Telonics Inc.) were deployed on five common minke whales in West Greenland, Svalbard/Norwegian waters and Iceland during 1998–2002. The transmitters were equipped with two lithium thianyl batteries (M1) and were pre-programmed to be on for 24 hours and off for 72 hours. The transmitters had a conductivity switch (salt water switch) that allowed transmission if the transmitter was out of the water for more than approximately 250ms. The tags were attached to a spear that acted as an anchor in the blubber. The actual transmitter was located on the outside of the skin of the whale (see Heide-Jørgensen *et al.*, 2001; 2003 for details). The repetition period of the transmissions was 45s. The salt-water switch was positioned 11cm off the whale skin allowing for longer detection of dry periods.

The transmitters collected information on the duration when the salt water contacts were dry, interpreted as the fraction of the surfacing time for the whale. Dry periods were sampled as the total time between transmissions where the salt water switch was dry, i.e. out of the water. The accumulated numbers of seconds with dry readings of the salt water switch were transmitted to the satellites. Based on the proportion between the accumulated number of seconds with dry readings and the elapsed time between transmissions (determined by the satellite) the fraction of time the whale spent out of the water was calculated. Data were collected and transmitted every fourth day. Data collected between days with scheduled transmissions were excluded. The reception of the data was determined by the passage of a satellite and the sampling time therefore was of

Table 1

The sequence of surfacing and diving states used to describe a surfacing minke whale (n = 29). Each image in a sequence of images was categorised by a single surfacing or diving state. The surfacing sequence is defined by the period from 'emerging' to 'back breaking surface', and the diving sequence is defined by the period from 'back breaking surface' to 'vanishing'.

	Emerging period			Submerging period				
Sea state	Emerging	Surfacing	Head breaking	Back breaking	Just dived	Diving	Emerging time	Submerging time
0	–	–	–	2.62	2.66	1.32	–	6.60
1		2.84	2.10	–	–	–	4.94	–
1	1.35	1.36	1.36	–	–	–	4.07	–
1	–	–	–	0.94	1.03	1.03	–	3.00
2	–	–	–	2.63	0.90	0.90	–	4.43
2	–	–	–	1.35	2.52	1.27	–	5.14
2	–	–	–	2.53	1.26	1.26	–	5.05
2	1.27	1.26	1.26	–	–	–	3.79	–
2	0.93	0.93	1.40	1.40	0.94	0.94	3.26	3.28
2	–	–	–	–	–	–	–	–
2	0.69	1.31	1.31	–	–	–	3.31	–
2	0.71	0.71	0.71	0.94	0.94	0.94	2.13	2.82
2	–	–	–	0.50	0.50	0.50	–	1.50
2	0.89	0.89	0.89	1.34	1.34	0.00	2.67	2.68
2	1.28	1.29	1.29	0.00	2.53	1.28	3.86	3.81
2	–	–	–	0.52	0.52	0.52	–	1.57
				n			**8**	**10**
	ss<3			**Mean**			**3.5**	**3.3**
				cv			**0.09**	**0.12**
3	0.95	0.95	0.95	–	–	–	2.85	–
3	–	–	–	2.47	1.24	1.24	–	4.95
3	0.58	2.55	2.55	–	–	–	5.68	–
3	0.58	0.58	0.58	0.78	0.78	0.78	1.74	2.34
3	–	–	–	0.94	0.94	0.94	–	2.82
3	0.69	0.69	0.69	–	–	–	2.07	–
3	1.50	1.50	0.76	0.76	0.76	0.76	3.76	2.28
3	0.69	0.69	0.69	0.68	0.68	0.68	2.07	2.04
3	0.75	0.75	0.75	0.75	0.75	0.75	2.25	2.25
4	–	–	–	2.62	0.86	0.86	–	4.34
4	1.26	1.26	1.28	–	–	–	3.80	–
4	–	–	–	0.90	0.90	0.90	–	2.70
4	–	–	–	2.62	1.33	1.33	–	5.28
				N			**15**	**21**
	All			**Mean**			**3.15**	**3.51**
				cv			**0.09**	**0.09**

variable length. The sampling was independent of the whale's behaviour.

Correction for non-instantaneous availability

Common minke whales are available for detection for a short period of time during aerial surveys (i.e. some whales may be seen ahead of the plane). Therefore, the probability that an animal is available is different from being available at a randomly-chosen instant in its dive cycle. Laake *et al.* (1997) derived an equation for estimating the average probability of detecting a whale at the surface to correct for this:

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

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

Fully corrected strip census estimation

All of the common minke whale sightings in the survey in 2007 were made within 300m from the trackline and it was assumed that there is a constant probability within that strip width (Fig. 2). Thus a strip census estimate was developed with a simple arithmetic mean of the group size across all strata ($\hat{E}[a]$). A Chapman estimate was used to correct for perception bias ($\hat{p}'$) by the observers:

$$\hat{p}' = \frac{\sum n}{\dfrac{(S_1+B+1)\,(S_2+B+1)}{(B+1)} - 1}$$

where n is the total number of sightings, S_1 and S_2 are the sightings by observer platform 1 and 2 only and B is the sightings by both platforms (Magnusson *et al.*, 1978). Variance of ($\hat{p}'$) was estimated with Jackknife methods.

Individual animal abundance in stratum A was then developed from:

$$N' = \frac{\left(\dfrac{n}{2\cdot L\cdot 0.300}\,\hat{E}[a]\cdot A\right)}{\hat{p}'}$$

It is assumed that the whales were only available for detection when tags were dry and that the time spent dry ($\hat{a}'$) was known from photographic recordings of surfacing

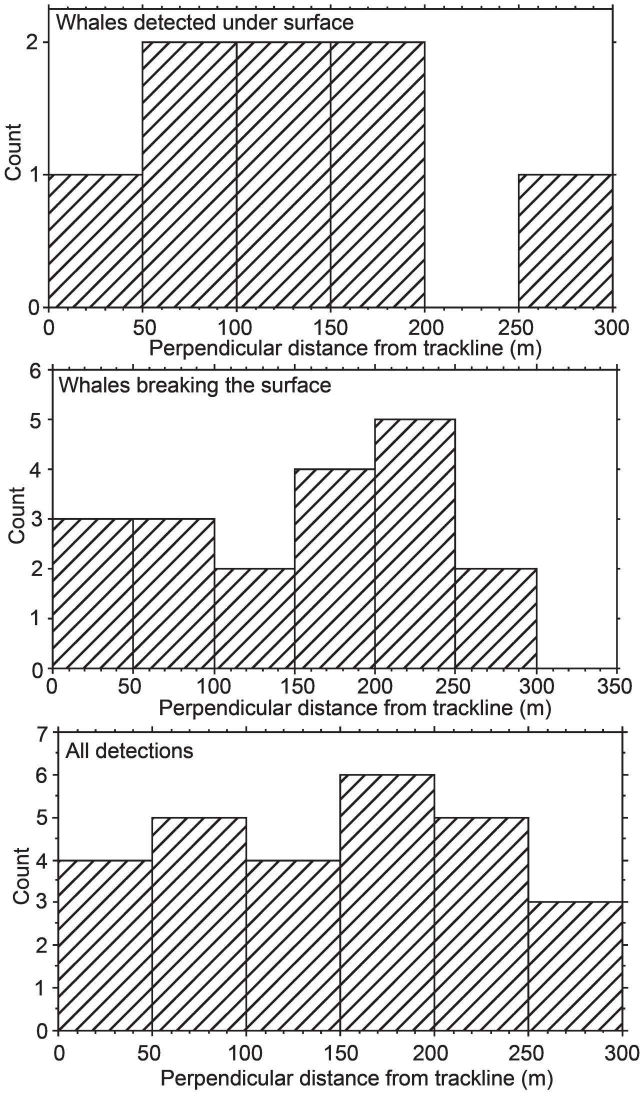

Fig. 2. Distribution of detections of minke whale sightings in 2007 ($n = 27$) for Method 1 (upper panel, whales detected below the surface), Method 2 (middle panel, whales breaking the surface), and all detections (lower panel).

common minke whales (Method 1) or from satellite linked-data recorders (Method 2). In order to account for this availability bias, corrected abundance (denoted by the subscript 'c') was estimated by:

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

with estimated CV

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

RESULTS

A total of 8,670km of survey effort was conducted in sea states <5, covering 11 strata with a total stratum area of 213,807 km^2 (Fig. 1), with only 66% of the effort in sea state <3 (Fig. 3). Due to unfavorable weather conditions during the survey period the area west of Disko Bay (stratum 4) had low coverage. Common minke whales were widely distributed in the surveyed area and were found in most strata coastally and offshore (Fig. 3). Out of the 35 sightings of common minke whales, 27 on-effort sightings were obtained within a strip width of 300m. The perpendicular distribution of sightings demonstrated that the detection probability for common minke whales was constant out to a distance of 300m (Fig. 2) and therefore the survey was analysed as a strip census with a fixed strip width of 300m. Few sightings were made ahead of the plane and the overall average time from first detection to the sighting passed abeam was 1.7s thus cue counting estimates were not pursued further.

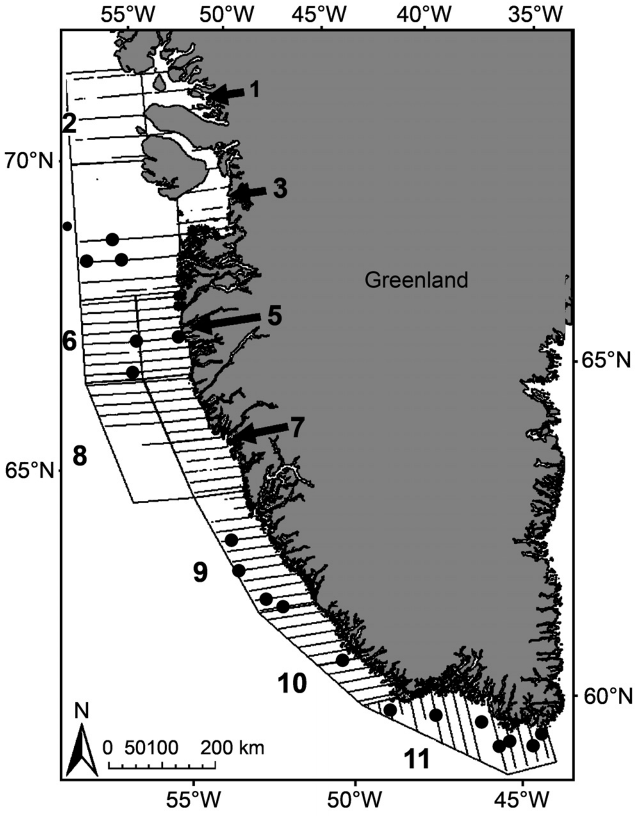

Fig. 3. Effort in sea state <5 and sightings of minke whales by strata off West Greenland during the aerial survey in 2007.

Two fully corrected abundance estimates were developed from the strip census estimates of 'at-surface' abundance (Table 2), one for each method.

Method 1

The first method was independent of whether the whales were breaking the surface when detected and relied on the photographic method for estimating the fraction of whales available to be seen by the observers. All sightings were used and of the 27 sightings of common minke whales detected within the strip width of 300m, 7 were seen by the front observers, 3 by the rear observers, and 17 by both observers (Table 3). The mark-recapture correction factor for perception bias was 0.96 (CV = 0.03) for sea states <5 and 0.98 (CV = 0.02) for sea state <3.

There were 39 image sequences with surfacing and/or diving common minke whales; one sequence included two whales while all other sequences included only one whale. An average availability time of 6.7s was estimated (CV = 0.06, Table 1) when using the photographic sequences for sea states <5. When using only image series from sea states <3 this increased to 6.8s (CV = 0.11). Heide-Jørgensen

Table 2

Effort, area, sightings and abundance estimates from 11 offshore strata covered in sea states <3 during the aerial survey in West Greenland in 2007. Additional 808 km of effort in inshore strata (7,117km^2) without sightings of minke whales are not shown here. CV's indicated in parenthesis.

				All detections within 240m (group size 1.2, CV = 0.10); $\hat{p}'$ = 0.98, se 0.02				Only detections of whales breaking the surface within 300m (group size 1.2, CV = 0.13); $\hat{p}'$ = 0.98, se 0.02			
Stratum	Effort (km)	Area (km^2)	Transects	Sightings	$\hat{N}$	$\hat{N}'$	$\hat{N}'_c$	Sightings	$\hat{N}$	$\hat{N}'$	$\hat{N}'_c$
1: Uummannaq Fjord	153	8,404	3	–	–	–	–	–	–	–	–
2: 71°30'–69°45'N	282	22,631	5	–	–	–	–	–	–	–	–
3: Disko Bay and Vaigat	274	14,653	8	1	130 (0.79)	133 (0.79)	1,156 (0.84)	1	108 (0.80)	110 (0.80)	2,115 (0.86)
4: 69°45'–68°N	360	34,272	5	3	694 (0.56)	708 (0.56)	6,180 (0.63)	2	385 (0.96)	393 (0.96)	7,535 (1.02)
5: 68°–66°30'N offshore	478	16,226	9	1	83 (1.12)	84 (1.12)	735 (1.16)	1	69 (0.92)	70 (0.92)	1,344 (0.98)
6: 68°–66°30'N inshore	621	14,902	9	3	175 (0.54)	179 (0.54)	1,559 (0.61)	3	146 (0.55)	149 (0.55)	2,851 (0.63)
7: 66°30'–64°N offshore	439	22,085	6	–	–	–	–	–	–	–	–
8: 66°30'–64°N inshore	540	20,264	12	–	–	–	–	–	–	–	–
9: 64°–62°N	692	20,334	12	6	429 (0.65)	438 (0.65)	3,817 (0.71)	5	298 (0.46)	304 (0.46)	5,818 (0.56)
10: 62°–60°30'N	741	15,951	10	1	52 (1.02)	53 (1.02)	466 (1.06)	–	–	–	–
11: 60°30–59°N	580	24,085	12	3	303 (0.52)	303 (0.52)	2,697 (0.60)	2	168 (0.71)	172 (0.71)	3,288 (0.78)
Sum	5,160	213,807	91	18	1,866 (0.30)	1,904 (0.30)	16,609 (0.41)	14	1,174 (0.39)	1,198 (0.39)	22,952 (0.51)

Table 3

Number of sightings seen by each observer and the number of duplicates (seen by both observers). The 'Total' column shows the number of sightings seen by observer 1 and observer 2 with the sightings seen by both removed. CVs are in parenthesis.

Pod size	Observer 1	Observer 2	Seen by both	Total	Perception bias $\hat{p}'$
All detections					
1	22	18	15	25	–
2	1	1	1	1	–
3	1	1	1	1	–
Total	24	20	17	27	0.96 (0.03)
In ss<3	20	18	16	22	0.98 (0.02)
Only detections of whales breaking the surface					
1	14	12	9	17	–
2	1	1	1	1	–
3	1	1	1	1	–
Total	16	14	11	19	0.94 (0.05)
In ss<3	13	11	10	14	0.98 (0.02)

and Simon (2007) estimated a cue rate of 46.1 cues per whale per hour (CV = 0.11) for common minke whales in West Greenland. The fraction of time a common minke whale will be available for an instantaneous sighting process in sea states <3 was estimated at 0.088 (CV = 0.16) under the assumption that each cue has the same availability as determined from the photographic sequences. The average time a common minke whale was visible for detection from the plane before passing abeam was 2.2s (bootstrapped CV = 0.26) when the longest period was used for each observer (Table 4). The sighting process cannot be considered perfectly instantaneous. Adjusting for a non-instantaneous sighting process with a surface time of 6.8s and a visibility period of 2.2s results in an availability correction factor of 0.12 (CV = 0.28).

In order to ensure that the visual detectability was similar to the detectability obtained from the photographic method, a strip width of 240m was used. This is the same strip width on either side of the plane covered by the images (480m), and it results in an 'at-surface' abundance of 1,866 whales (CV = 0.30). Corrected for perception bias this results in 1,904 (CV = 0.30) common minke whales (Table 2). Applying the availability correction factor to the 'at-surface' estimate corrected for perception bias results in a total abundance of 16,609 (95% CI 7,172–38,461, 90% CI 8,316–33,173) common minke whales in West Greenland.

Method 2

The alternative method for correcting for availability bias assumes that all common minke whale detections are animals breaking the water surface because the correction is based on the time the whales are dry at the surface. Only detections where it was specifically noted that the whale was breaking the surface were included in this estimate. This reduces the number of sightings to 19 with 9 detections by both observers, 5 by the front observer, and 3 by the rear observer in sea states <5. In sea states <3 this results in 14 sightings with 3 front, 1 rear and 10 duplicates (Table 3). The mark-recapture estimate of perception bias for sea states <5 is 0.94 (CV = 0.05) and 0.98 (CV = 0.02) for sea states <3.

The sampling periods of the dry time readings from the satellite-linked recorders of common minke whales varied from 45s to several thousand seconds (Fig. 4). Most of the periods sampled for surfacing time lasted less than 1,000s for all whales and this probably corresponds to representative sampling during the passage of a satellite, whereas the longer sampling period happens between passages of satellites. Periods when the whales spent more time at the surface will always favour signal reception by the satellites thus averages over longer periods are preferable. All the whales had a clear prevalence for short surfacing times of less than 4% of the total time they were monitored (Fig. 4).

For samples >500s the average time the whales were available to be seen at the surface was 1.95s (CV = 0.14, Table 5) and the average time a common minke whale was available for detection during the survey was 2.6s (CV = 0.29, Table 4). This adjusts the availability correction to 0.05 (CV = 0.33) for a non-instantaneous sighting process with a surface time of 1.52 s and an average dive time of 76.6s (Table 6). The 'at-surface' abundance estimate with a strip width of 300m was 1,174 (CV = 0.39) whales and corrected for perception bias resulted in 1,198 (CV = 0.39) whales. Further correction for availability bias resulted in a

Table 4

List of all sightings with details on duplication and on time from first detection to when the sighting has passed abeam. Underlined visibility times for front and rear observers were used in Method 2 for estimating the average time a minke whale is visible to the observers before passing abeam.

Stratum	Pod size	Distance (m)	Obs no.	Sea state	Break surface	Seen front	Seen rear	Seen both	First detection front	Abeam front	First detection rear	Abeam rear	Front time	Rear time
3	1	230	199	1	1	1	1	1		15:55:15	15:55:12	15:55:15	0	3
4	1	44	65	2	1	1	1	1	16:44:29	16:44:29	16:44:25	16:44:32	0	7
4	1	152	66	1	1	1	0	0		17:05:33			0	
4	1	122	67	1	0	1	1	1		17:40:45		17:40:47	0	0
5	1	76	22	2	0	1	0	0		15:05:04			0	
5	1	299	45	2	1	0	1	0				17:00:57		0
6	1	233	13	2	1	1	1	1		18:39:55		18:40:00	0	0
6	1	122	200	2	1	1	1	1		15:09:36		15:09:38	0	0
6	1	299	201	3	1	0	1	0				15:20:17		0
6	1	117	202	2	1	1	1	1	15:21:58	15:22:00	15:22:02	15:22:17	2	5
9	3	193	71	2	1	1	1	1	15:37:32	15:37:39		15:37:40	7	0
9	1	245	78	2	1	1	1	1	17:10:40	17:10:44		17:10:45	4	0
9	1	74	159	1	1	1	1	1		11:57:59	11:57:56	11:57:59	0	3
9	1	18	160	1	0	1	1	1		11:58:04		11:58:07	0	0
9	1	115	161	1	0	1	1	1		11:58:12		11:58:13	0	3
9	2	233	162	1	1	1	1	1		11:58:26	11:58:18	11:58:23	0	5
9	1	36	179	1	1	1	0	0		14:36:02			0	
10	1	82	135	2	0	1	1	1	18:42:40	18:42:46		18:42:47	4	0
11	1	286	82	2	0	1	1	1		11:34:01		11:34:05	0	0
11	1	195	84	3	0	1	0	0		12:05:36			0	
11	1	176	88	3	1	1	0	0		12:28:34			0	
11	1	233	97	3	1	1	0	0		13:19:57			0	
11	1	89	100	3	1	1	1	1		14:17:03		14:17:09	0	0
11	1	163	104	1	1	1	0	0		15:07:56			0	
11	1	192	123	2	0	1	1	1	11:30:38	11:30:45		11:30:46	7	0
11	1	84	124	2	1	1	1	1		11:53:44		11:53:43	0	0
11	1	36	222	5	1	0	1	0				18:21:01		0

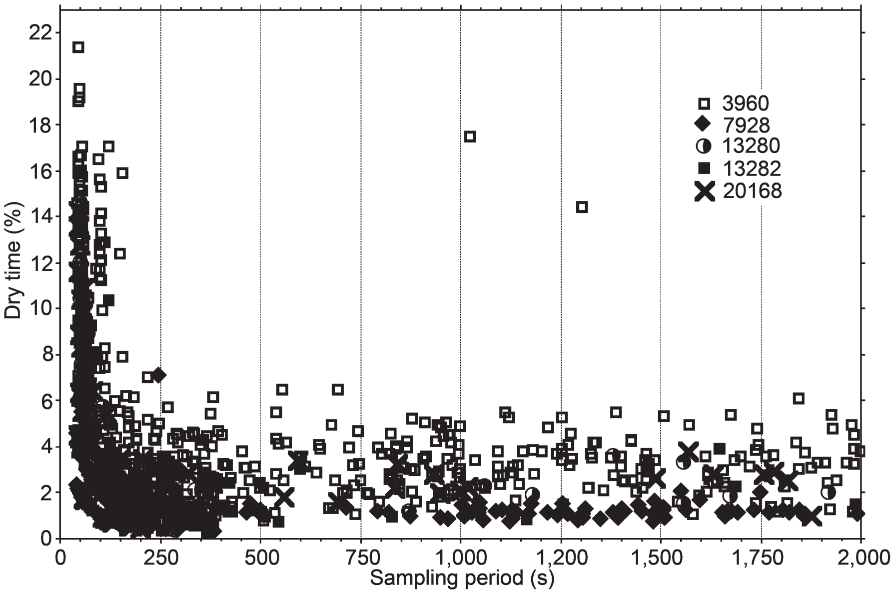

Fig. 4. Proportion of dry time for different sampling periods for five minke whales (see Table 5)

Table 5

Average percentage of dry time for five minke whales instrumented with satellite transmitters. Only samples between 09.00 and 18.00 local time were included.

		All	*n*	SD	>500s	*n*	SD	Sum of dry time	Sum of sampling time	Ratio	Reference
20168	1998, W Greenland	2.39	82	0.03	2.36	46	0.01	9,956	483,835	0.0206	Heide-Jørgensen (unpubl. data)
7928	1999, Norway	1.12	191	0.02	1.15	133	0.01	20,612	1,901,427	0.0108	Heide-Jørgensen *et al.* (2001)
13282	2001, Iceland	1.68	166	0.03	1.66	93	0.02	90,452	5,611,340	0.0161	Vikingsson and Heide-Jørgensen (unpubl. data)
13280	2001, Iceland	1.85	44	0.04	1.85	30	0.01	64,316	2,168,010	0.0297	
3960	2002, Iceland	2.74	531	0.05	2.73	253	0.01	189,671	6,984,198	0.0272	
Mean		**1.96**			**1.95**					**0.0209**	
CV		**0.14**			**0.14**					**0.17**	

Table 6

Overview of the estimation of availability correction factors for the two correction methods for minke whales in West Greenland compared to observations in Norway. CVs are in parenthesis.

	West Greenland	Norwegian observations (Øien *et al.*, 2008)
Method 1		
Time visible at surface	6.8s (0.11) from Table 1	
Surfacings per hour	46.1 (0.11, Heide-Jørgensen and Simon, 2007)	47.5 (0.05)
Proportion of time at surface	46.1*6.8/3,600 = 0.0871	
Availability correction for 2.2s search time	0.1146 (0.36)	
Method 2		
Proportion of time at surface (= dry time)	0.0195 from Table 5	
Surfacings per hour	46.1 (Heide-Jørgensen and Simon, 2007)	47.5 (0.05)
Duration of surfacings	3,600*0.0195/46.1 = 1.52s	
Duration of dives	3,600*0. 9,805/46.1 = 76.6s	75.8 s (0.05)
Availability correction for 2.6s search time	0.0522 (CV = 0.33)	

fully corrected estimate of 22,952 (95% CI 7,815–67,403; 90% CI 9,585–54,960) common minke whales in West Greenland in 2007 (Table 2).

DISCUSSION

The distribution of sighting distances from the trackline in the 2007-survey was very different from the distributions in previous aerial surveys for common minke whales in West Greenland. Most sightings in the 2005 survey were detected between 300 and 500m from the trackline with some as far away as 1.6km (Heide-Jørgensen *et al.*, 2008). However, in the 2007 survey the same narrow strip width was also evident from the sightings of other species; e.g. humpback whales, *Megaptera novaeangliae* (Heide-Jørgensen *et al.*, in press) and fin whales, *Balaenoptera physalus* (Heide-Jørgensen *et al.*, 2010). The observers were instructed to monitor the trackline closely and to collect cues of whales rather than sightings. Two of the observers were trained as harbour porpoise (*Phocoena phocoena*) observers which probably explains the narrow search profile. It was also evident that the common minke whale sightings were detected almost instantaneously (mean time before passing abeam <2s) and that very few sightings were missed by both observers (<4%) compared to previous surveys where <50% of the animals were seen by both observers (Heide-Jørgensen *et al.*, 2008). These survey characteristics suggest that the search profile of this survey had a narrow search width and was close to being instantaneous (i.e. with little searching ahead). Nevertheless, a correction was applied to adjust for the time the observers were able to detect common minke whales and this reduced the availability correction between 32 and 167% for the two methods.

The encounter rate was the largest contributor to the variance of the estimates, which was not unexpected as despite the large survey effort in 2007, low encounter rates have been a common feature of all past surveys of common minke whales in West Greenland. Increasing survey effort would ideally reduce the variance on the encounter rate but must be balanced against the logistic difficulties of conducting the survey over a short period of time and in optimal conditions. Another major contributor to the uncertainty of the corrected estimates was the variance of the time from first detection to when the whales passed abeam. This contributed about 82% of the availability correction factor and was therefore a major contributor to the uncertainty in the corrected estimates. The small sample size had a large impact on the variance estimates and a better model for the forward detection would be desirable. As applied, the forward detection was assumed to have a flat functional form up to the average time a common minke whale was available for detection. More realistically the detection is declining at some distance forward from the plane perhaps with an initial ‘shoulder’ (hazard rate function), but the number of detections when sorted for sea state does not allow for fitting more complex functional forms of the forward detection.

The estimates derived from the two methods are not statistically different. The point estimates from the two approaches should in theory have been closer to each other and the difference may be due to different approaches with the correction factors. Method 1 used a photographic technique, where whales were identified on images taken at an altitude of 519m with an image footprint of 480m. Information on the surfacing time of common minke whales in Iceland in 2003 were combined with cue rates collected in West Greenland in 1996 and 2006 and assumed to be representative of the proportion of time a common minke whale would be available to be seen during the survey in 2007. This is certainly less than ideal but the large variance should cover differences between areas and years.

The availability correction factor using Method 1 utilised all sightings and the correction included submergence to the depth at which common minke whales can be detected on aerial photographs. It assumed an even detectability of submerged common minke whales across the strip width similar to the footprint of the images. Ideally, only measurements from whales detected at the centre (on the trackline) of the images should be included in the calculation of the availability bias.

The availability correction factor of Method 2 utilised only sightings where the whales were breaking the surface and no whales detected below the surface were included in the estimation. The sightings for this survey were collected as cues of common minke whales, defined as the dorsal fin breaking the surface (i.e. the period the whale is dry). The satellite transmitters deployed monitored the periods the five whales were dry and resulted consistently in dry periods of less than 4s for whales instrumented at three localities in the North Atlantic (Svalbard/Norway, Iceland and West Greenland). Only one of the whales was instrumented in West Greenland and it is assumed that the dry times from the three areas combined are representative of the dry time for common minke whales in West Greenland. The whales were tracked in the same summer feeding season as in West Greenland, and are likely exhibiting similar behaviour. The number of measurements of dry periods was considerable and the large variance around the estimate should span any difference in the proportion of dry time between areas.

With Method 2 it can be argued that the dry time collected by satellite transmitters is sensitive to the position of the transmitters on the whale. During the deployment period the transmitters will migrate vertically out through the whale's skin and eventually fall out. At the end of a transmitter's life the tag may sit lower on the whale thus giving fewer signals and dry period readings. However, it must also be noted that transmissions and relay of dry periods is only possible when the transmitters are dry during the surfacing of the whales. The outward migration of the transmitters may increasingly expose the transmitter to be dry slightly more frequently; however the amount of dry time affected by this change is negligible. The long measurement periods with similarly long dry periods are indicative of poor transmission performance (i.e. poor positioning of the tag on the whale), but when included, add to the negative bias of the correction factor.

Despite the effort put forth in this study to correct for biases, the estimates of abundance of common minke whales in West Greenland presented here are still negatively biased because survey coverage was poor in the areas west of stratum 9–11. Hence no abundance estimate was included for that area. Nevertheless, the abundance estimates from the 2007 survey are the largest ever obtained in West Greenland and are probably also the most complete in terms of bias corrections that negatively affect the abundance estimates.

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Abundance of fin whales in West Greenland in 2007

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ABSTRACT

An aerial line transect survey of fin whales (*Balaenoptera physalus*) conducted off West Greenland in 2007 was used to estimate the current abundance of fin whales on the summer feeding ground. A total of 24 sightings of fin whale groups were collected during 8,632km of survey effort in sea states <5. Based on conventional distance sampling techniques an abundance of 4,359 whales (95% CI 1,879–10,114) was estimated. The survey was conducted as a double platform survey and mark recapture distance sampling techniques were used to correct for perception bias which resulted in an estimate of 4,468 whales (95% CI 1,343–14,871). Both estimates are negatively biased because no corrections were applied for whales that were submerged during the passage of the survey plane. The abundance estimate furthermore only represents the coastal areas of West Greenland. The sightings at the westernmost border of the strata suggest that the entire Baffin Bay-Davis Strait summer abundance of fin whales could be considerably larger. Based on comparison with previous surveys in West Greenland in 1987/88 and 2005 it appears that the fin whale abundance in West Greenland has increased.

KEY WORDS: FIN WHALE; ABUNDANCE ESTIMATE; SURVEY-AERIAL; WEST GREENLAND; NORTHERN HEMISPHERE

INTRODUCTION

Exploitation of fin whales (*Balaenoptera physalus*) in West Greenland began around 1919 with pelagic Norwegian whaling in the Davis Strait (Kapel, 1979). In 1924 coastal whaling along West Greenland was initiated and during 1919–39 approximately 1,200 fin whales were taken in West Greenland and the Davis Strait. Approximately 300 fin whales were taken during 1946–58, primarily along the coast of West Greenland. From 1959 to 1976 catches remained low with <2 catches per year and in 1977 the first quota was installed by the International Whaling Commission (IWC). Catches have remained stable at a mean of 12 per year for the period 1977–2007.

Fin whales are primarily hunted in West Greenland during summer and early autumn. Although their occurrence in West Greenland likely spans most of the year, West Greenland must still be considered a summer feeding ground for fin whales that generally spend the winter at more southern latitudes in the North Atlantic. The stock delineation of fin whales in the North Atlantic is unresolved but it is currently considered that fin whales in West Greenland comprise an isolated stock with limited exchange with the East Greenland-Iceland stock or the Newfoundland-Labrador stock even though genetic studies indicate a large exchange of individuals between areas (Bérubé *et al.*, 2006; IWC, 1992).

Despite many attempts between 1982 and 2007 only two surveys obtained enough sightings to allow for calculation of the abundance of fin whales in West Greenland. In 1987/88 fin whale abundance was estimated at 1,100 whales (95% CI 520–2,100) from an aerial cue counting survey (IWC, 1992). In 2005 the abundance was estimated at 3,218 whales (95% CI 1,431–7,240) from an aerial line transect survey with independent observers that allowed for correction of whales missed by the observers (Heide-Jørgensen *et al.*, 2008). A ship-based survey also conducted in 2005 gave a smaller abundance estimate (1,980, 95% CI 913–4,296) than the aerial survey (Heide-Jørgensen *et al.*, 2007).

In 2004, the IWC's Scientific Committee expressed concern that the available abundance estimates for fin whales in West Greenland were outdated and too imprecise to be used for generating advice on sustainable takes (IWC, 2005). For continued advice on the sustainability of the harvest in West Greenland it is important to determine if the abundance of fin whales in Baffin Bay-Davis Strait is stable, fluctuating in relation to climatic or ecological changes, or in a decline. A survey conducted at regular intervals is one way to update our knowledge on the status of fin whales in West Greenland. Here we report on an aerial survey of fin whales conducted off West Greenland in 2007 as part of the Trans North Atlantic Sightings Survey (TNASS; an international whale survey in 2007 that covered large parts of the Northern Atlantic).

METHODS

An aerial line transect survey of large whales in West Greenland was conducted between 25 August and 30 September 2007. The survey platform was a Twin Otter plane from Air Greenland, with long-range fuel tank and two independent pairs of observers all with bubble windows. Sightings and a log of the cruise track (recorded from the aircrafts GPS) were recorded on a Redhen msDVRs system that also allowed for continuous video recording of the trackline as well as vertical digital photographic recordings. The declination angle to sightings was measured with Suunto inclinometers when sighting was abeam (i.e. perpendicular to the trackline) and a time stamp (from the microphone switch) on the recordings was used to determine the moment when the sighting was abeam. Declination angles were

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converted to perpendicular distance of the animal to the trackline using an equation that adjusts for earth curvature (Buckland *et al.*, 2001). Target altitude and speed was 213m and 167km hr^{-1}, respectively.

Survey conditions were recorded at the start of the transect lines and whenever a change in sea state, horizontal visibility or glare occurred. For the analysis only effort in sea states <5 was included. The survey was designed to systematically cover the area between the coast of West Greenland and offshore (up to 100km) to the shelf break (i.e. the 200m depth contour, Fig. 1). Following previous survey designs transect lines were placed in an east-west direction except for South Greenland where they were placed in a north-south direction. This design ensured that the transects were perpendicular to the bathymetric gradients and did not follow depth contours. The surveyed area was divided into 11 strata plus several inshore strata that are not included here because of the absence of sightings (Fig. 2). The southern strata were planned to be covered first.

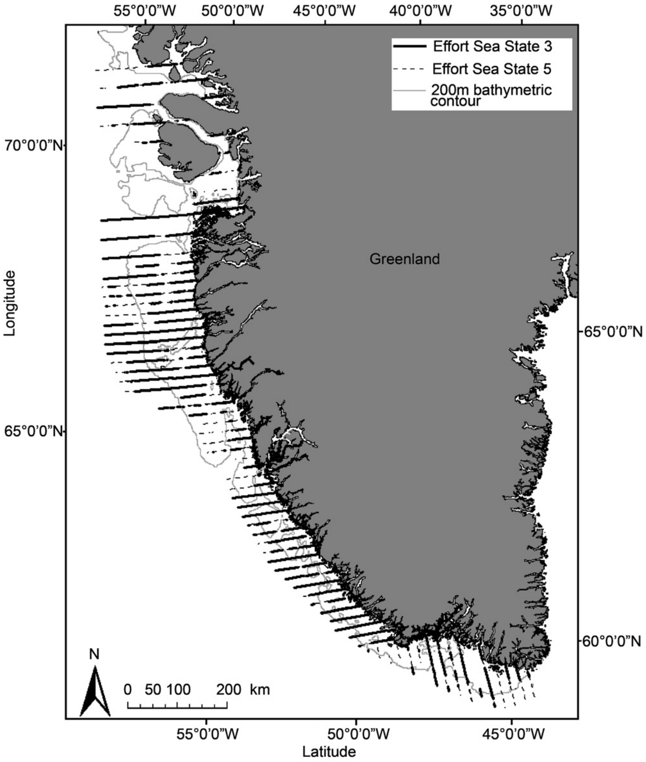

Fig. 1. Survey effort in sea states <3 and <5.

Conventional distance sampling abundance estimator

Using conventional distance sampling (CDS) methods, where detection on the trackline is assumed to be certain (denoted by $g(0) = 1$), animal abundance in each stratum was estimated by

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

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

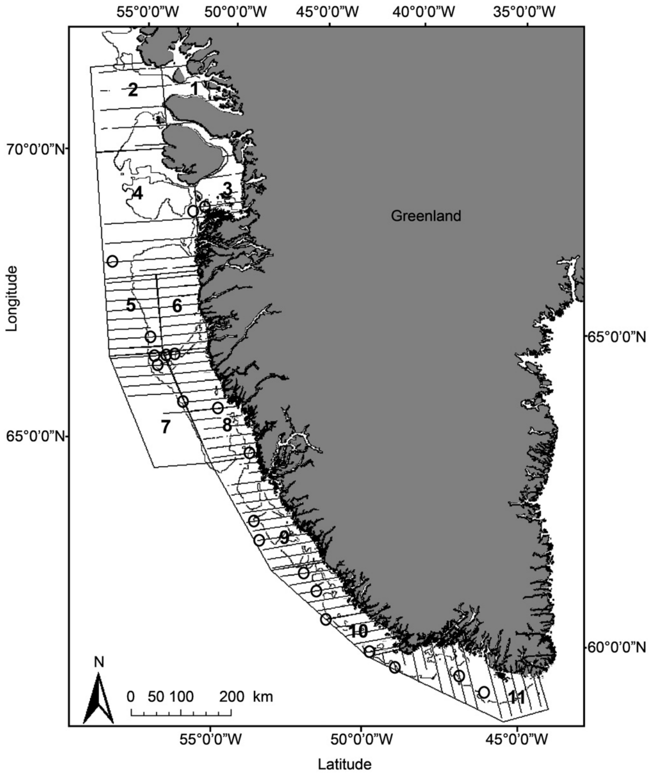

Fig. 2. Strata and transect lines and sightings of fin whales during the 2007 aerial survey.

Correction for perception bias

In this survey mark-recapture (MR) and DS methods were used which allowed detection on the trackline to be estimated and thus abundance could be estimated without assuming that $g(0) = 1$. However, this method of analysis (point independence) relies on having enough sightings to be able to estimate the parameters in the fitted models.

The search method used an independent observer configuration where the primary observers in the front seats acted independently of the secondary observers in the rear seats. Detections of animals by the primary observers serve as a set of binary trials in which a success corresponds to a detection of the same group by secondary observers. The converse is also true because the observers are acting independently; detections by the secondary observers serve as trials for the primary observers. Analysis of the detection histories using logistic regression allows the probability that an animal on the trackline is detected by an observer to be estimated, and thus, abundance can be estimated without assuming $g(0)$ is one (Buckland *et al.*, 2001).

Abundance of groups was estimated in each stratum using

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

where w is the truncation distance, and $\hat{p}_i$ is the estimated probability of detecting group i obtained from the fitted mark-recapture distance sampling (MRDS) model. Individual animal abundance is given by

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

where s_i is the size of the group *i*. The estimated group size in the stratum is given by

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

RESULTS

The total survey effort in sea states <5 was 8,632km of which 66% was in sea states <3 (Fig. 1). Although the southern strata were planned to be covered first, the actual succession of the effort was weather dependent and the effort had to be allocated to strata with sufficiently low sea states. Therefore, strata 3, 5, 6 and 8 had some coverage between 25 August and 1 September, strata 4, 5, 7, 8, 9, 11 were partially covered during 4–11 September, strata 1, 2, 3, 4, 6, 8, 9 and 10 had some effort during 11–24 September and some transects in strata 8, 10, 11 were also flown during 28–29 September.

A total of 24 fin whale sightings in nine strata were obtained (Fig. 2, Table 1). One duplicate sighting had a missing declination angle and was assigned the same angle as the other record in the duplicate pair. The observers searched independently and for some duplicate sightings, the observers recorded different declination angles or group sizes. There did not appear to be any systematic bias between duplicate pairs of perpendicular distance or school size. Thus the mean perpendicular distance and mean group size of the duplicate pairs was used.

One large school of fin whales detected at 36m from the trackline in stratum 9 was estimated by the primary observer to consist of 15 whales and by the secondary observer to be 25 whales and the average was used for analysis. Shortly after, an additional 8 whales (at 770m) and 3 whales (at 2m) were seen by observers on either side of the plane. A video sequence obtained off effort of this fin whale aggregation confirmed that about 50 whales were present in 8 smaller groups at that location (63°332'N 52°707'W). Aside from this aggregation, the vast majority of sightings were single animals.

The distribution of perpendicular distances of sightings (Fig. 3) shows that there were a large number of sightings close to the trackline indicating that there was not a blind spot for observers beneath the plane. To fit the CDS methods both hazard rate and half normal functional forms were considered and a half-normal model was chosen on the basis of AIC (Fig. 3, Table 2). A truncation at 250m was chosen to avoid the long tail in the distribution of sightings and based on the remaining 18 sightings, an effective search half-width of 134m (CV 0.21) was estimated. The mean group size across all strata was 2.3 (CV 0.21) and the abundance of fin whales was 4,359 animals (CV 0.45; 95% CI 1,879–10,114).

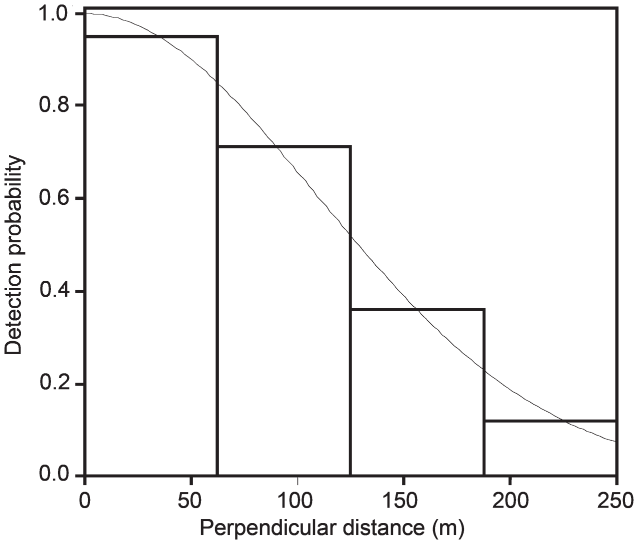

Fig. 3. Perpendicular distance distribution and fitted detection probability model fitted using CDS methodology to the fin whale sightings. Note that the histogram bars are scaled in order to place them on a comparable scale with the detection function.

Table 1

Summary of strata information including size of strata, number of transects (*k*), total length of transects and total number of sightings (without truncation).

Stratum	Area (km^2)	*k*	Length (km)	Fin whale sightings	Number of fin whales
1	8,404	3	191		
2	22,631	5	508		
3	14,653	9	532	1	2
4	34,272	4	545	3	3
5	16,226	9	863	1	1
6	14,902	9	973	1	1
7	22,085	6	551	2	2
8	20,264	12	1,345	5	8
9	20,334	12	998	5	37
10	15,950	10	932	3	6
11	24,085	16	1,194	3	3
Total	213,806	95	8,632	24	63

Stratum 4 contributed 37% of the total abundance but this stratum had a considerably lower coverage than the other strata (Fig. 1 and Table 1). In order to assess if the overall estimate was affected by the low coverage of stratum 4, a CDS analysis that treated all of West Greenland as one stratum was conducted. The abundance attained from this alternative analysis was 3,556 whales (CV 0.34) or 800 whales less than the stratified estimate. The coverage in stratum 4 was biased towards the southern portion and given that the neighbouring stratum 2 to the north had no sightings it seemed appropriate to limit the stratum to the area where transects were flown (i.e. 50% of the stratum). This reduced the CDS estimate by 19%. Stratum 7 also suffered from biased coverage but there were sightings both south and east of the stratum and it only contributes 16% of the total abundance, so no corrections were applied here.

There were 18 detections by the primary observers, 15 by the secondary and 9 by both observers (Table 3). The explanatory variables available to be included in the MRDS models were, in addition to perpendicular distance to sightings; group size, Beaufort sea state (as a factor variable with 4 levels) and observer (2 levels). The final model (Fig. 4) included distance and was chosen based on AIC (Table 4).

The final MRDS model indicated that the primary and secondary observers had similar probabilities of detection on the trackline; 0.62 (CV 0.17) and that the estimate for both observers combined was 0.86 (CV 0.09, Fig. 4). In the MRDS analysis, the data were truncated at 800m excluding one duplicate sighting that was seen >2km away – leaving 23 sightings and 9 duplicates for analysis. A further

Table 2

Abundance estimates using CDS methodology showing the encounter rate (n/L), effective strip half-width (esw) and estimates for group size $E[s]$, group density D_G, group abundance N_G , animal density D, and animal abundance N. Strata without sightings are not shown although the total densities take all strata into account. CVs are given in parentheses. Portion (a) shows the preferred analysis whereas portion (b) shows the analysis with group size estimates for each strata with both the preferred CDS left truncation at 250m and a left truncation at 800m that is compatible with the MRDS analysis.

								Percentage contribution to the variance of N		
Stratum	esw (km) n/L (groups/km)	250m truncation	$E[s]$	D_G (groups/km^2)	N_G (groups)	D (animals/km^2)	N (animals)	esw	n/L	$E[s]$
(a)										
3	0.0019 (0.76)	0.134 (0.21)	2.256 (0.21)	0.0070 (0.79)	103 (0.79)	0.0169 (0.82)	232 (0.82)	6.5	87.1	6.4
4	0.0055 (0.81)			0.0206 (0.84)	706 (0.84)	0.0496 (0.86)	1,592 (0.86)	5.8	88.4	5.8
5	0.0012 (0.98)			0.0043 (1.00)	70 (1.00)	0.0105 (1.02)	159 (1.02)	4.1	91.8	4.1
6	0.0010 (0.90)			0.0038 (0.92)	57 (0.92)	0.0093 (0.95)	129 (0.95)	4.8	90.4	4.8
7	0.0036 (0.59)			0.0136 (0.63)	300 (0.63)	0.0327 (0.66)	676 (0.66)	9.8	80.4	9.8
8	0.0015 (0.52)			0.0056 (0.56)	113 (0.56)	0.0134 (0.60)	254 (0.60)	12.1	75.8	12.0
9	0.0040 (0.72)			0.0150 (0.75)	305 (0.75)	0.0338 (0.78)	687 (0.78)	7.1	85.9	7.0
10	0.0021 (0.58)			0.0080 (0.62)	128 (0.62)	0.0193 (0.65)	289 (0.65)	10.1	79.9	10.0
11	0.0017 (0.51)			0.0063 (0.55)	151 (0.55)	0.0151 (0.59)	340 (0.59)	12.6	74.9	12.5
Total	0.0019 (0.18)			0.0088 (0.40)	1,933 (0.40)	0.0211 (0.45)	4,359 (0.45)	8.1	74.9	12.5

Stratum	esw (km) 250m truncation	$E[s]$	N (animals)	esw (km) 800m truncation	N (animals)
(b)					
3	0.134 (0.21)	2.0 (0.0)	206 (1.00)	0.175 (0.34)	158 (1.03)
4		1.0 (0.0	706 (0.96)		541 (0.99)
5		1.0 (0.0)	70 (1.03)		54 (1.06)
6		1.0 (0.0)	57 (1.00)		44 (1.03)
7		1.0 (0.0)	300 (0.65)		230 (0.70)
8		1.0 (0.0)	113 (0.64)		259 (0.70)
9		6.25 (0.74)	1,904 (1.08)		1,926 (1.02)
10		1.0 (0.0)	128 (0.65)		147 (0.57)
11		1.0 (0.0)	151 (0.67)		173 (0.63)
Total			3,635 (0.63)		3,532 (0.65)

truncation at 500m excluded one additional sighting but resulted in practically no difference in the abundance estimate. The additional truncation would have reduced the number of duplicates which was already small.

The abundance of fin whales was 4,468 animals (CV 0.68; 95% CI 1,343–14,871) using MRDS methods with a right truncation at 800m (Table 5). The contribution from stratum 4 with the biased coverage was only 14% and a correction for the unsurveyed northern part of the stratum similar to the CDS analysis above reduced the MRDS estimate by 7%. The large aggregations of fin whales in stratum 9 made up half the estimate from the MRDS analysis and similarly for the CDS estimates with stratum specific group sizes (Table 2b).

The data in the CDS estimator was truncated at 250m and so the encounter rates are slightly lower than the MRDS estimate. However, the average expected school size used in the CDS estimator is higher than the average school size in the MRDS estimator and this resulted in higher animal abundance in most strata (see Tables 2 and 5). If for the comparison a truncation at 800m and mean group sizes for each stratum were used in the CDS analyses, a total of 3,532 (0.65) fin whales were obtained which is compatible with a perception bias of approximately 0.86 in the MRDS analyses (Table 2).

Table 3

Number of sightings seen by the primary and secondary observers and the number of duplicates (seen by both). The Total column reports number of sightings seen by observer 1 plus observer 2 minus sightings seen by both.

Group size	Primary observer	Secondary observer	Seen by both	Total
1	15	10	7	18
2	1	2	1	2
3	1	1		2
8		1		1
25	1	1	1	1
Total	18	15	9	24

Table 4

MRDS models fitted to the data for fin whales truncated at 800m. D is distance to sightings and O is observer.

Distance sampling model	Mark recapture model	Akaike Information Criteria	ΔAIC
Half Normal: D	D	343.92	5.81
Hazard rate: D	D	338.11	0.00
Hazard rate: D	$D + O$	338.95	0.85

DISCUSSION

The estimate of fin whale abundance provided here only covered the coastal areas of West Greenland and must be considered an absolute minimum for the abundance in Baffin Bay and Davis Strait. The main reason for this is that fin whales were observed at the westernmost point of the transects several times and the survey strata clearly did not cover the entire fin whale summer distribution in Baffin Bay and Davis Strait. Satellite tracking of fin whales has also demonstrated their capacity to move from the coastal areas

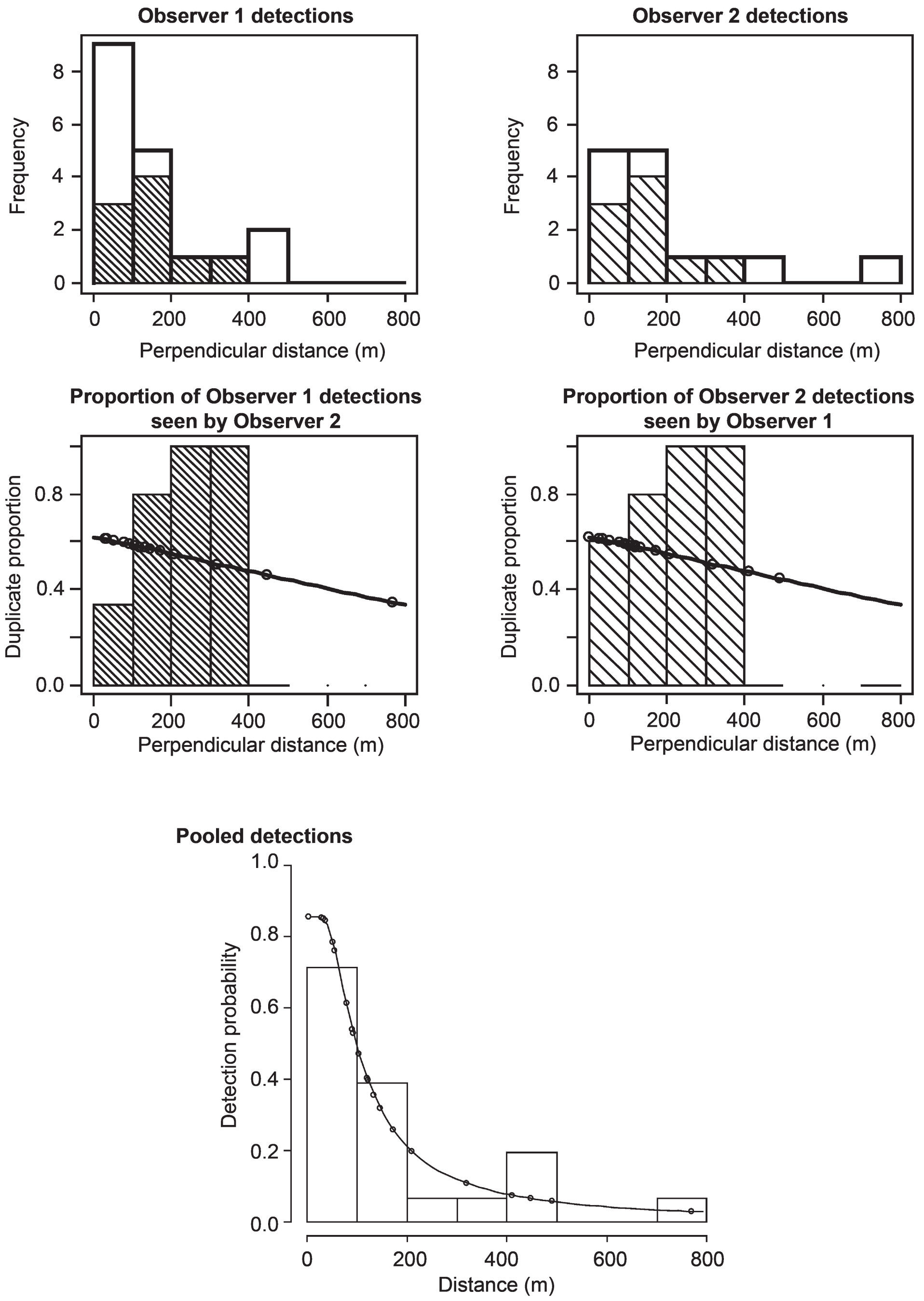

Fig. 4. Detection function plots for the MRDS analyses. Duplicate detections are indicated in the shaded areas; as a number in the top plots and as a proportion in the middle plots. The points are the probability of detection for each sighting given its perpendicular distance and the lines are the fitted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

of West Greenland to offshore areas west of the range of the surveys (Heide-Jørgensen *et al.*, 2003).

Large aggregations of fin whales were detected in stratum 9 and similar large groups were also detected in an aerial survey in 2005 (Heide-Jørgensen *et al.*, 2008). Stratum 9 contributed about half the total abundance when using stratum-specific mean group size estimates, but only 16% of the total abundance when averaging group sizes across all strata. However, it seems reasonable to restrict the effect of the large group sizes to stratum 9 since mostly solitary whales were detected in the other strata. The reason for the large congregations of fin whales in recent years in West Greenland is likely due to large concentrations of krill (*Meganyctiphanes norvegica* and *Thysanoessa sp.*) stimulated by increased advection and warmer sea temperatures in West Greenland (Laidre *et al.*, 2010). Schooling fin whales have been shown to feed on these krill concentrations in West Greenland (Laidre *et al.*, 2010).

Both the MRDS and the CDS analysis are negatively biased due to the lack of correction for whales that were submerged and therefore invisible to the observers. The relatively low number of primary sightings prevented the use of cue counting techniques that could correct for whales that were submerged during the passage of the survey plane. It must be assumed that only a fraction of the fin whales were available for detection at the surface. No availability factors

Table 5

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

							Percentage contribution to the variance of N			
Stratum	n/L (groups/km)	D_G (groups/km^2)	N_G (groups)	D (animals/km^2)	N (animals)	$E[s]$	esw	n/L	$E[s]$	$\hat{p}$
3	0.0019 (0.98)	0.0063 (1.04)	92 (1.04)	0.0126 (1.04)	185 (1.04)	2.00 (0.87)	16.4	81.9	0	1.2
4	0.0055 (0.94)	0.0184 (1.00)	632 (1.00)	0.0184 (1.00)	632 (1.00)	1.00 (0.66)	14.9	84.7	0	1.1
5	0.0012 (1.00)	0.0039 (1.06)	63 (1.06)	0.0039 (1.06)	63 (1.06)	1.00 (0.30)	10.5	88.9	0	0.7
6	0.0010 (0.98)	0.0034 (1.04)	51 (1.04)	0.0034 (1.04)	51 (1.04)	1.00 (0.54)	12.3	86.0	0	0.9
7	0.0036 (0.61)	0.0122 (0.70)	268 (0.70)	0.0122 (0.70)	268 (0.70)	1.00 (0.21)	24.3	73.1	0	1.7
8	0.0030 (0.51)	0.0100 (0.62)	202 (0.62)	0.0149 (0.64)	303 (0.64)	1.50 (0.41)	28.3	52.7	21.9	2.1
9	0.0050 (0.80)	0.0168 (0.87)	341 (0.87)	0.1107 (1.03)	2,592 (1.03)	7.60 (0.45)	12.0	70.0	9.4	0.9
10	0.0032 (0.46)	0.0108 (0.58)	172 (0.58)	0.0108 (0.58)	172 (0.58)	1.00 (0.12)	35.6	65.1	0	2.5
11	0.0025 (0.54)	0.0084 (0.64)	203 (0.64)	0.0084 (0.64)	203 (0.64)	1.00 (0.00)	14.3	85.1	0	1.0
Total	0.0024 (0.26)	0.0092 (0.49)	2,024 (0.49)	0.0187 (0.68)	4,468 (0.68)	2.21 (0.50)	14.3	85.1	0	1.0

are available from fin whales in West Greenland or other areas and there is a need to develop methods for collecting this information. Furthermore the CDS estimate is negatively biased due to the lack of correction for whales at the surface that are missed by the observer. MRDS includes correction for this and must be considered the most complete of the two analyses.

Nevertheless, the present abundance estimate is the largest abundance ever recorded for West Greenland. Abundance estimates from surveys in July and August 1987/88 for West Greenland were developed from cue counting techniques and fin whale abundance was estimated at 1,100 (95% CI 520–2,100) (IWC, 1992). In September 2005 a ship-based line transect survey covered the shelf areas out to the 200m depth contour and an abundance of 1,980 (95% CI 913–4,296) fin whales was estimated for West Greenland (Heide-Jørgensen *et al.*, 2007). Simultaneously an aerial line transect survey gave a similar estimate of 1,652 (95% CI 811–3,367) fin whales (Heide-Jørgensen *et al.*, 2008). Correction of the 2005 aerial survey for perception bias increased the abundance estimate to 3,218 fin whales (95% CI 1,431–7,240). The 1987/88 estimate of 1,100 (95% CI 520–2,100) fin whales in West Greenland (IWC, 1992) was a cue counting estimate but did not correct for perception bias. However, considering that the current uncorrected estimate is considerably larger (4,359 whales, 95% CI 1,879–10,114) than the earlier estimates corrected for availability bias (by the cue counting technique in 1987/88) or for perception bias (by independent observers in 2005), it seems likely that the occurrence and abundance of fin whales in West Greenland is under a long-term increase (as also observed in East Greenland – Víkingsson *et al.*, 2009), perhaps stimulated by the recent increase in density of krill on the feeding banks off West Greenland (Laidre *et al.*, 2010).

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Abundance of Bering-Chukchi-Beaufort bowhead whales (*Balaena mysticetus*) in 2004 estimated from photo-identification data

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ABSTRACT

Ice-based surveys near Point Barrow, Alaska, have been used to obtain most estimates of abundance for the Bering-Chukchi-Beaufort (B-C-B) stock of bowhead whales, but global warming has raised concerns that ice-based surveys may not be practical in the future. Aerial photographic surveys provide an alternative method for obtaining abundance estimates and may replace ice-based surveys. Aerial photographic surveys were conducted near Point Barrow during the spring migrations of bowhead whales in 2003 and 2004 and, in 2005, in the northern Bering Sea in spring and near Barrow in fall. The 2003 survey was the most complete photographic survey of the population conducted to date. These surveys provided photo-identification data for use in capture-recapture analyses. A screening procedure was used to define which whales captured in 2003, 2004 and/or 2005 were marked and could be reidentified if photographed on another occasion. An estimate of the number of marked whales was obtained using a closed population model for capture-recapture data. Several models were investigated, including models that accounted for heterogeneity in capture probabilities, but a simple model with no covariates produced the most precise estimate. To account for unmarked whales, the estimate of marked whales was divided by an estimate of the proportion of the bowhead population that was marked based on the 1989–2004 spring photographic surveys near Point Barrow. Abundance of the B-C-B bowhead population in 2004 (excluding calves) was estimated to be 12,631 with CV 0.2442, 95% bootstrap percentile confidence interval (7,900; 19,700) and 5% lower limit 8,400. These results were compared with results that used approximate variance expressions for the estimates of the number of marked whales, the proportion of the population that was marked and population abundance instead of using the bootstrap. The estimates of abundance in 2004 computed for comparison included one based on a modified Petersen estimate of the number of marked whales that omitted the 2005 data as well as the estimate of 12,631 described above. The comparison estimates also included estimates of abundance in 1985 computed from 1984–87 photographic survey data using the same methods. All the abundance estimates computed from photographic data were consistent with expectations based on independent abundance and trend estimates from the ice-based surveys conducted from 1978 to 2001.

KEYWORDS: ABUNDANCE ESTIMATE; MARK-RECAPTURE; SURVEY-AERIAL; PHOTO-ID; BOWHEAD WHALE; ARCTIC; BEAUFORT SEA

INTRODUCTION

Aerial photography projects conducted from 1981–2000 have provided much of the life history data that are available on the Bering-Chukchi-Beaufort (B-C-B) stock of the bowhead whale (Angliss *et al.*, 1995; da-Silva *et al.*, 2007; Koski *et al.*, 1992; 1993; 2006; Miller *et al.*, 1992; Nerini *et al.*, 1984; Rugh *et al.*, 1992b; Zeh *et al.*, 2002; 1993). The last major photographic effort during that period was conducted in 1992, although smaller scale photography projects were conducted during 1994 and 1998–2000.

The 1985 and 1986 photography projects also provided data that were used to make abundance estimates (da Silva *et al.*, 2000; da-Silva, 2003; da-Silva *et al.*, 2003; da-Silva and Tiburcio, 2010; Schweder, 2003) using closed population capture-recapture models. These estimates and their precision were similar to estimates from ice-based surveys in 1985 and 1986 (da Silva *et al.*, 2000). The capture-recapture estimates were based on photographic images of the midback zone of the whales scored as being of acceptable quality and identifiability (Rugh *et al.*, 1998). Zeh *et al.* (2000; 2002) developed a data screening method that allowed natural marks[1] in all four zones (rostrum, midback, lower back and flukes) to be used without risking failure to recognise recaptures because different zones of the whale were visible in images taken on different sampling occasions. This screening method provided larger sample sizes of naturally marked whales and increased precision of estimates based on their images. It was used to estimate annual survival probability of bowheads by Zeh *et al.* (2002) and da-Silva *et al.* (2007) using open population capture-recapture models; da-Silva *et al.* (2007) showed that accounting for heterogeneity in capture probabilities between moderately and highly marked whales improved precision of the survival estimate.

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[1] 'Natural' marks include scars resulting from encounters with propellers, bullets and fishing gear as well as ice and killer whales. Since researchers do not capture, mark and release the whales, the term 'capture-recapture' rather than 'mark-recapture' is used in this paper. A naturally marked whale is 'captured' by obtaining a photograph of adequate quality to allow the whale to be categorised as marked during data screening and 'recaptured' when recognised in a subsequent photograph. An 'unmarked' whale is one with a photograph of adequate quality to determine that the screening method does not categorise it as 'marked'.

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It was recognised that continuation of bowhead photography studies would provide information that would allow better definition of life history parameters of bowhead whales as has been done for other species of baleen whales such as right and humpback whales (Barlow and Clapham, 1997; Best *et al.*, 2001; Cooke *et al.*, 2001; Gabriele *et al.*, 2007; Payne *et al.*, 1990). In addition, there are concerns that global warming and unstable shore-fast ice might prevent successful completion of future ice-based surveys. This made it important to determine whether photographic data collected in two consecutive years and analysed using capture-recapture methods could provide adequately precise abundance estimates (i.e. sufficient for use in management as input data for the *Bowhead Strike Limit Algorithm* – e.g. IWC, 2003) to justify replacing ice-based with photographic surveys. The ice-based surveys are dependent on stable ice and weather conditions since they require observers to count whales from perches on the shore-fast ice that are close to leads through which the whales travel. In addition, it is important for the ice-based effort to include hydrophones to record whales that pass beyond viewing range. Snow, persistent fog and shifting ice can lead to failure of an ice-based survey. The aerial photography approach to estimating abundance is less sensitive to vagaries in ice cover but does require weather conditions suitable for conducting flights.

Long gaps between photographic surveys result in less precise estimates and difficulties in analysing data. Thus aerial photographic studies were conducted near Point Barrow, Alaska, during the spring bowhead migration in 2003 (12 April to 6 June) and 2004 (18 April to 7 June) to continue collection of photographs that could be used for better definition of life-history parameters and estimation of abundance. In addition, in connection with investigations of the structure of the B-C-B stock of bowheads, aerial photographic studies were conducted in 2005 in the northern Bering Sea (9 April to 2 May) and near Barrow prior to the main fall migration (6 to 9 September) (Koski *et al.*, 2007).

The 2003 data and data from the earlier spring photographic surveys near Point Barrow were used by Schweder *et al.* (2010) to estimate abundance, population growth rate and mortality. Their approach eliminated the need for data screening by modelling the probability of recognising a recapture as a function of degree of marking of the whale and quality of the images. However, they were not able to obtain capture-recapture estimates of 2003–05 abundance because the 2004 and 2005 data were not yet available and the 2003 data had not been checked for matches with other years.

Koski *et al.* (2008) computed modified Petersen estimates (Chapman, 1951) of the number of naturally marked bowheads for the only two pairs of years when photographic surveys provided adequate numbers of photographic captures and recaptures to support such estimates: 1985–86 and 2003–04. These were preliminary estimates because data from the 2005 surveys were not yet available and checking of data from the earlier surveys was ongoing. In addition, analytical methods were still under development. Koski *et al.* (2008) noted that their abundance estimates were completely independent from ice-based survey estimates used by the International Whaling Commission Scientific Committee (IWC SC) for giving management advice (IWC, 2003). The estimates from the two independent methods agreed well. In this paper, abundance estimates based on the modified Petersen estimate for 1985–86 and 2003–04 using updated data and methods are presented in order to facilitate comparisons with ice-based survey estimates and estimates based on three instead of two years of surveys.

Koski *et al.* (2008) suggested that a more precise estimate of 2004 abundance might be obtained without additional surveys by accounting for heterogeneity in capture probabilities as a function of predictors such as whether whales were highly or only moderately marked (da-Silva *et al.*, 2007; Schweder *et al.*, 2010). They also observed that an estimate based on 2005 as well as 2003–04 data would be more precise. These ideas are pursued in this paper. Methodological improvements have also been made. Most important are refinement of the method for estimating the proportion of whales that are marked and development of a bootstrap approach for assessing precision in addition to the approach based on the delta method. Estimates based on 1989–2005 data are compared with estimates based on 1984–87 data computed using the same methods.

METHODS

Collecting and processing of images

Field and laboratory methods for the pre-2003 surveys (1984–94) have been documented (Angliss *et al.*, 1995; Koski *et al.*, 1992; Rugh *et al.*, 1992a; 1998) and described (Koski *et al.*, 2006). The 2003–05 aerial photographic studies were conducted jointly by LGL Limited (LGL), the North Slope Borough Department of Wildlife Management (NSB-DWM) and the Alaska Fisheries Science Center's National Marine Mammal Laboratory (NMML) with support from the Minerals Management Service (MMS). Field and laboratory methods were similar to those of the earlier studies.

Following each field season, the film was developed, labelled, duplicated and stored in acid-free archive sheets for future analyses. The data documenting each image were entered into an *Excel* spreadsheet for future integration into the 'Bowhead Whale Photography Database' described in Koski *et al.* (2006). Images obtained in 2003–05 were digitised at 4,000 dots per inch; most of the digitised images were cropped and printed to nearly fill 12.7cm × 17.8cm (5in × 7in) colour prints, which are suitable for comparing images to identify matches i.e., recaptures (Rugh *et al.*, 1992a). Printed images were checked against the original film transparencies and the data files to ensure that all images were scanned and printed.

Researchers at LGL and NMML have shared all tasks. NMML researchers have taken the lead on scoring images for photo quality and identifiability (as per Rugh *et al.*, 1998). LGL researchers have taken the lead on within-year matching for the 2003–05 studies, assembling the database, and measuring whales. NMML researchers did within-year matching of images from 2004 for verification of the same effort at LGL. Researchers at both NMML and LGL provided final determination of within-year matches. LGL and NMML researchers independently identified between-year matches. After both groups completed their matching efforts, match results were compared and discussed, and final match determinations were made.

Images were screened using the method of Zeh *et al.*

(2000; 2002) to determine whether they were of acceptable quality for use in capture-recapture analyses and, if so, whether they were of marked or unmarked whales. Quality is scored as 1+ (best), 1–, 2+, 2– or 3 (worst) in each of four zones on the whale's body: rostrum, midback, lower back and flukes. If a zone is scored as 3, it is not acceptable for use in defining the whale as marked for capture-recapture analyses except in the rare cases in which identifiability is scored as H+, H– or M+. Identifiability in each zone is scored as H+ (highly marked), H–, M+ or M– (moderately marked); U+, U– or U (unmarked); or X meaning the zone is not depicted clearly enough in the photo to determine mark status. Scores of X almost always correspond to quality 3. It is assumed that if a zone scored as quality 3 receives an identifiability score of M+ or better, it can be used in defining a whale as marked because that whale would be recognised in a subsequent image of the zone.

In defining the whale (as opposed to the zone) as marked, whales marked in the midback zone are first defined as marked. Then whales with a midback image quality of at least 2+ that were never scored as marked in the midback zone are defined as marked if they are marked on the rostrum. Whales are added to the list of marked whales similarly if they are adequately marked on the flukes or lower back and unmarked in the zones already considered. The end product of the screening process is a list of marked whales that is used in the capture-recapture analysis. This screening method, as well as the natural differences in how well marked individual whales are, leads to heterogeneity in capture probabilities that should be accounted for in analyses (da Silva *et al.*, 2000; da-Silva *et al.*, 2007; Schweder *et al.*, 2010). Covariates created during the screening process can be used to account for heterogeneity under the model used for estimating abundance of the marked population.

Estimating abundance of the 1+ population

An estimate N of bowhead abundance can be computed from photo-identification data using a closed population capture-recapture model to obtain an estimate N^m of the number of naturally marked whales and accounting for unmarked whales by dividing by an estimate p^* of the proportion of the bowhead population that is naturally marked. This abundance estimate is:

$$N = N^m / p^* \tag{1}$$

See p.72 of Seber (1982) or equation (1) of da Silva *et al.* (2000).

A rough estimate of the variance of N can be derived using the delta method under the assumption that N^m and p^* are statistically independent (Seber, 1982). It can be written as

$$V(N) = V(N^m) / (p^*)^2 + (N^m)^2[V(p^*) / (p^*)^4] \tag{2}$$

The square root of the right-hand side of equation (2) provides an estimate of the standard error (SE) of N. Calves are not included in computing either N^m or p^*, so N is an estimate of the size of the 1+ (non-calf) population.

Precision of N can also be assessed using a bootstrap procedure. This is not simple given equation (1) because a bootstrap for N^m is based on sampling capture histories of individual marked whales (Buckland and Garthwaite, 1991) while p^* is computed from images of marked and unmarked whales and the effort expended to collect those images. There can be several photographic images of an individual marked whale in a given year and no images in another year included in its capture history. Some images contributing to the capture history of a marked whale are not included in computing p^*, and no images of unmarked whales contribute to the capture histories. The natural sampling unit for a bootstrap on p^* is a survey flight because hours of effort are recorded for each survey flight. While some survey flights produce no images, most produce images of both marked and unmarked whales.

In a given bootstrap replicate, some marked whales with images from a given flight may be represented in the bootstrap sample of capture histories and others may not. If a marked whale with images from a given flight is indicated by the bootstrap sample of capture histories to have been seen in the year of the flight, the flight must be part of the sample of flights. This is because in most cases whales were seen in only one flight in a given year. Although there may be multiple photographs of an individual whale from a single flight, most animals are migrating, so there is a low probability that they will still be in the area during a subsequent flight. If a marked whale photographed on an included flight is not represented in the capture history sample, images of that whale (and a proportional number of unmarked whale images from the flight) must be omitted because the whale cannot both be and not be in the bootstrap replicate. In the next three sections, we describe in more detail how this is accomplished.

Once the bootstrap samples have been defined N^m, p^* and N can be computed for each bootstrap replicate. The standard deviations of the bootstrap values provide standard errors; e.g. if there are *nboot* replicates, the SE of N is given by the standard deviation (SD) of the *nboot* values computed for N.

Estimating abundance of the marked population

The estimate N^m can be obtained using the closed capture model of Huggins (1989; 1991) as implemented in Program MARK (White and Burnham, 1999). The 2003–05 data on marked whales can be treated as representing three sampling occasions (if spring and fall 2005 samples are combined) or four occasions. Recapture probabilities $c(t)$ can be treated as equal to or different from initial capture probabilities $p(t)$, where t denotes the sampling occasion. In initial analyses of the capture-recapture data, spring and fall 2005 were treated as separate sampling occasions, Sp2005 and Fa2005. All 5 recaptures and 49 of the initial captures in 2005 occurred in Sp2005; only 12 initial captures were in Fa2005. When the same models for $p(t)$ and $c(t)$ were fit to the three-occasion and four-occasion data, the estimates N^m of the number of marked whales were generally similar, but N^m from the three-occasion model was somewhat more precise. This is to be expected since the three-occasion model has one less capture probability parameter to estimate than the four-occasion model. Therefore, four-occasion models were not considered further.

Linear or logit models for $p(t)$ and/or $c(t)$ can include covariates that differ among the whales and are expected to influence these capture and/or recapture probabilities, e.g. the identifiability scores that indicate how well marked the whales are. Except in the case of the simplest model discussed below, the parameters that determine $p(t)$ and/or $c(t)$ are estimated via maximum conditional likelihood while N^m is obtained using a method of moments (Huggins, 1989). Either AIC (Akaike, 1974) or the Bayesian Information Criterion (BIC – Schwarz, 1978) can be used in selecting the best model. In this paper, BIC is used because it chooses more parsimonious models. Models with lower BIC explain the data better than those with higher BIC. However, BIC is a function of the maximised likelihood, which involves only $p(t)$, $c(t)$ and any covariates, along with the model assumed for them. Since N^m, the parameter of primary interest, is a derived parameter, a measure of how well the model permits it to be estimated is also needed. Its CV is used for this purpose. An over-parameterised model may produce $p(t)$ and $c(t)$ that fit the data well, but if CV(N^m) is too large, it is not a useful model for our purposes.

The simplest defensible model for the bowhead data, since different numbers of hours of survey effort and different survey conditions characterised the three years, is a model with different values for $p(2003)$, $p(2004)$ and $p(2005)$ with $c(2004) = p(2004)$ and $c(2005) = p(2005)$. This is the model discussed in Chapter 4 of Seber (1982) as the generalised hypergeometric model (Chapman, 1952; Darroch, 1958). White *et al.* (1982) and Buckland and Garthwaite (1991) refer to this model as Model M_t. It will be referred to as Model M_t in this paper. Under this model, Program MARK computes the maximum likelihood estimate N^m as the largest root of the quadratic equation

$$(N^m)^2\,(m_2 + m_3) - N^m\,(n_1n_2 + n_1n_3 + n_2n_3) + n_1n_2n_3 = 0 \quad (3)$$

where n_1 is the number of naturally marked whales photographed in 2003, n_2 the number photographed in 2004, n_3 the number photographed in 2005 and m_2 and m_3 the number of recaptures in 2004 and 2005 respectively. The estimated variance $V(N^m)$ of N^m is computed as in Seber (1982) using an asymptotic variance derived by Darroch (1958):

$$V(N^m) = 1 / [1/(N^m - r) + 2 / N^m - 1 / (N^m - n_1) - 1/(N^m - n_2) - 1 / (N^m - n_3)] \quad (4)$$

where r is the number of different whales caught during the three sampling occasions. As noted in the previous section, this variance can also be estimated as the variance of *nboot* bootstrap values N^m. However, the variance of N^m is of less interest when the bootstrap is used because the bootstrap provides a direct estimate of the variance of N in place of the function of N^m, p^* and their variances given by equation (2).

Seber (1982) gives an expression for the bias b of N^m from an asymptotic result of Darroch (1958) which for our case of three sampling occasions reduces to

$$b = \{[2 / N^m - 1 / (N^m - n_1) - 1 / (N^m - n_2) -1 / (N^m - n_3)]^2 + [2 / (N^m)^2 - 1 / (N^m - n_1)^2 - 1 / (N^m - n_2)^2 - 1 / (N^m - n_3)^2]\} / \{2[1 / (N^m - r) + 2 / N^m - 1 / (N^m - n_1) - 1 / (N^m - n_2) - 1 / (N^m - n_3)]^2\} \quad (5)$$

As already noted, equations (3) and (4) assume that the population of naturally marked bowheads is closed, i.e. the effects of emigration, immigration, mortality and recruitment on the size of the marked population are negligible so that this size can be assumed to be constant over the period during which the data are collected, e.g. 2003–05. This bowhead population has a high survival rate (Zeh *et al.*, 2002), a modest annual rate of increase (George *et al.*, 2004; Zeh and Punt, 2005), a consistent migration pattern that brings it past Point Barrow and into the Beaufort Sea each spring which makes it easy to photograph (Braham *et al.*, 1984; Moore and Reeves, 1993) and stable natural markings that permit the whales to be identified over periods of many years (Koski *et al.*, 1992; Rugh *et al.*, 1992a; 2008; 1992b). It has been shown via simulations based on bowhead photo-identification and natural history data by da Silva *et al.* (2000) that the closed population assumption does not lead to biased estimates over a two-year sampling period in the bowhead case.

Thus the closed population assumption over a three-year sampling period seems reasonable. Comparing abundance estimates based on two-year capture histories, where N^m is the modified Petersen estimate (Chapman, 1951), with those based on three-year capture histories, where N^m is obtained by subtracting the bias given by equation (5) from N^m given by equation (3), provides a check on this assumption. It is important to correct the Model M_t estimate for bias to make the comparison valid because the modified Petersen estimate can be assumed to have negligible bias unless there are fewer than seven recaptures (Robson and Regier, 1964).

If the population continued to increase in 2003–05 as in 1978–2001 (George *et al.*, 2004), the assumed constant abundance would be most representative of 2004. Therefore, the abundance estimate was assigned to that year. Using the same reasoning, the abundance estimates based on 1985–86 and 1984–86 capture histories were assigned to 1985; 1984 was chosen as the additional year for the latter estimate because the number of marked whales successfully photographed in 1984 was similar to the number in 2005.

Bootstrap on capture histories to obtain bootstrap values

Buckland and Garthwaite (1991, pp.257–9), describe how to carry out either a parametric or a nonparametric bootstrap on the capture histories under Model M_t. Capture probability in sample t is estimated by n_t / N^m where n_t is the number of marked whales actually captured in sample t and N^m is the estimate of the number of marked whales, in our case the estimate given by equation (3) corrected for the bias estimated from equation (5). The probability of each possible capture history, including the capture history of marked whales that were never captured in a photograph, is estimated from the n_t / N^m values under a multinomial model. Seber (1982) notes that this multinomial model and Model M_t lead to the same maximum likelihood estimates N^m of abundance.

Buckland and Garthwaite (1991) favour a parametric bootstrap carried out by drawing N^m capture histories from the assumed multinomial distribution. However, we needed to draw from the observed capture histories of the marked whales in order to determine which whales were, and which were not, included in each bootstrap sample. An entry 000 for the never captured whales was added to the observed capture histories and sampled with probability $(1 - n_1 / N^m)$ $(1 - n_2 / N^m)$ $(1 - n_3 / N^m)$.

The single marked whale captured in 2003, 2004 and 2005 (capture history 111) was sampled with probability (n_1 / N^m) (n_2 / N^m) (n_3 / N^m). Each other observed capture history was represented by more than one marked whale, so the corresponding multinomial model probability was divided among the whales. For example, eight whales were captured in 2003 and 2004 but not 2005, so each of those whales was sampled with probability $[(n_1 / N^m)\,(n_2 / N^m)\,(1 - n_3 / N^m)] / 8$ to represent capture history 110.

Estimating the proportion of the population that is marked

Koski *et al.* (2008) used data from spring, summer and autumn photographic surveys from 1981 to 2004 to estimate proportion marked. In this paper, data from 1984–87 spring photographic surveys near Point Barrow were used to estimate the proportion of the bowhead population that is naturally marked for 1985 abundance estimates. Data from 1989–92 and 1994 spring surveys as well as the 2003 and 2004 surveys were used for 2004 abundance estimates. These are the most appropriate surveys to use for this purpose because they were designed to sample the entire migrating population. Data from the 2005 surveys cannot be used for estimating proportion marked because those surveys were not conducted during the spring migration near Point Barrow. The Sp2005 survey was designed to sample naturally marked whales, and the Fa2005 survey covered only a few days prior to the main fall migration. Although summer/autumn surveys in earlier years attempted to sample the whole population, they did not always succeed due to age segregation on the summering grounds.

As in Koski *et al.* (2008), separate surveys were used for the 1985 and 2004 abundance estimates so that those estimates would be statistically independent. In this paper, more years were assigned to the 2004 estimate to increase its precision.

The estimate p^* is based on all images with midback quality better than 3 and midback identifiability better than X. The data screening procedure of Zeh *et al.* (2000; 2002) that was used results in the majority of marked whales being marked on their midbacks, and to qualify for the list of marked whales on the basis of marks in another zone, they must be unmarked on their midbacks. Therefore images of the midback zone scored X do not contribute to defining whales as marked or unmarked. The restriction to quality better than 3, not imposed by Koski *et al.* (2008), is to avoid positive bias in p^* due to well marked whales recognisable as marked even in some images of lowest quality.

After the restriction to the images just described, each image was given a weight. That weight was 1.0 for the vast majority of the images. However, following Koski *et al.* (2006), images of cows accompanied by calves were given less weight because of increased effort to photograph cow-calf pairs and the greater amount of time spent at the surface by calves. Cows and yearlings travelling together were given intermediate weight because, like cows with calves, increased effort is made to photograph them, but their surface times are similar to other non-calves. Summing these weights is equivalent to counting the images with each weight, multiplying by the weight and summing the weighted counts. Koski *et al*. (2008) computed p^* as

$$p^* = (\textit{sum of weights for images of marked whales}) / (\textit{sum of weights for all images}) \qquad (6)$$

They used images collected before 1988 to compute p^* for their 1985–86 abundance estimate and those collected after 1988 for the 2003–04 estimate. They used the same cow-calf and cow-yearling weights for both estimates.

In this paper, following Koski *et al.* (2004), time at the surface was estimated from data on surfacing, respiration and diving (SRD) behaviour during the spring migrations of 1989–91 and 1994. Durations of surfacings and dives were recorded for 248 calf SRD cycles and 302 SRD cycles of other whales. Calves were found to spend 1.71 times as long at the surface as other whales, with SE = 0.14 based on 2000 bootstrap replicates. To account for uncertainty in this factor, values were drawn from the bootstrap values used to obtain the SE just cited when a bootstrap analysis was conducted to obtain standard errors for N^m, p^* and N.

To allow for the possibility of changes over time in the extra effort expended to photograph cow-calf pairs, this factor was computed separately from the 1984–87 spring surveys and the 1989–2004 spring surveys. The ratio of images per whale for cows with calves to images per whale for whales not accompanied by a calf or yearling during the part of the migration when calves were seen defines the factor. It was 1.56 in 1984–87 and 1.46 (SE = 0.09) in 1989–2004. The SE of the latter value was estimated via the bootstrap by calculating the ratio from just the eligible images included in each bootstrap sample. A bootstrap analysis was not conducted for estimates obtained from the 1984–87 data because there were many complications to be dealt with, including shifts in migration timing in 1985 (Koski *et al.*, 2006) and 1987. Thus the weights for the 1984–87 calculations were 0.641 = 1/1.56 for cows and yearlings seen together and 0.375 = 1/1.56 × 1/1.71 for cows seen with calves. The corresponding 1989–2004 values were 0.685 = 1/1.46 and 0.401 = 1/1.46 × 1/1.71.

Seventeen whales not accompanied by calves or yearlings that lingered near Point Barrow for three days or more between 19 May and 6 June 2004, a behaviour almost never observed in other years, were omitted from the 1989–2004 calculations described in the previous paragraph. These whales were photographed as many as 17 times on as many as 6 different days, on average 4.99 times as often as other whales not part of a pair. Images of these whales were given weight 0.200 = 1/4.99 in computing p^*.

As in Koski *et al.* (2006), the migration was divided into ‘weeks’ and the weeks’ proportions of marked whales combined to obtain the overall proportion. This approach avoids positive or negative bias in p^* that could result if a week with unusually large numbers of marked whales was oversampled or undersampled, respectively, and (6) was used to compute p^*. The weeks for 1989–2004 are the seven weeks in Koski *et al.* (2006). The more limited sample for 1984–87 required reducing the number of weeks to five by merging the first week with the second and the penultimate with the last. Dates for 1985 were shifted by 9 days as in Koski *et al.* (2006) to account for the late migration that year. Koski *et al.* (2006) did not examine 1987 data because usable lengths were not obtained in 1987. We found that the 1987 migration appeared to be late by about 6 days and shifted its dates accordingly.

Data are available on the number of hours of photographic survey effort for each of the spring surveys near Point

Barrow. The hours of effort for each week were summed over the relevant survey years to obtain $effort_w$ = total hours of effort for week w. It was assumed that if each week had the same amount of effort, the number of images per week would be related to the fraction of the bowhead population migrating past Point Barrow during that week. Under this assumption, p^* can be computed as follows:

$$p^* = [\Sigma(M_w / effort_w)] / [\Sigma(A_w / effort_w)] \quad (7)$$

where M_w = sum of weights of week w images of marked whales, A_w = sum of weights of all week w images and Σ represents summation over weeks.

A rough estimate $V(p^*)$ of the variance of p^* can be computed under the assumption that M_w follows a binomial distribution with parameters A_w, p_w as

$$V(p^*) = \Sigma W_w^{\,2}\, p_w\,(1 - p_w) / A_w \quad (8)$$

where $p_w = M_w / A_w$ and $W_w = (A_w / effort_w) / \Sigma(A_w / effort_w)$.

The variance of p^* was also estimated as the square of the SD of p^* values computed from the images and effort in bootstrap samples for the 1989–2004 data. For each bootstrap replicate, the sample of capture histories was drawn first as described in the previous section. For each week, flights which obtained images of whales included in the capture history sample were included in the sample of survey flights for the week. Flights which obtained images of marked whales, none of which were included in the capture history sample, were excluded from the sample of survey flights, along with all images obtained on those flights. Among the included flights, if some marked whales photographed were and others were not included in the capture history sample, images of those that were not were excluded. A proportional number of images of unmarked whales chosen at random from the same flight were also excluded in order to keep the proportion marked for images from the flight unchanged. The remaining flights to make up the correct total number of flights for the week were sampled, with replacement, from the flights not already included or excluded, i.e. flights in 2003 and 2004 during which no usable photographs of marked whales were obtained and all flights near Point Barrow during the 1989–92 and 1994 surveys.

Once the sample of flights for each bootstrap replicate was defined, the factor representing the extra effort expended to photograph cow-calf and cow-yearling pairs was computed from the images obtained on the sampled flights as described above and used instead of 1.46. A bootstrap value for calves' extra time at the surface was used instead of 1.71. Then p^* was computed from equation (7) using these bootstrap values and the images of adequate quality and hours of effort from the sampled flights.

Using covariates to account for heterogeneity in capture probabilities

The covariates considered to model differences in capture probabilities among whales were

- *ib* best identifiability score in any of the four zones (b midback, r rostrum, f fluke, l lower back);
- *brfl* zone that defined the whale as marked;
- *zib* best identifiability score in the zone that defined the whale as marked;
- *zqb* best quality score in the zone that defined the whale as marked;
- *nz* number of zones with marks;
- *photos* maximum number of acceptable quality photos of the whale per sampling occasion.

These covariates were considered singly, and all possible pairs were considered. Various codings for each covariate were considered. Covariates were coded to values between 0 and 1 to avoid the need for standardisation within Program MARK. After initial exploratory analyses, we considered only three-occasion models for the 2003–05 data, with recapture probability the same as initial capture probability on each sampling occasion after the first, i.e. $c(t) = p(t)$, t = 2, 3. Zeh *et al.* (2002) noted that the assumption $c(t) = p(t)$ is appropriate for photo-identification data because the animals are not physically captured and there is no reason to suppose that the act of photographing a whale should make it more or less likely to be photographed on another occasion as might happen with captured animals. Both linear and logit models were considered. When it was possible to hypothesise which covariate values were expected to lead to higher capture probabilities, the covariate was coded so that its coefficient would likely be positive if the hypothesis was correct. E.g. both *ib* and *zib* were coded with M– = 0, M+ = 0.1, H– = 0.2 and H+ = 0.3 or with M (– or +) = 0 and H (– or +) = 1.

Initial exploratory analyses included attempts to model capture probability as a function of hours of photographic survey effort instead of allowing a different model intercept for each sampling occasion t. These were unsuccessful because of differences in the surveys not reflected in hours of effort. The 2003 survey covered the early part of the migration, when young unmarked whales predominate, more thoroughly than the 2004 survey. Consequently fewer marked whales per hour of effort were captured in 2003 than in 2004. The Sp2005 survey, which accounted for over 80% of the 2005 captures, targeted marked whales. However, high winds reduced the quality of the photos (Koski *et al.*, 2007). Since there were relatively few usable photos, the number of marked whales captured per hour of effort in 2005 was low. Thus all models discussed below include a different intercept for each t.

A covariate coding or a pair of covariates was rejected if its use resulted in a failure by Program MARK to fit the model successfully. In some cases, MARK provided error messages indicating that the model could not be fit. These included 'no numerical convergence', 'numerical convergence suspect', 'beta number x is a singular value' and 'error number x from VA09AD optimisation routine' with x an integer indicating the offending parameter or error. For example, when *nz* was coded 1 = 0.1, 2 = 0.2, 3 = 0.3 and 4 = 0.4 there was no numerical convergence. In other cases, MARK provided no message indicating problems in fitting the model, but output values provided a clear indication of failure. Such output values included SE = 0 for most or all of the estimated parameters, BIC values more than 300 times as large as those from successful fits and estimates N^m smaller than the number of marked whales with capture histories in the data. For example, when *photos* was coded 1 = 0.1, 2 = 0.2, 3 = 0.3, 4 = 0.4 and >4 = 0.5 MARK provided no error message and reported BIC = 955.8, but all parameter estimates had SE = 0.

If none of these obvious failures occurred, BIC and CV(N^m) were used to evaluate covariate codings and models. BIC = $-2\ log(L) + n_{par}\ log(n)$, where L is the likelihood of the model for capture probability, n_{par} the number of parameters and n the sample size. MARK computes n as (number of sampling occasions) × (number of marked whales providing capture histories). When no covariates were used, $n_{par} = 3$ since the model included only the intercept parameter for each t. Each coding for each covariate required only a single parameter for the covariate, so $n_{par} = 4$ if a single covariate was used and $n_{par} = 5$ if a pair of covariates was used. CV(N^m) evaluates the additional parameter N^m. For each covariate, it was possible to find at least one coding producing BIC ≤ 973.1 and CV(N^m) ≤ 0.2707. These 'best' codings all came from linear models, so logit models were not considered further. In cases where one coding was better in terms of BIC and another better in terms of CV(N^m), results are reported for both if BIC ≤ 973.1 and CV(N^m) ≤ 0.2707.

Computing confidence intervals

Buckland (1992) was followed in using the method of Burnham *et al*. (1987) to compute confidence intervals (CI). For example, a 95% CI for N is

$$(N / C,\ N \times C), \text{ where } C = \exp\left[1.96 \sqrt{\log_e (1 + V(N) / N^2)}\right] \quad (9)$$

The percentiles of sorted bootstrap values also provide confidence limits (Buckland and Garthwaite, 1991).

RESULTS

The number of images in the Bowhead Whale Photography Database, the number suitable for use in estimating proportion marked and the number of marked whales from the photographic studies in 1989–92, 1994 and 2003–05 are shown in Table 1 by year. For each of the years 2003–05 used in the capture-recapture analyses in this paper, the number of marked whales identified for the first time in each year and the recaptures are also shown. The analogous 1984–87 data are shown in Table 2. Table 2 is slightly more complicated than Table 1. In Table 1, 2003 is the first year for both the modified Petersen estimate and the Model M_t estimate. In Table 2, 1985 is the first year for the modified Petersen estimate while 1984 is the first year for the Model M_t estimate, so for the latter estimate both 1985 and 1986 have recaptures of whales captured in 1984.

For 2003–05, as shown in Table 1, the method of data screening used in Zeh *et al*. (2000; 2002) produced a sample with $n_1 = 150$ marked whales captured in 2003, $n_2 = 210$ in 2004 and $n_3 = 66$ in 2005, representing 412 different marked whales with capture histories for 2003–05. Among these histories, $m_2 = 9$ whales were recaptured in 2004 and $m_3 = 5$ whales in 2005. The 14 recaptures were of 13 different whales; only one whale was recaptured in both 2004 and 2005.

Different models for capture probabilities and the resulting estimates of the number of marked whales N^m were explored only using the 2003–05 data. Table 3 summarises N^m and its precision obtained from different models, both with and without a covariate characterising individual whales. The estimate N^m from the model without a covariate is given by equation (3). No bias corrections were used for N^m and its CV in Table 3. Equation (5) provided an estimate of bias for N^m given by equation (3), but estimates of bias for the models in Table 3 with a covariate were not available.

The models for capture probabilities in Table 3 were ranked by BIC, so the first model in the table explains capture probabilities best and the last model in the table is the worst based on that criterion. The best model involving each covariate singly was included. All were linear rather than logit models. All had BIC ≤ 973.1 and CV(N^m) ≤ 0.2707. The rank of CV(N^m) is also shown in Table 3, with 1 the best (lowest CV) and 10 the worst of the models shown. For all models in which a pair of covariates was considered, both BIC and CV(N^m) were the same or larger than for the best model involving one of the covariates singly. Consequently, no models with two covariates were included in Table 3.

Recall that covariates were coded such that a positive coefficient would represent the expected result. Coefficients were considered statistically significant (indicated by a Yes under Sig?) if they were significantly different from zero at the 5% level. The *ib* and *zib* coefficients in Table 3 indicate that more highly marked whales are more likely to be captured, though only the *zib* coefficient obtained when *zib* = 0 for moderately marked whales and *zib* = 1 for highly marked whales is statistically significant.

The model best in terms of BIC is worst in terms of CV(N^m), so it is clearly not the best model for the purpose of abundance estimation. That model and the third best model in terms of BIC involve the *photos* covariate. One would expect that having more than one photograph of a whale on a sampling occasion would make it easier to determine if that

Table 1

Numbers of images and marked whales by year and in total used in the 2004 abundance estimates. The 1989–2004 data are from surveys near Point Barrow during the spring migration. The 2005 data are from a spring survey in the Bering Sea and flights in early September near Point Barrow. In 2003–05 initial captures and recaptures that provided the data for estimating the number of marked whales in 2004 are also shown. The modified Petersen estimate used only 2003 and 2004 captures and recaptures while the Model M_t estimate used 2003–05 captures and recaptures. Initial captures and recaptures are not shown for years not used in the capture-recapture analyses to emphasise that matching to determine which whales captured in 2003–05 were first captured before 2003 has not yet been done.

	1989	1990	1991	1992	1994	2003	2004	2005	Total
Number of images	705	677	615	670	283	1,455	1,766	1,081	7,252
Number of images for computing p^*	419	409	402	384	156	967	1,295	0	4,032
Number of marked whales photographed	88	60	69	61	16	150	210	66	720
Initial captures	–	–	–	–	–	150	201	61	412
Recaptures	–	–	–	–	–	0	9	5	14

Table 2

Number of images and marked whales by year and in total used in the 1985 abundance estimates. The images for computing p^* are from surveys near Point Barrow during the spring migration. The numbers of initial captures and recaptures in each of the years used in estimating the number of marked whales in 1985 are also shown. The captures in the first year used in each capture-recapture analysis are treated as initial captures even though some of the whales were captured prior to that year. No captures before the first year used in the analysis are considered in defining whales as recaptured, e.g. eight whales captured in both 1984 and 1985 and four captured in both 1984 and 1986 are treated as initial captures for the modified Petersen estimate, which is based only on 1985 and 1986 capture-recapture data.

	1984	1985	1986	1987	Total
Number of images	1,156	2,788	1,450	403	5,797
Number of images for computing p^*	12	774	508	226	1,520
Number of marked whales photographed	63	254	162	24	503
Initial captures, modified Petersen estimate	–	254	143	–	397
Recaptures, modified Petersen estimate	–	0	19	–	19
Initial captures, Model M_t estimate	63	246	139	–	448
Recaptures, Model M_t estimate	0	8	23	–	31

whale was marked and hence to capture or recapture it. Both codings for *photos* shown in Table 3 were based on that expectation. Nevertheless, *photos* had a significant negative coefficient in both cases. This may be because this covariate represents a property of the sampling occasion rather than the whale. Among the whales captured on only one sampling occasion, 76% of the marked whales captured in Sp2005 had only one photo, compared to 41% to 47% on the other occasions. The negative coefficient apparently allowed for a better model for capture probabilities but resulted in estimates N^m with relatively poor precision.

One would also expect that having more zones marked would increase the probability of capture. However, the relatively large BIC and insignificant negative coefficient of *nz* in Table 3 suggest that it is not a useful covariate. It is less clear how *brfl* should be coded. Its position at the bottom of Table 3 suggests it is not a useful covariate. Its insignificant negative coefficient may reflect the relative ease of obtaining images of the midback compared to the lower back. Similarly, *zqb* does not appear to be a useful covariate; whale identifiability was a better predictor of capture probability than photo quality.

Model M_t with no covariates and N^m obtained from equation (3) had the lowest CV(N^m) and was second best in terms of BIC. Although Table 3 suggests that some of the covariates considered might contribute to a better model when matching of the 2003–05 data with the 1981–2000 data is complete and the full dataset is available, N^m from equation (3) provides the best estimate among those in Table 3. As shown in Table 3, $N^m = 3{,}909$ and SE(N^m) = 993. The bias of N^m from equation (5) is $b = 250$, so the bias-corrected estimate of the abundance of the marked population is 3,659. We correct for the estimated bias so that N based on the Model M_t estimate will be comparable to N based on the unbiased modified Petersen estimate.

The modified Petersen estimate based on the 2003 and 2004 captures and recaptures was 3,185 (SE = 906). It was estimated to be unbiased using an approximation due to Robson and Regier (1964) given by Seber (1982), p. 60. The estimated proportion of the bowhead population that is naturally marked to be used in equation (1) to obtain 2004 abundance estimates is $p^* = 0.28968$. This estimate was computed from equation (7) using data from the 1989–92, 1994, 2003 and 2004 surveys conducted near Point Barrow during spring migration. Using $V(p^*)$ given by equation (8), it was estimated that SE$(p^*) = 0.00707$. The corresponding values obtained from the 1984–87 data for 1985 abundance estimates are $p^* = 0.33937$ and SE$(p^*) = 0.01225$. Thus total 1+ abundance in 2004 is estimated as $N = 3{,}185/0.28968 = 10{,}995$ using the modified Petersen estimate and as $N = 3{,}659/0.28968 = 12{,}631$ using the Model M_t estimate. These values of N–with delta method CVs and confidence limits based on equations (2), (8) and (9) and the estimate v^* (Seber, 1982, p. 60) for the modified Petersen estimate or equation (4) for the Model M_t estimate–are shown in Table 4. The corresponding results for 1985 are also shown in

Table 3

Estimates N^m of the number of marked whales for various models for capture probabilities $p(t)$ and recapture probabilities $c(t)$ as a function of sampling occasion and whale-specific covariates (Huggins, 1989; 1991). For each sampling occasion t after the first, it is assumed that $c(t) = p(t)$.

Covariate	N^m	SE(N^m)	CV(N^m)	CV rank	BIC	ΔBIC	Coefficient + or – Sig?	Deviance
Photos 1, 2, >2 coded as 0.1, 0.2, 0.3	4,466	1,209	0.2707	10	955.6	0.0	– Yes	927.2
None	3,909	993	0.2540	1	966.9	11.3	N/A	945.5
Photos >1 versus 1 coded as 1 versus 0	4,128	1,066	0.2582	8	967.9	12.3	– Yes	939.4
zib H versus M coded as 1=H– or H+, 0=M– or M+	4,111	1,063	0.2586	9	968.2	12.6	+ Yes	939.7
ib H versus M coded as 1=H– or H+, 0=M– or M+	4,031	1,032	0.2560	7	969.9	14.3	+ No	941.4
zib M–, M+, H–, H+ coded as 0.0, 0.1, 0.2, 0.3	3,991	1,019	0.2553	4	971.0	15.4	+ No	942.5
nz 1, 2, >2 coded as 0.0, 0.1, 0.2	4,007	1,025	0.2558	6	971.5	15.9	– No	943.0
ib M–, M+, H–, H+ coded as 0.0, 0.1, 0.2, 0.3	3,969	1,012	0.2550	3	971.9	16.3	+ No	943.4
zqb 3, 2–, 2+, 1–, 1+ coded as 0.0, 0.1, 0.2, 0.3, 0.4	3,973	1,015	0.2555	5	972.5	16.9	– No	944.1
brfl b, r, f, 1 coded as 0.1, 0.2, 0.3, 0.4	3,950	1,006	0.2547	2	973.1	17.5	– No	944.6

Table 4

Estimates N of B-C-B bowhead 1+ abundance in 1985 and 2004 with CVs and confidence limits based on the delta method or bootstrap. Estimates that include data from two years are based on the modified Petersen estimate of the number of marked whales. Estimates that include data from three years are based on the Model M_t estimate of the number of marked whales. Confidence limits based on the delta method CV are computed using equation (9). Bootstrap percentile confidence limits are shown when the CV is based on the bootstrap SE. Lower and Upper denote the ends of a 95% confidence interval in either case.

			Confidence limits		
Estimate	N	CV	Lower	Upper	Lower 5th percentile
1985–86 estimate, delta method	6,120	0.1997	4,150	9,020	4,420
1984–86 estimate, delta method	6,129	0.1695	4,410	8,520	4,650
2003–04 estimate, delta method	10,995	0.2855	6,400	19,000	6,900
2003–05 estimate, delta method	12,631	0.2727	7,500	21,300	8,100
2003–05 estimate, bootstrap	12,631	0.2442	7,900	19,700	8,400

Table 5

Means and standard deviations (SD) over 2,000 bootstrap replicates for key parameter estimates used in computing the Table 4 estimate of B-C-B bowhead 1+ abundance in 2004 based on Model M_t with CV and confidence limits estimated via the bootstrap. The bootstrap CV of N is SD(N)/N with N the estimate and SD(N) from this table. The confidence limits in Table 4 are from percentiles of the sorted bootstrap replicate values N.

Parameter	N	N^m	b	p^*
Estimate	12,631	3,909	250	0.28968
Mean over bootstrap replicate values	12,307	3,880	271	0.29345
SD over bootstrap replicate values	3,084	1,081	189	0.00715

Table 4. For both 1985 and 2004, the addition of a third year of data improved precision as measured by the delta method CVs.

Because the delta method estimate of the variance of N given by equation (2) and $V(N^m)$ and $V(p^*)$ given by equations (4) and (8) are only rough estimates based on assumptions that may not hold, variances for N, N^m and p^* were also obtained directly via the bootstrap procedure described above for the estimate of abundance in 2004 based on Model M_t. In order to obtain reliable percentile bootstrap confidence limits, *nboot* = 2,000 bootstrap replicates were used (Buckland and Garthwaite, 1991; da Silva *et al.*, 2000). The means and SDs over the bootstrap replicate values for N, N^m, bias b from equation (5) and p^* from equation (7) are shown in Table 5. Recall that in the absence of bias, the mean over the bootstrap replicate values should be close to the corresponding estimate and the SD gives the SE of the estimate. The resulting bootstrap CV for N and percentile bootstrap confidence limits are given in Table 4.

DISCUSSION

The estimates of total 1+ abundance and measures of their precision in Table 4 are consistent with our expectations concerning bowhead abundance based on completely independent ice-based survey data (George *et al.*, 2004; Zeh and Punt, 2005). George *et al.* (2004) estimated 2001 abundance as 10,470 with SE = 1,351 (CV = 0.129) and 95% CI 8,100 to 13,500. They estimated the annual rate of increase for the population from 1978 to 2001 as 3.4% (95% CI 1.7% to 5%). The estimate of Zeh and Punt (2005) was 10,545 (CV = 0.128) for 2001. If the trend line fit by George *et al.* (2004) is projected forward, the expected abundance in 2004 is 11,811; the point on the trend line for 1985 is 6,295. The 2004 abundance estimates in Table 4 are about 800 whales away from 11,811 and their average is 11,813. The 1985 estimates in Table 4 are within 175 whales of the trend line value. In other words, all the estimates N in Table 4 are considerably closer to the values expected based on the ice-based surveys than the CVs in Table 4 indicate they might be.

The CVs in Table 4 are higher than CVs for the 1988, 1993 and 2001 abundance estimates from ice-based surveys in Table 4 of Zeh and Punt (2005). Those ice-based surveys had more comprehensive acoustic monitoring of whales that passed too far offshore to be seen than the earlier surveys, leading to improved precision. However, our Table 4 CVs are comparable to or lower than their Table 4 CVs for the ice-based survey estimates obtained before 1988. E.g. the 1985 estimate in Table 4 of Zeh and Punt (2005) has a CV of 0.253, and the remaining pre-1988 CVs range from 0.215 to 0.345. The 1985 estimate based on Model M_t in our Table 4 has a CV of 0.1695.

The CVs in our Table 4 that are lower than the pre-1988 ice-based survey CVs are those of the 1985 estimates N. This is because, as can be seen by comparing Table 2 with Table 1, there were more initial captures and recaptures for both the Petersen estimate and the Model M_t estimate N^m for 1985 than for 2004. There were no summer surveys in 2003–05 and only one brief September survey. This contrasts with 1984–86, when summer and autumn photographic surveys in the Beaufort Sea in addition to spring surveys were conducted. The 1985 surveys were particularly comprehensive. Images from these summer and autumn surveys provided many of the initial captures and recaptures of marked whales for the 1985 estimates. There were many fewer images available from spring surveys near Point Barrow for computing p^* for the 1985 estimates, but this had relatively little impact on their precision.

Since the 1985 estimates in Table 4 are the most precise, they are the most useful for comparing the estimates based on the modified Petersen estimate computed from two years of capture-recapture data with those from Model M_t based on three years of capture-recapture data. This comparison is of interest as a check on whether the closed population assumption on which both estimates are based is acceptable over three years for bowheads. The very close agreement between the two values of N suggests that it is.

Recall that the bootstrap analysis was based on the assumption that the true number of marked whales in 2004 was 3,659. This is $N^m = 3{,}909$ from Model M_t, corrected for bias $b = 250$. The corresponding means over the bootstrap replicate values in Table 5 are $N^m = 3{,}880$ and $b = 271$, both quite close to the expected values. SD(b) in Table 5 indicates high variability of the estimated bias over the bootstrap replicates; b is always estimated to be positive as expected, ranging from 51 to 2,279. The mean of p^* over the bootstrap replicate values is 0.29345, close to the estimate $p^* = 0.28968$. The mean over the bootstrap replicate values of N in Table 5 is 12,307, very close to (3,880 – 271) / 0.29345 = 12,299 and reasonably close to the estimate $N = 12{,}631$ in Table 4. None of the Table 5 means suggest problems with the bootstrap analysis. It is interesting that the median of the bootstrap replicate values of N is 11,767. This is very close to the value of 11,811 in 2004 predicted from the trend in the ice-based survey estimates. From Table 5 the estimate SE(N) = 3,084 is obtained. It is similar to the delta method SE of 3,444 computed from equation (2). Taking the above discussion into account, we recommend using the bootstrap CV and percentile method confidence limits in Table 4 for the estimate $N = 12{,}631$ of total 1+ abundance in 2004.

Using a model for heterogeneity in capture probabilities under which whales highly marked on the midback were more likely to be captured than those only moderately marked, da Silva *et al.* (2000) showed via simulation that a capture-recapture estimate of abundance that does not account for heterogeneity in capture probabilities when present can be slightly negatively biased. An estimate that accounts for the heterogeneity may be slightly positively biased. However, the biases were small compared to the SE of the estimates. The estimate that accounted for heterogeneity was slightly more precise. The simulated data from which these results were obtained had many more captures and recaptures than even the 1984–86 data shown in Table 2.

The estimates N^m in Table 3 based on assuming and attempting to account for heterogeneity in capture probabilities are somewhat larger than the estimate that assumes homogeneity. This is consistent with the bias results of da Silva *et al.* (2000). However, the estimates that account for heterogeneity are slightly less precise than the one that does not. Recall that da-Silva *et al.* (2007) showed that accounting for heterogeneity in capture probabilities between moderately and highly marked whales improved precision of the estimate of annual survival probability using a much larger dataset. More captures and recaptures than are available in the 2003–05 dataset are needed to assess covariate effects on capture probabilities and abundance estimates. It may be necessary to use an open population model (da-Silva *et al.*, 2007; Schweder *et al.*, 2010) and many more than three years of data to obtain an adequate number of captures and recaptures.

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A simulation-based approach to evaluating population structure in non-equilibrial populations

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ABSTRACT

The standard null model of panmixia used to test for population subdivision is based on a set of assumptions that can be violated given recent events likely to result in non-equilibrial genetic composition coupled with the complex life histories of many species. Bowhead whales (*Balaena mysticetus*) represent such a species. Bowhead whales also have a well-documented history of severe commercial harvest in the recent past which would be expected to leave a population out of genetic equilibrium. They also have a very long life span, overlapping generations, and age and sex-structured migrations. In addition, samples come from whales killed in a hunt known to be non-random with respect to size at different whaling villages. Sampling of such a population could lead to erroneous conclusions regarding population structure, which could have real consequences for aboriginal whaling. To better interpret the results of standard population genetic analyses, an individual-based model of bowhead whale population dynamics and genetics was created using the R package *rmetasim*. The model re-created as closely as possible all aspects of the demography, genetics, and whaling history of bowhead whales. Simulated datasets were generated by sampling from the simulated population in a way that matched the age, sex and geographic distribution of empirically collected samples. The empirical bowhead datasets were compared to null distributions generated from the simulated datasets for a variety of genetic analyses. The analysis indicates that the empirical genetic data sampled from the Bering-Chukchi-Beaufort (BCB) stock of bowhead whales are more consistent with the model of a population with the same whaling history and demographic composition as BCB whales than they are with a single, randomly-mating population in genetic equilibrium under a standard Wright-Fisher model. Additionally, it was demonstrated that by failing to account for the unique features of the population dynamics of the species, standard tests of genetic differentiation based on panmixia may produce misleading results. The approach outlined will likely prove useful for evaluating population structure in other species likely to be out of equilibrium.

KEYWORDS: WHALING – ABORIGINAL; WHALING – HISTORICAL; ARCTIC; MANAGEMENT; MODELLING; AGE DISTRIBUTION; GENETICS; BOWHEAD WHALE; BERING SEA; CHUKCHI SEA; BEAUFORT SEA; NORTHERN HEMISPHERE

INTRODUCTION

The Wright-Fisher model of population genetics (Fisher, 1930; Wright, 1931) forms the basis of the null hypotheses describing no population structure for most genetic analyses. Under this model, the hypothetical single population is assumed to be at genetic equilibrium (the rate of genetic drift equals that of mutation), is panmictic (every individual has an equal chance of mating with every other individual), has non-overlapping generations, and experiences no immigration or emigration. While not an explicit assumption of the Wright-Fisher model, most studies also assume that samples have been collected at random and thus accurately represent the genetic frequency distribution in the population at large.

In most real populations, one or more of these assumptions are often not met, potentially leading to problems in interpreting the results of standard genetic tests. Bowhead whales (*Balaena mysticetus*) represent a good example of such a population. In the late 19th and early 20th centuries, bowhead numbers were very rapidly reduced by whaling followed by a recovery in only two and a half generations (Bockstoce, 1986; Bockstoce and Burns, 1993; Brandon and Wade, 2006), guaranteeing the population or populations to be strongly out of genetic equilibrium. Sampling is also not random. Most samples are from animals killed by Alaskan native subsistence hunters, with some villages preferring to kill large (and hence older) whales, while others prefer smaller (younger) whales (Noongwook *et al.*, 2007; Suydam and George, 2004). Further, hunting primarily occurs during migration and often in short time periods, and whales are known to segregate by size and reproductive condition during migration (Angliss *et al.*, 1995). Thus, samples of bowhead whales stratified by sampling location could represent different demographic components of the population.

Results of previous analyses of bowhead whales migrating past Barrow, Alaska have been interpreted to suggest that more than one stock may exist in the Beaufort-Chukchi-Bering (BCB) Sea (Jorde *et al.*, 2007). However, these results could also reflect age stratification of migration. Bowhead whales can live for over 100 years (George *et al.*, 1999), thus it is likely that some whales that were born prior to the end of commercial whaling are still alive today. Their genes represent frequencies of the unexploited population, while those of recent cohorts represent the smaller, yet still diverse, gene pool that survived commercial whaling. These differences between genetic frequencies of cohorts resulting from non-equilibrial dynamics are called the Generational Gene Shift (GGS) hypothesis. In addition to GGS, it has been demonstrated that both non-random sampling as well as sampling from age-structured populations can lead to results

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that differ significantly from those expected from a panmictic population (Waples, 1990; Waples and Teel, 1990; Waples and Yokota, 2007). It is possible that all of these factors are present in the bowhead whale data.

In this paper, an individual-based simulation is described that attempts to both capture the population dynamics that lead to GGS and non-equilibrial genetic samples, and match the non-random empirical samples as closely as possible with respect to birth year and sex. The aim is to generate an alternative to the standard null distribution that will allow testing for population structure without assuming equilibrium conditions, panmixia, or random sampling. The analyses conducted include evaluations of Hardy-Weinberg equilibrium and measures of population structure (F_{st}, χ^2, and Φ_{st}) using strata considered possible for bowhead whales. A single population was simulated and evaluated the likelihood of obtaining observed results without invoking a multiple-stock scenario. Issues with applying the approach to multiple stocks are addressed in the discussion.

METHODS

The simulation is based on the *rmetasim* package (version 1.1.008 – Strand, 2002), run in the R statistical environment (version 2.4.1 – R Development Core Team, 2006). *Rmetasim* is a library of functions that performs individual-based population genetic simulations. Each individual has a multi-locus genotype and a mitochondrial DNA (mtDNA) haplotype. Individuals are structured demographically with a stage-based matrix population model (see 'Demography' section below; Caswell, 2001). At each time step individuals are randomly assigned their births, stage transitions and deaths according to the rates specified in the matrix model (used as distributions to incorporate demographic stochasticity). Offspring genotypes are determined by parental genotypes assuming random mating, independently segregating alleles, and neutrality of markers. For all parameters not explicitly defined here the program default values were used.

During the simulation, a set of individuals are selected to mimic the 1,099 BCB bowhead whales in the recorded harvest between 1937 and 2006 (Braund *et al.*, 1988; Suydam and George, 2004). While the analysis of Braund *et al.* (1988) cautioned that 'these data represent minimum numbers' of landed whales and some landed whales likely went unrecorded, harvest numbers were relatively low in the 1930s-60s and in many years fewer than 10 were taken, so the overall number of missed harvests through this period should be very small. Harvests increased significantly in the 1970s, but it is unlikely that any landed whales went unrecorded, due to careful monitoring by NOAA; however a few struck but lost whales may not have been reported during this period. Potential mortalities from these events were not simulated.

During the last 25 years (and predominantly during the last decade), tissue samples were collected both from whales killed during Alaskan subsistence hunts as well as from biopsies of live whales (O'Hara *et al.*, 1998; Suydam and George, 2004). As noted above, this sampling was not random, due to hunting preferences, biopsy opportunities, and important aspects of bowhead whale migratory behaviour and distribution. A variety of life history data was also collected from many of the whales killed during the hunts, some of which were used to characterise the demographic composition of the simulated population as described below.

Demography

Rmetasim version 1.1.008 incorporates density dependent population growth, as described in Martien (2006). Density dependence is implemented by interpolating between matrices that represent survival and reproduction rates at carrying capacity and near zero population density. Although this version of *rmetasim* only allows for linear interpolation between these matrices, the program was modified to allow for non-linear density dependence. The value of a given element (the probability of transition between stages) of the life history matrix in year *t* is given by:

$$x_t = x_0 + (x_{\max} - x_0)\left(1 - \left(\frac{N_t}{K}\right)^z\right)$$

where:

x_t is the value of the element in year *t*
x_0 is the value of the element at carrying capacity
$x_{\max}$ is the maximum value of the element (near zero population size)
N_t is the size of the population at the start of year *t*
K is the carrying capacity of the population
z is the shape parameter.

The demographic matrices used for this study are for a stage-based model with the following 7 stages: 5 juvenile stages (J1–J5), adult females (F), and adult males (M) (Ripley *et al.*, 2006). Juvenile stages were added to assure that individuals did not remain or advance through being juveniles in a biologically unrealistic way while allowing the model to avoid having a different stage for all 120 ages (most of which have identical probabilities of birth and death). Stage transition probabilities were calculated using the fixed stage duration method (Caswell, 2001). The life history parameter estimates presented in Brandon and Wade (2006) were used to develop two matrices, one for which the intrinsic population growth rate $\lambda = 1.00$, the other for which $\lambda = 1.042$ (Table 1). These matrices were used to represent vital rates (age at sexual maturity, juvenile and adult survival, timing of transition from juvenile to adult survival rates, and

Table 1

Demographic parameters at carrying capacity (λ=1.00) and near zero population size (λ=1.042). For each stage, stage duration (T) and age-specific survival (σ) are used to calculate the matrix model parameters P (survival in stage) and G (stage transition probability) according to the fixed stage duration model (Caswell 2001; Ripley *et al.* 2006).

	λ=1.00				λ=1.042			
Stage	*T*	σ	*P*	*G*	*T*	σ	*P*	*G*
J 1	4	0.800	0.661	0.139	2	0.925	0.490	0.435
J 2	4	0.978	0.741	0.236	3	0.985	0.675	0.310
J 3	4	0.978	0.741	0.236	3	0.985	0.675	0.310
J 4	4	0.978	0.741	0.236	3	0.985	0.675	0.310
J 5	4	0.978	0.741	0.118	3	0.985	0.675	0.155
F	50	0.978	0.967	0.011	50	0.985	0.981	0.004
M	50	0.978	0.967	0.011	50	0.985	0.981	0.004

reproductive rates) at carrying capacity and near zero population size, respectively. z was set to 4, which is the posterior median from Brandon and Wade's (2006) backward projection model (referred to as '1848DD' in their paper).

Genetic initialisation and burn-in

The simulated populations were initialised using mitochondrial haplotype and microsatellite allele frequency distributions generated by the coalescent program *SIMCOAL* v2.1.2 (Laval and Excoffier, 2004). Initialising from a coalescent rather than with random allele and haplotype frequencies greatly reduced the number of generations required for the simulations to reach equilibrium (Martien *et al.*, 2009). In order to initialise *SIMCOAL*, the average effective population size (Ne) at carrying-capacity was estimated using *rmetasim*.

The relationship between a change in heterozygosity and effective population size is given by,

$$E\left[\frac{H_t}{H_0}\right] = \left(1 - \frac{1}{2N_e}\right)^{\frac{t}{g}}$$

where:

H_0 = initial heterozygosity
H_t = heterozygosity at time t
t = elapsed time in years
g = generation time

After rearranging the above and including a multiplier *(m)* chosen to start the simulation burn-in phase close to equilibrium, N_e was estimated as,

$$N_e = \frac{m}{2 \cdot \left(1 - \left(\frac{H_t}{H_0}\right)^{\frac{g}{t}}\right)}$$

A generation time (g) of 37 years was used, representing the average age of reproductive females (Taylor *et al.*, 2007). A value for m of 1.45 was empirically found to be satisfactory and was used in all simulations. N_e was estimated for mtDNA and microsatellites separately. For microsatellites, the above equation actually estimates $2N_e$, which is the value required by *SIMCOAL*. The average effective population size ($\tilde{N}_e$) used to initiate *SIMCOAL* was the harmonic mean of N_e from 20 *rmetasim* population projections at carrying capacity, each initialised with the same survival and reproduction matrices as in the full simulation, and lasting 4,000 years (t). The sample size generated by SIMCOAL was $\tilde{N}_e$ for the mtDNA sequences and the smaller of $\tilde{N}_e$ and 1,000 for the microsatellite loci.

Parameters for both mtDNA sequences and microsatellite loci were set to mimic the empirical data as closely as possible. The mtDNA sequence was specified to be 397bp, with a Ts:Tv of 10:1, and a mutation rate of 9.4×10^{-3} (LeDuc *et al.*, 2005; LeDuc *et al.*, 2008). For the microsatellites, two groups of loci were simulated representing 11 'original' loci which were typed from a variety of different cetaceans including bowhead whales, and 22 'new' loci which were screened from a CA-enriched library using bowhead whale samples. A detailed description of the development of these two sets of loci can be found in Givens *et al.* (2010) and Huebinger *et al.* (2006). Average mutation rates were set at 3.0×10^{-4} and 1.5×10^{-3} for the original and new loci respectively. Mutation parameters were tuned to produce diversity comparable to that observed in the empirical bowhead dataset, as has been done previously (Taylor *et al.*, 2000). The same mutation rates that were used in *rmetasim* were used in the *SIMCOAL* initialisations.

In order to ensure that the simulated populations were in equilibrium, a burn-in phase was conducted following initialisation. Previous examinations of the trajectories of the number of mtDNA haplotypes, microsatellite alleles, and heterozygosity in both markers indicated that 4,000 years was a sufficient amount of time to ensure that these values were relatively stable (Fig. 1). A sample of all markers was independently generated from *SIMCOAL* for each burn-in replicate.

Simulated whaling and sampling

For each burn-in replicate, multiple replicates of simulated harvest of whales designed to mimic the historical kill were conducted. The historical kill encompasses the commercial harvest and Russian and Alaskan subsistence catches from 1848 to 2006. The harvest data used in the model are the same data being used in the IWC Aboriginal Whaling Management Plan (IWC, 2003). In each year of a whaling replication, the first whales removed from the simulated populations were those included in the empirical genetic dataset. These consisted of whales for which biological samples and measurements were collected from the Alaskan subsistence catch (available from 1974 to 2006). For each sampled whale in the empirical dataset, an individual of the same age and gender was randomly selected from the simulated population. If the gender of the sampled whale was unknown, then it was randomly selected using the ratio of known-gender whales killed in that year. A 50:50 ratio was assumed if no known-gender whales were available in a particular year (empirical sex ratio for all whales harvested from 1974–2006 for which sex was identified was 487(F):468 (M), i.e. very close to parity).

In order to match the age of simulated individuals to those of harvested whales, the age of each harvested whale was determined in a hierarchical fashion based on the quality of data available. Many of the whales included in the empirical dataset were aged and had estimates of standard errors from one of the methods given in Lubetkin and Zeh (2006). For these whales, ages were randomly sampled from a normal distribution and rounded to the nearest whole age.

For whales that were not aged, a Classification and Regression Tree (CART – Breiman *et al.*, 1984), as implemented in the R package *rpart* v3.1–34 (Therneau and Atkinson, 2006), was used to estimate the age bin to which they belonged based on morphological characteristics (gender, body length, baleen length, anterior flipper length, peduncle girth, and length of the peduncle white patch). The CART tree was created from 177 known-aged samples using ten age bins (Fig. 2), which were selected from an exploratory series of CART regression trees. Bins were selected probabilistically based on the distribution of bin membership from the training data in the node to which an unknown sample was assigned (Table 2). The age for each sample was then chosen at random from all individuals in the simulated population within the chosen age bin. If the

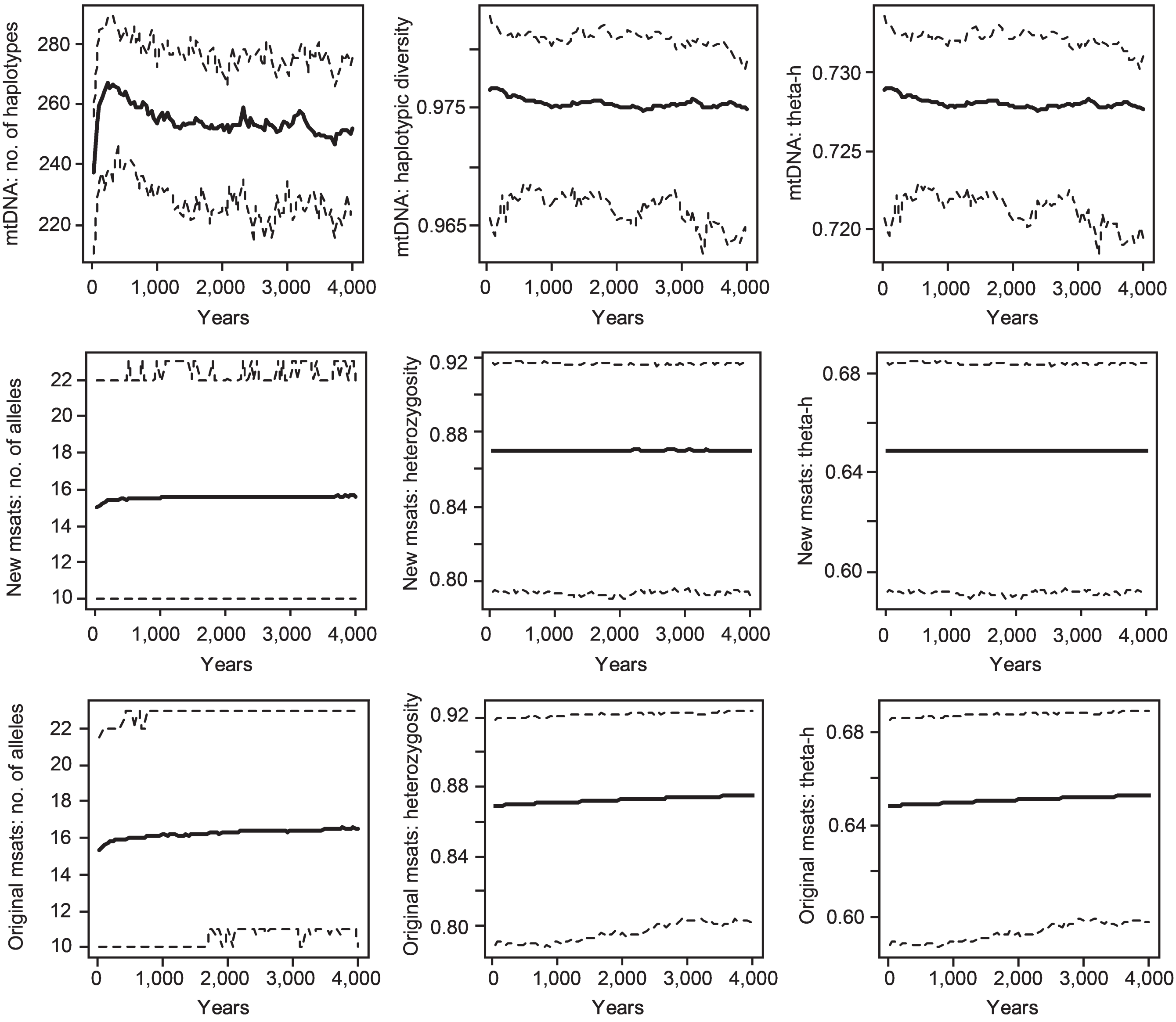


Fig. 1. Mean values (solid lines) and 95-percentiles (dashed lines) for number of haplotypes (mtDNA) and alleles (microsatellites), heterozygosity, and Theta (θ)-h during 50 burn-ins.

morphometric data necessary to classify a sample at a particular split in the CART tree was missing, surrogate variables were used if available. If there was insufficient morphometric data for the CART algorithm, then an age was chosen at random from the simulated population. In all cases, the age distribution being chosen from was that of the simulated population immediately following burn-in, which was considered a stable age distribution.

In some cases, no individuals in the simulated population were found to match the age and gender of a harvested whale exactly. When this occurred, all individuals within a progressively increasing age window around the whale under consideration were examined. In each age window, probabilities were assigned to each individual based on their gender and the size of the window. The probability of choosing an individual of the same sex as the sample under consideration ranged from one for an age window of zero (all simulated individuals were of the same age as the sampled whale) to 0.5 when all individuals in the population were considered. The probability of choosing an individual of the opposite sex was one minus this value. If no individuals in the window had probabilities greater than a randomly chosen value, then the age window was increased and the new set of individuals were reconsidered. In this manner, all simulated individuals were matched to a unique sampled whale.

Following the removal of any biologically sampled whales, the un-sampled portion of the recorded catch in that year was then removed from the simulated populations. In all cases, whaling was restricted to individuals older than one year. The genetic data of the simulated whales selected to be killed each year were saved if genetic data were available for their matched harvested counterparts. If biopsies were collected in a given year, the genetic data of an equivalent number of randomly selected simulated individuals still alive in the population were also saved. Following a simulated year of whaling and sampling, the population was projected forward one year and the whaling for the next year would occur as described above.

In order to ensure that the abundance trajectories from the simulations were similar to those of historical trend analyses (Brandon and Wade, 2006), two abundance ‘gates’ were

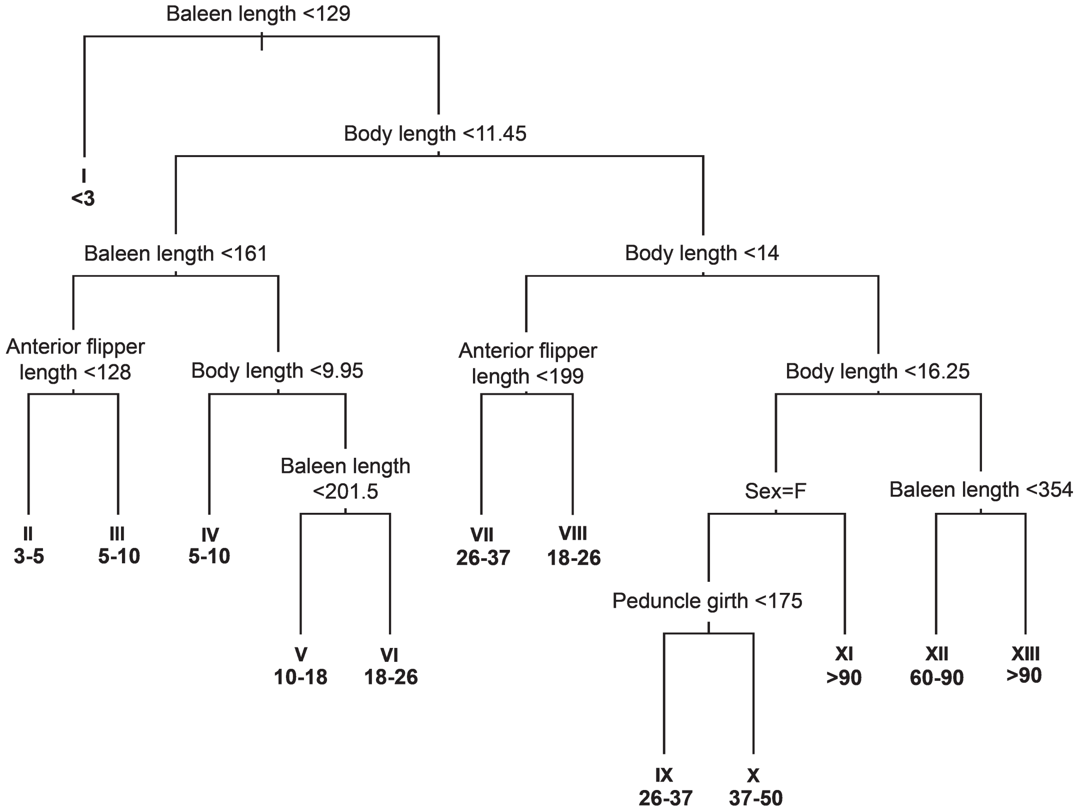


Fig. 2. CART tree with primary splits used for age estimation. Cases meeting the criteria at a node are sent down the left. Roman numerals are leaf identifiers corresponding to rows in Table 2. Values below leaf identifiers are estimated age bin of leaf.

established that replicates had to pass through. Replicates that had trajectories outside of the 99% confidence intervals of the first and last years of estimated population abundance (1978 and 2001), including those that went extinct, were discarded. For each of 50 burn-in replicates, the first ten successful whaling replicates were saved, producing a total of 500 replicates. The final output of each replicate was a simulated genetic sample representing the demographic composition of the empirical harvest sample and all individuals surviving in each of the simulated populations. Annual population abundances were saved for comparison with trajectories from historical trend analyses (Brandon and Wade, 2006).

Introduction of errors

Microsatellite datasets inevitably contain genotyping errors. Error rates reported in the literature range from 0.1% to 48% (Morin *et al.*, 2009). To examine the effect of genotyping errors on the analytical methods applied to the bowhead whale dataset, genotyping errors were introduced into the simulated dataset. By comparing genotypes for duplicate samples included in the original empirical dataset, Morin *et al.* (2009), estimated an overall error rate of 0.01 for the bowhead whale microsatellite data. Of these, 40% were apparent cases of allelic dropout, i.e. the individuals were scored as homozygotes in one genotyping attempt and as heterozygotes in another.

Table 2

Probability of assignment to age bins for leaves of the CART tree in Fig. 2. Bins are inclusive of the lower boundary.

	Age bin									
Leaf	< 3	3-5	5-10	10-18	18-26	26-37	37-50	50-60	60-90	≥ 90
I	0.84	0.11	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00
II	0.00	0.86	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00
III	0.21	0.21	0.36	0.21	0.00	0.00	0.00	0.00	0.00	0.00
IV	0.00	0.06	0.88	0.00	0.00	0.00	0.06	0.00	0.00	0.00
V	0.00	0.00	0.36	0.57	0.00	0.00	0.07	0.00	0.00	0.00
VI	0.00	0.00	0.33	0.00	0.50	0.17	0.00	0.00	0.00	0.00
VII	0.00	0.00	0.00	0.33	0.17	0.50	0.00	0.00	0.00	0.00
VIII	0.00	0.00	0.00	0.13	0.53	0.27	0.00	0.00	0.07	0.00
IX	0.00	0.00	0.00	0.00	0.00	0.53	0.29	0.18	0.00	0.00
X	0.00	0.00	0.00	0.00	0.00	0.14	0.43	0.29	0.00	0.14
XI	0.00	0.00	0.00	0.11	0.00	0.00	0.22	0.11	0.22	0.33
XII	0.00	0.00	0.00	0.00	0.00	0.11	0.11	0.11	0.67	0.00
XIII	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.17	0.17	0.50

The number of genotyping errors introduced into a simulated dataset was determined by drawing a random deviate from a binomial distribution given the overall error rate (0.01) and the number of alleles in the dataset (18,314). The alleles to which the errors were applied were chosen at random from the entire dataset. When an error occurred, it had a 0.4 probability of being an instance of allelic dropout, in which case the allele in question was set equal to the other allele the individual possessed at that locus, making the individual homozygous at that locus. Otherwise, the allele was replaced by a different allele chosen at random from the allele frequency distribution for the appropriate locus.

Genetic analyses

A suite of standard population genetic algorithms were used to analyse both the genetic samples from the simulations as well as the matching empirical genetic data. *Genepop* v3.3 (Raymond and Rousset, 1995) was used to run the Hardy-Weinberg test of heterozygote deficiency on the 213 samples from Barrow using both the 11 'original' and 22 'new' loci. For this test, an MCMC burn-in of 30,000 iterations was used, with a final chain length of 10,000 and batch size of 100. The Hardy-Weinberg disequilibrium was also calculated across all loci using Fisher's method (Ryman and Jorde, 2001).

To examine the effects of GGS, several stratification schemes were used. In the first, in order to examine the magnitude of extreme GGS, samples were stratified into three age cohorts based on the year of catch and the estimated ages of the samples (George *et al.*, 1999; Lubetkin and Zeh, 2006; Rosa *et al.*, 2004). The first stratum was composed of animals born prior to 1950, encompassing animals born during the low point in the population's history (prior to 1918). The second stratum, those born 1950–79, represented animals born during the rapid growth phase. The final stratum was those born after 1979, representing animals born recently during the period when most of the samples were taken.

Additionally, to replicate actual analyses that have been conducted previously, stratifications based on sampling site (Barrow versus St. Lawrence Island) were also examined, as well as those based on season of collection (spring or autumn) at each of those sites. Fig. 3 shows the distribution of body lengths of samples from each of these three stratifications.

For the village and season comparative tests, all empirical samples were used. For the tests comparing cohorts only whales that were actually aged were used in order to reduce the large uncertainties that are introduced when using length to approximate age.

The F_{st} for mtDNA and microsatellites was calculated following Weir and Cockerham (1984), and χ^2 for both sets of markers was calculated following Roff and Bentzen (1989). The AMOVA Φ_{st} metric was calculated for mtDNA data using the R package *ade4* (Chessel *et al.*, 2004).

For each test, the empirical test statistic was compared to null distributions generated by 500 replicates of standard permutation methods (representing a null model of panmixia) and the distribution generated by the simulation. For both comparisons, p-values reported in this paper refer to the proportion of replicates with test-statistics equalling or exceeding the value obtained from the empirical data using the same (matched) samples; p-values ≤0.05 were considered to indicate empirical results inconsistent with the model.

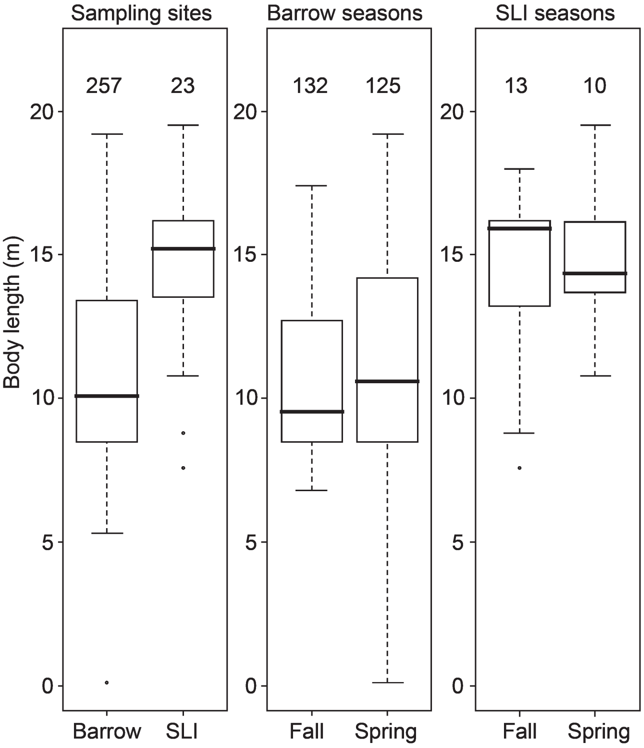


Fig. 3. Distribution of body length of samples stratified by sampling site, and season of collection within each site. Numbers above each distribution indicate sample size. 'SLI' = St. Lawrence Island.

To evaluate the relative support for the panmixia and simulation null models, the ratio between the likelihoods of each model given the empirical data for each pairwise test conducted was calculated. In order to estimate likelihoods, a Gamma distribution (chosen because of its' relative flexibility) was fitted to the distribution of test statistics from replicates in each null model. As both F_{st} and Φ_{st} can have negative values, each null distribution was rescaled to have a minimum value of zero prior to fitting the gamma. Using the estimated parameters of the gamma distribution the likelihood of the observed test statistic plus the fixed rescaling constant was then calculated. Finally, the log of likelihood(data|panmixia)/likelihood(data|simulation) was calculated. Log-likelihood ratios less than one support the simulation model, while those greater than one support the panmixia model.

RESULTS

Simulation diagnostics

The population trajectories for the 500 replicates are given in Fig. 4. At the nadir, the median abundance was 1,197 with a range of 806–1,608. Four percent of the replicates ended with an abundance greater than 12,000 in 2006. Fig. 5 shows the distribution of ages within each stage at the end of burn-in (a) and at the end of the simulation (b). The mean age of all reproductive individuals was 48 (95-percentile = 13–129) at the end of burn-in and 33 (95-percentile = 12–76) at the end of the simulation. At the end of the simulation,

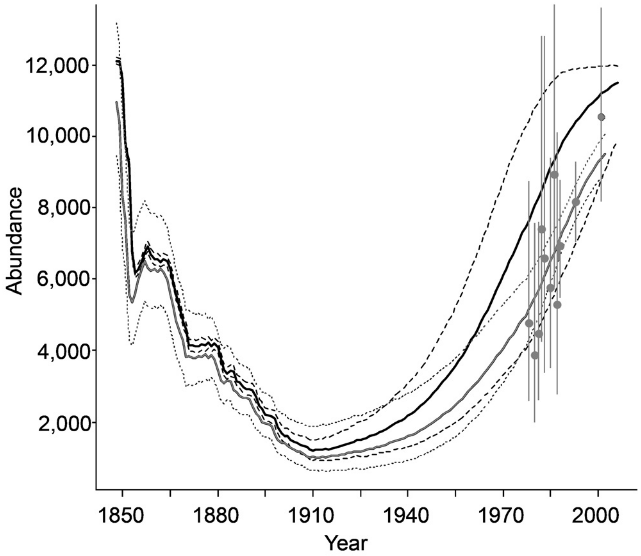


Fig. 4. Median population abundance for 500 simulation replicates from 1848 to 2006 shown in black. Dashed lines bound the 90-percentile of abundance in each year. Grey lines and points indicate trajectory and median abundance estimates from surveys with 90% CIs reproduced from Brandon and Wade (2006).

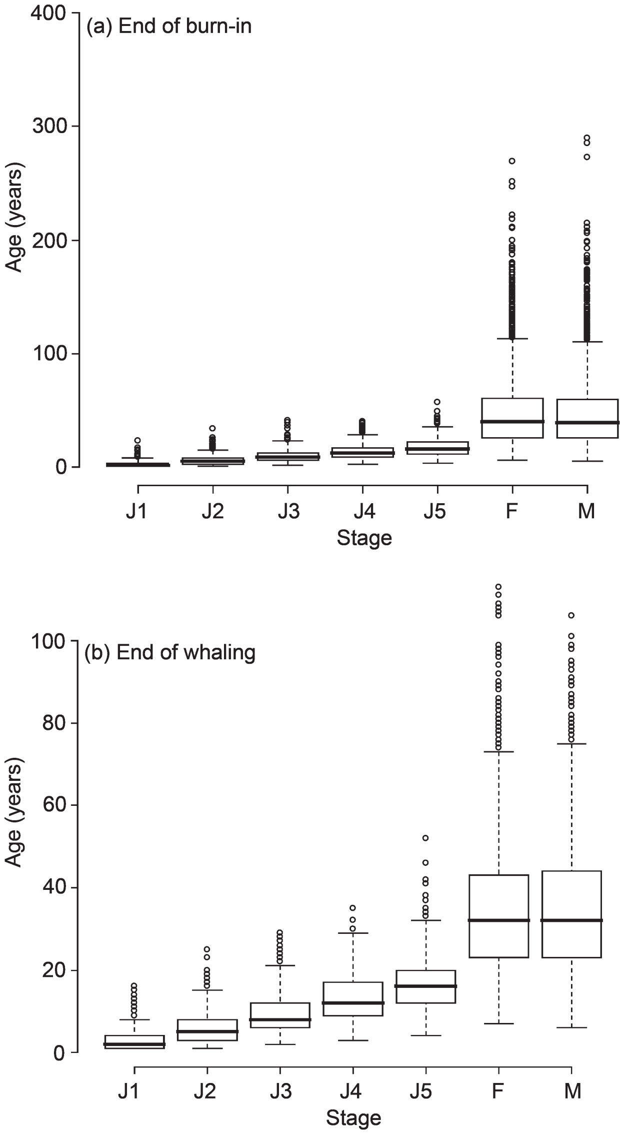


Fig. 5. Distribution of age within each demographic stage for all simulated individuals at the end of burn-in (a), and the end of whaling (b), for an example simulation replicate.

approximately 48% of the individuals were reproductive adults and the sex ratio was not significantly different from 50:50.

Genetic diversity of the empirical data, as measured by the number of alleles (haplotypes for mtDNA), heterozygosity, and Φ_H, was similar to the distributions of these metrics from the matched simulated samples (Fig. 6). Only measures of heterozygosity and Φ_H for mtDNA were outside of the simulated distributions, a result of the skewed haplotypic frequency distribution in the empirical data.

Genetic analyses

In the empirical data, nine of the 33 loci were found to be out of Hardy-Weinberg equilibrium (HWE) with a combined *p*-value using Fisher's method of 2.3×10^{-6}. In the simulation, the median number of loci out of HWE was two, with a maximum of five (Fig. 7a). When errors were added to the simulated data, the median number out of HWE increased to three with a maximum of 11 (Fig. 7b). The *p*-value for the test with errors was 0.006.

There was a relatively uniform distribution of MCMC HWE *p*-values across loci without errors included (Fig. 8a). The combined *p*-value using Fisher's method for the empirical data was 2.3×10^{-6}, which was less than the minimum value in the simulation of 0.0025. The 95-percentile of the simulated distribution was 0.022–0.989. When errors were introduced into the simulated data, the distributions of the MCMC HWE *p*-values and the Fisher's method *p*-values were highly skewed (Fig. 8b). The median of Fisher's method *p*-values was 2.5×10^{-2}, with a 95-percentile of 3.14×10^{-5}–5.1×10^{-1}. Sixty one percent of this distribution was $\leq$0.05. The empirical value was at the lower 1% of this distribution, making it inconsistent with the simulation.

In the analyses of the empirical data stratified by age cohorts, sampling sites, and seasons within sampling sites, only four of the 60 tests (30 pairwise tests each for panmixia and simulation null models) indicated significant genetic differentiation ($p \leq 0.05$) (Table 3). χ^2-tests of cohorts born before 1950 versus those born after 1979 for both mtDNA and microsatellites were significant using the permutation test for panmixia ($p = 0.012$ and 0.048 respectively) but not significant using the simulation generated *p*-value ($p = 0.186$ and 0.494 respectively). The likelihood for the simulation null model was 12.5 times more likely than panmixia for mtDNA and 3.4 times more likely for microsatellite data. The mtDNA χ^2-test between the 1950–79 and after-1979 cohorts, which had a small, but non-significant panmixia *p*-value (0.088) was also non-significant (0.312) under the better supported simulation null model. Conversely, the same test for microsatellites and the χ^2-tests between cohorts born before 1950 and those born 1950–79 supported the panmixia model. For both markers, F_{st}-tests supported the simulation model, while the three Φ_{st}-tests supported the panmixia model.

The other two tests that indicated significant differentiation were inconsistent with our simulation model. They were the mtDNA F_{st}-test between autumn and spring samples from St. Lawrence Island ($p = 0.008$), and the microsatellite F_{st}-test between Barrow and St. Lawrence Island ($p = 0.042$). In both of these comparisons, although

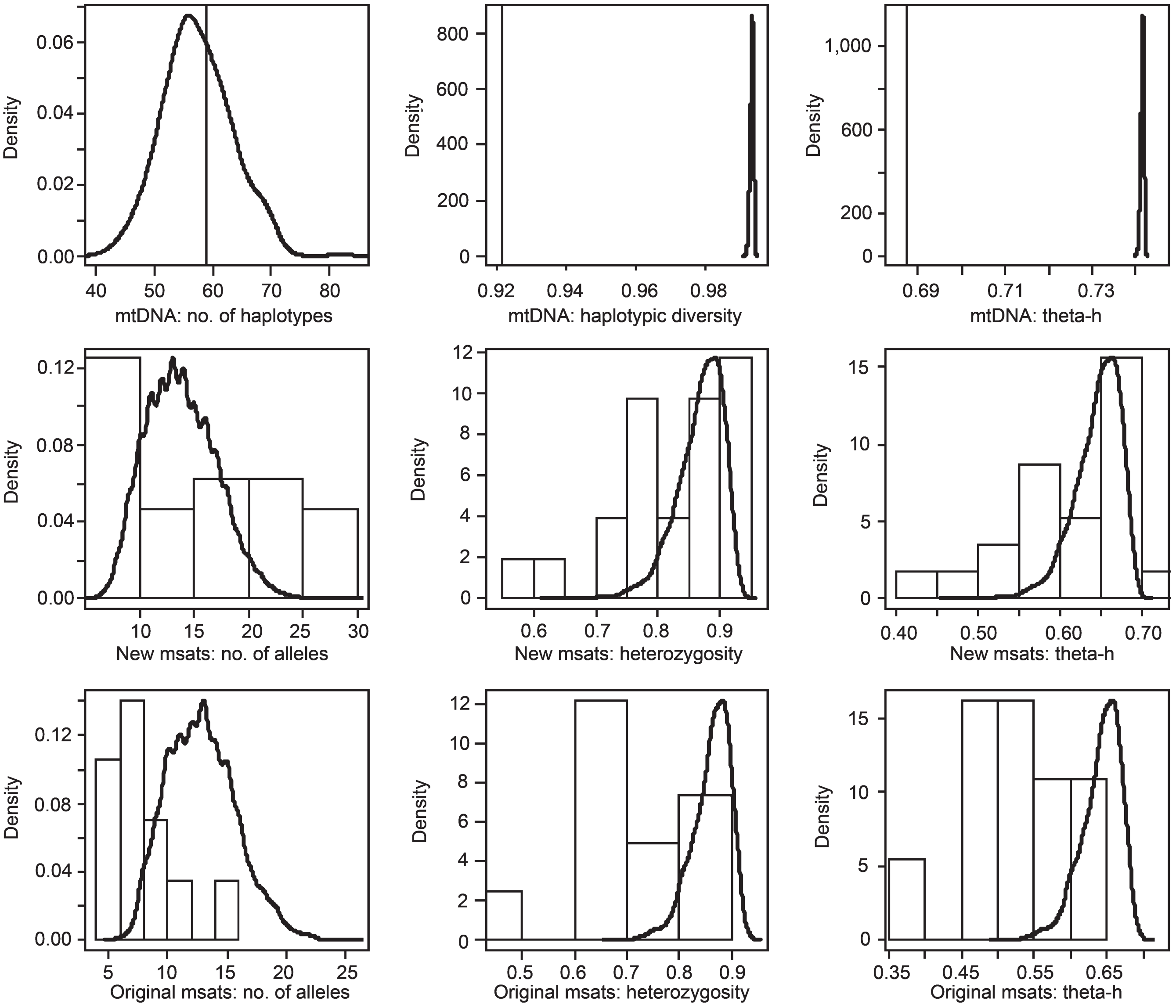


Fig. 6. Distribution of single-locus measures of genetic diversity in the empirical data (histograms over the 33 loci), and 500 replicates of the simulation (bold lines). For mtDNA, the empirical data value is given by a single line.

the *p*-value for panmixia was non-significant, the panmixia model was less than 1.4 times more likely than the simulation model. Additionally, the panmixia *p*-values for both microsatellite tests of the sampling sites were only slightly higher than the critical *α* ($p = 0.066$ for both).

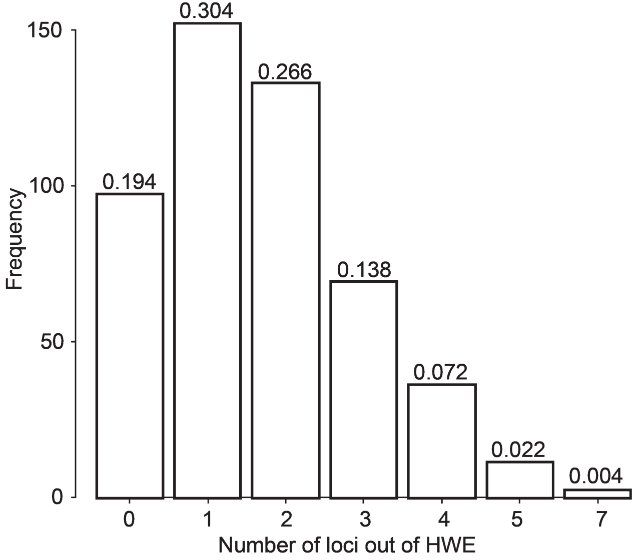
The introduction of errors into the simulated microsatellite data did not make a substantial change in the results of any of the F_{st} or χ^2-tests. While the *p*-value of some results changed slightly, there was not a consistent pattern in the direction of the change (results not shown).

DISCUSSION

Results indicate the benefit of using simulation models to develop null distributions when assumptions of Wright-Fisher null distributions are known to have been violated. The two significant permutation tests for panmixia (χ^2 for two extreme age cohorts) were not significant using the null distributions from the simulations and were also the tests which most strongly supported the simulation null model (i.e. had the largest negative log-likelihood ratio values). In many respects, the results of the analysis indicate that the empirical genetic data sampled from BCB bowhead whales are more consistent with the model of a single, randomly-mating population with a history of whaling and subsequent recovery mimicking the true bowhead whale history than they are with standard null distributions generated under assumptions of panmixia. None of the 15 pairwise cohort tests conducted (three comparisons for five measures of genetic differentiation) exhibited a significant difference between the simulated replicates and empirical data.

However, the number of loci actually out of HWE significantly exceeded the numbers estimated to be out of HWE in the simulations, which suggests that, in some respect, our model may not fully capture some component of the process that generated these samples. Given the findings of Morin *et al.* (2009), an attempt was made to simulate some of the genotyping errors that may lead to Hardy-Weinberg disequilibrium. However, when errors were introduced in the simulated data, the difference between the two decreased dramatically but remained significant. This was the only analysis for which the introduction of genotyping errors into the simulated datasets had a

(a) Without errors



(b) With errors

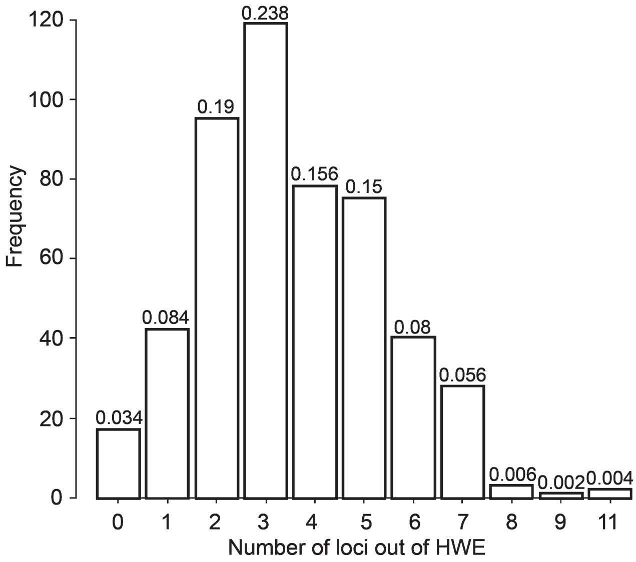


Fig. 7. Distribution of the number of loci out of Hardy-Weinberg equilibrium in the 500 replicates without (a) and with (b) errors included. Numbers above the bars are the fraction of the total number of replicates represented by that bar.

substantial impact on the results. While the comparison between the empirical and simulated results was still significant even with errors introduced, the results support those of Morin *et al.* (2009) in highlighting the sensitivity of HWE to genotyping errors. For instance, in the simulation without genotyping errors only 0.026 of the simulated datasets had five or more loci out of HWE. When genotyping errors were introduced, this frequency jumped to 0.298.

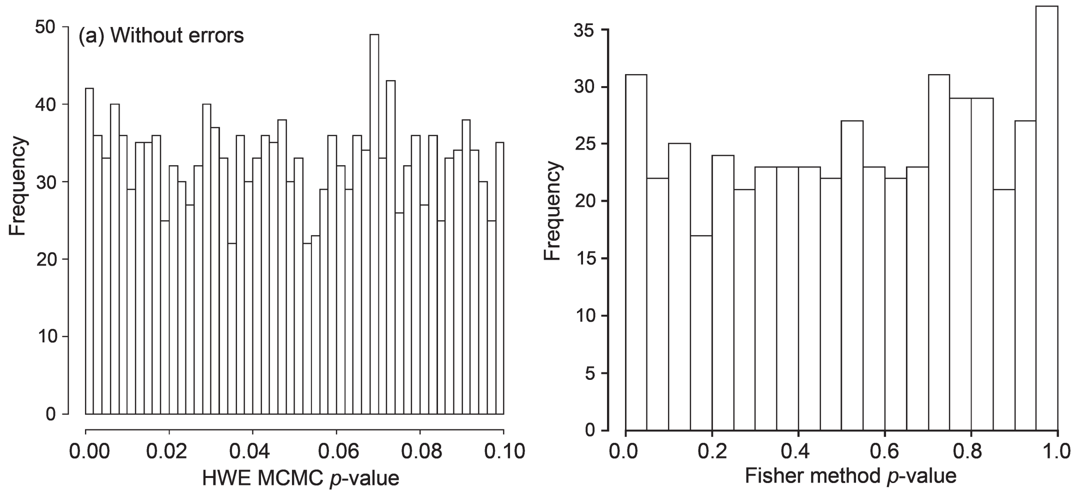
The introduction of errors showed a greater effect on the distribution of the overall Fisher's method p-value for HWE. Without errors, this distribution was relatively uniform as would be expected under a standard null hypothesis. When errors were included, the distribution became highly skewed towards very small p-values. While this skew was not large enough to make the empirical finding of overall Hardy-Weinberg disequilibrium consistent with our model, the implication is that with even the relatively low error rate identified by Morin *et al.* (2009), there is a large probability (61% of the replicates had a $p \leq 0.05$) of falsely assessing widespread disequilibrium.

A very simplistic model was used for introducing genotyping errors to the simulated datasets. Though the estimated allelic dropout rate from the empirical data was incorporated, all errors were random with respect to the loci at which they occurred and the alleles and individuals that were affected. In reality, genotyping errors are often not random (Bonin *et al.*, 2004; Gagneux *et al.*, 1997; Morin *et al.*, 2009). Some loci or samples may be more susceptible to errors than others. Allele length and frequency may also affect the likelihood of the allele being correctly scored. Stutter bands and slippage would result in the mis-scored allele being very close in length to the correct allele, rather than reflecting the overall allele frequency at the locus. Since it was not possible to quantify the various biases inherent in genotyping errors, a simplistic model was chosen that only included allelic dropout and random errors. If other realistic biases had been incorporated into the simulated genotyping errors, an even stronger impact on the expected distribution of the number of loci out of HWE (Morin *et al.*, 2009) would have been expected. The susceptibility of HWE to genotyping errors makes reliance on this metric as the sole source of data indicating population structure questionable practice.

The second analysis that indicated a lack of consistency between the empirical data and simulation model was the F_{st} test of mtDNA sequences from samples taken at St. Lawrence Island in the autumn and spring. The magnitude of the observed mtDNA F_{st} value (0.054) in this test results from the difference in the frequency of one haplotype (BH42) between spring and autumn samples (6 in autumn, 1 in spring). Given that five of the six autumn samples that possessed haplotype BH42 came from one location in St. Lawrence Island (Savoonga), and sample sizes are relatively small in both strata, it is possible that these samples do not adequately represent the haplotypic distributions of St. Lawrence Island whales in these seasons.

The final analysis that was inconsistent with the model described here was the F_{st} test between Barrow and St. Lawrence Island for the microsatellite markers. It is possible that this result is being influenced either by the unusual distribution of the autumn Savoonga samples mentioned above or by the loci that were found to be out of HWE in the Barrow samples. The effect of the latter were partially examined by running this analysis again after removing the six samples most influential on HWE, which were identified by Morin *et al.* (2009). The removal of these samples did not significantly change the lack of consistency between the empirical and simulated data either with or without errors introduced into the simulated data.

By mimicking the demographic composition and whaling history of BCB bowhead whales, the model was able to capture non-equilibrial effects such as GGS that a standard panmixia null model could not. This was most clearly shown in the extreme example of the age cohort analyses. However, it was also evident in analyses which compared whales sampled in Barrow versus those sampled from St. Lawrence Island. Although the microsatellite F_{st} test indicated significant differentiation using the simulated null



(b) With errors

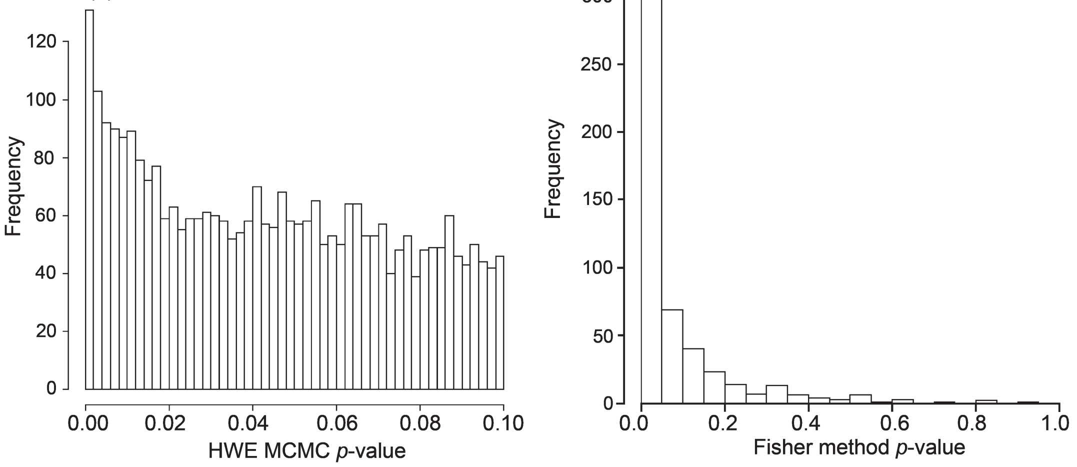


Fig. 8. Distribution of p-values for Hardy-Weinberg equilibrium (HWE) without (a) and with (b) errors included. Figures on left are distributions of locus *p*-values from *Genepop* (truncated to values ≤ 0.1). Figures on right are distributions of overall *p*-value using Fisher's method.

distribution, the likelihood ratio suggests that the panmixia model is only very slightly favoured. Given that there is a significant difference in ages (as inferred from length – Fig. 3) between these two sites, it is expected that this stratification would behave more like the cohort analyses. Additionally, the St. Lawrence Island microsatellite sample size was small ($n = 25$) relative to mtDNA ($n = 52$), so conclusions must be treated as preliminary. Genotyping of more samples from this region with Single Nucleotide Polymorphisms (SNPs) is underway which ought to provide more resolution.

The fact that both microsatellite panmixia test results are only slightly greater than the critical α could lead one to incorrectly infer the presence of population structure were there is none. Thus, the results presented here suggest that in some cases where standard permutation tests for panmixia may indicate significant genetic differentiation, if the population demographic history is taken into account, the simulated distribution will more appropriately reflect the genetic distribution of the null model being tested.

Simulation construction

The simulation described in this paper represents a null hypothesis based on a very specific model of a single population that is out of genetic equilibrium due to its population history. One of the strengths of this simulation is that by matching the age and sex characteristics of the empirical samples where possible, this null hypothesis inherently incorporates any potential demographic biases in the sampling process. The model relies on several parameters controlling the population dynamics and genetic diversity. When possible, empirical data and parameter values from independent sources were used. When these were not available, parameters were iteratively tuned to ensure that other aspects of simulation either fit published results or matched the empirical data as closely as possible. It is important to note that this process does not ensure that the parameter values are accurate with respect to a 'true' single population; the current best statistical estimates of stock structure and biological/demographic parameters are of varying precision.

An example is the procedure by which carrying capacity (K) was selected. With the value of the logistic growth shape parameter (z) set at the median posterior value from Brandon and Wade's (2006) backward projection model, a value of K was selected such that the majority of the replicates did not go extinct and passed through the abundance 'gates'. Under these constraints it can be seen that many of the population dynamics parameters, most notably K, z, and the population growth rate (r – not specified in the model, but resulting from

Table 3

Comparison of panmixia and simulation null models for tests of genetic differentiation of several stratifications of the data. Sample size of each strata given in parentheses. Panmixia and simulation *p*-values are from 500 replicates of each test. Likelihoods estimated from gamma distributions fit to replicates from each null model. Log-likelihood ratio is log(Panmixia likelihood/Simulation likelihood). Log-likelihood ratios less than 1 support the simulation model, while those greater than 1 support the panmixia model. Pairwise comparisons within each marker type are sorted by increasing Log-likelihood ratio. Values in grey indicate *p*-values ≤ 0.05. SLI=St. Lawrence Island.

Stratification	Strata	Test	Observed value	Panmixia *p*-value	Simulation *p*-value	Panmixia likelihood	Simulation likelihood	Log-likelihood ratio
(a) mtDNA								
Age cohorts	Before 1950 (21) v. after 1979 (34)	χ^2	35.582	0.012	0.186	0.004	0.048	0.08
	1950-1979 (25) v. after 1979 (34)	χ^2	34.331	0.088	0.312	0.039	0.058	0.67
	Before 1950 (21) v. after 1979 (34)	F_{st}	0.009	0.190	0.186	16.031	20.528	0.78
	1950-1979 (25) v. after 1979 (34)	F_{st}	0.007	0.261	0.216	20.523	25.555	0.80
	Before 1950 (21) v. 1950-79 (25)	F_{st}	-0.007	0.631	0.728	29.291	35.237	0.83
	Before 1950 (21) v. after 1979 (34)	Φ_{st}	0.012	0.230	0.242	11.580	9.223	1.26
	1950-1979 (25) v. after 1979 (34)	Φ_{st}	-0.015	0.778	0.658	27.910	20.842	1.34
	Before 1950 (21) v. 1950-79 (25)	Φ_{st}	0.005	0.321	0.284	14.524	10.299	1.41
	Before 1950 (21) v. 1950-79 (25)	χ^2	22.758	0.842	0.844	0.083	0.054	1.54
Sampling sites	Barrow (258) v. SLI (52)	F_{st}	-0.002	0.655	0.772	119.446	125.890	0.95
	Barrow (258) v. SLI (52)	χ^2	52.939	0.780	0.802	0.030	0.025	1.20
	Barrow (258) v. SLI (52)	Φ_{st}	-0.002	0.575	0.482	75.804	56.751	1.34
Barrow seasons	Autumn (133) v. Spring (125)	F_{st}	0.000	0.355	0.406	142.269	179.073	0.79
	Autumn (133) v. Spring (125)	Φ_{st}	0.002	0.218	0.232	57.302	48.569	1.18
	Autumn (133) v. Spring (125)	χ^2	57.078	0.573	0.586	0.053	0.040	1.33
SLI seasons	Autumn (13) v. Spring (11)	χ^2	16.519	0.172	0.672	0.126	0.131	0.96
	Autumn (13) v. Spring (11)	Φ_{st}	-0.014	0.485	0.492	8.479	6.949	1.22
	Autumn (13) v. Spring (11)	F_{st}	0.054	0.080	0.008	2.318	1.673	1.39
(b) Microsatellites								
Age cohorts	Before 1950 (14) v. after 1979 (24)	χ^2	355.637	0.048	0.494	0.004	0.014	0.29
	Before 1950 (14) v. 1950-79 (16)	F_{st}	-0.004	0.804	0.844	76.232	97.654	0.78
	Before 1950 (14) v. after 1979 (24)	F_{st}	0.002	0.335	0.272	71.310	88.219	0.81
	1950-1979 (16) v. after 1979 (24)	F_{st}	-0.003	0.790	0.858	107.732	118.951	0.91
	1950-1979 (16) v. after 1979 (24)	χ^2	324.783	0.281	0.888	0.015	0.007	2.14
	Before 1950 (14) v. 1950-79 (16)	χ^2	269.402	0.774	0.998	0.015	0.001	15.00
Sampling sites	Barrow (213) v. SLI (25)	χ^2	464.636	0.066	0.126	0.003	0.005	0.60
	Barrow (213) v. SLI (25)	F_{st}	0.002	0.066	0.042	89.679	72.476	1.24
Barrow seasons	Autumn (115) v. Spring (98)	χ^2	425.940	0.206	0.374	0.010	0.011	0.91
	Autumn (115) v. Spring (98)	F_{st}	0.001	0.128	0.098	301.650	293.580	1.03
SLI seasons	Autumn (14) v. Spring (11)	F_{st}	-0.007	0.934	0.988	43.487	17.524	2.48
	Autumn (14) v. Spring (11)	χ^2	254.095	0.978	1.000	0.003	$1.22 \cdot 10^{-4}$	24.59

the reproduction and survival matrices), will be closely correlated such that multiple combinations would work. While the goal was not to estimate these parameters, through iterative testing it was determined that, given the historical catch record, there was a small range over which they could vary and still meet the extinction and abundance constraints. In the tests, choices of *K* outside of the range of approximately 11,900–12,400 would not produce useable replicates. This range is well within the 95% credibility interval for *K* (9,112–13,610) from the Brandon and Wade (2006) assessment model most similar to the simulation used in this study, which is expected given that this study used the same historical catch and abundance data.

In this simulation, the carrying capacity of the population was assumed to be the same now as it was prior to the onset of commercial whaling. This could have been violated if there has been a substantial change in the ecosystem or the range of the population has either expanded or contracted. The 2001 abundance estimate of 10,545 suggests that the population is very close to the carrying capacity estimated in Brandon and Wade (2006), making it unlikely that there has been a decrease in carrying capacity. Moreover, estimates from George *et al*. (2004) indicate that the bowhead whale population continues to increase more than 3% annually. Among a variety of possible explanations for this finding would be an increase in carrying capacity. Whether or not there has indeed been a significant increase in carrying capacity will require future surveys.

Similarly, had bowhead whales been subjected to substantial population fluctuations prior to commercial whaling, some of the parameters used in the 4,000 year burn-in may not reflect reality as that phase simulated a population at demographic and genetic equilibrium. However, because the burn-in was tuned to produce a population with the approximate amount of diversity as seen in the current empirical data, deviations would not be expected to substantially affect the results. The difference between the actual effective population size (N_e) and what was calculated to initialise the population at equilibrium would be offset by a difference in the actual mutation rate and the one used in the study.

Another result of the model constraints is that it was not possible to directly control population abundance at the nadir or the range over which it varied. As a population reduced to a very small size will be unable to contain the entire genetic diversity of its larger progenitor, this factor is likely to greatly affect the degree of genetic disequilibrium within the population. The smaller the nadir, the stronger the signal of a GGS is expected to be, in which the genotypes of individuals born before and after the nadir will appear to have come from two different distributions. Therefore, it is important to note that the results of this study are conditional on the nadir being approximately 1,100. This is consistent with the suggestions that the population size might have been 1,000 or lower at the end of commercial whaling (Bockstoce and Botkin, 1983; Bockstoce and Burns, 1993).

In the absence of GGS, sampling from an age-structured population as well as non-random sampling can also lead to inferences of populations that are out of genetic equilibrium (Waples, 1998; Waples and Yokota, 2007). Though there is no evidence that whalers were intentionally selective in their hunting, the fact that bowhead whales segregate by age and sex during migration may have resulted in selectivity on the basis of availability (Bockstoce, 1986). Evidence for some selectivity can be found in the fact that the average size of whales killed decreased between the beginning of the fishery and 1874, the only period for which such data are available (Bockstoce and Burns, 1993). If a similar kind of selectivity continued throughout the commercial hunt, it would add to effects of GGS as the portion of the population that survived through the nadir would tend to represent younger cohorts. As a result of the complexity of this simulation and the constraints to mirror bowhead whale population trajectories as discussed above, the sensitivity of the results to parameters such as selectivity of harvest, differences in the age-structure of the population, or variance in reproductive success were not examined. These items are being further explored with a simpler form of the simulation previously described by Ripley *et al*. (2006) and presented in Martien *et al.* (2009).

In theory, the methods described here could be extended to construct any number of alternative null hypotheses. For example, while this simulation models a single stock, a variety of two-stock hypotheses have been proposed for BCB bowhead whales (IWC, 2008) and it would be a productive exercise to use the methods presented here to explore their relative likelihoods. Genetic simulations for any of these two-stock hypotheses would require several important refinements such as defining the population dynamics of each stock, as well as the annual partitioning of the historical catch among stocks. The stocks would also have to be initialised at their appropriate pre-whaling genetic conditions, which are a result of the relative abundances and degree of gene-flow. Finally, during the ‘whaling’ phase of the simulation, empirical samples and their simulated equivalents would need to be assigned to stock, introducing further uncertainty.

In summary, the creation of more appropriate null distributions for common tests for population structure is a potentially important strategy when there are known reasons for the population to be in disequilibrium due to historical or demographic factors. In such cases, the simulated null distributions may provide a better basis for inference than reliance on the standard Wright-Fisher assumption of equilibrium.

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Generalised additive models to investigate environmental drivers of Antarctic minke whale (*Balaenoptera bonaerensis*) spatial density in austral summer

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ABSTRACT

There is a need to characterise the physical environment associated with Antarctic minke whale density in order to understand long-term changes in minke whale distribution and density in open waters of the Southern Ocean during austral summer months. To investigate environmental drivers of Antarctic minke whale density, generalised additive models (GAMs) were developed, based on line transect data collected for the International Decade of Cetacean Research (IDCR) and Southern Ocean Whale Ecosystem Research (SOWER) programmes. The GAMs were fitted independently by survey year. Explained deviances ranged from 14.9% to 35.1%. Most models included covariates related to transition zones, such as distances to the continental shelf break and sea ice edge, both of which showed a predominantly negative relationship with whale density. This study suggests high variability in the relationships between Antarctic minke whale density and the environment. None of the selected covariates had a consistent qualitative relationship with density at either the circumantarctic or the regional scale. This in part may be explained by the changing ice-related boundaries of the surveys between years and hence differences in survey region. Another possible reason is that in absence of better data, most of the covariates considered were derived from remote sensing data. More localised surveys with comparable survey area conducted across the Southern Ocean, where whale sightings data are collected simultaneously with *in situ* non-biotic and prey data, are likely to provide a better assessment of the environmental determinants of whale density.

KEYWORDS: ANTARCTIC MINKE WHALE; SOUTHERN OCEAN; DISTRIBUTION; ICE; MODELLING; SOWER

INTRODUCTION

The Southern Ocean is the most important feeding ground for Antarctic minke whales (*Balaenoptera bonaerensis*). Mainly during the austral summer months, these whales predominantly feed on krill (Kawamura, 1994) and are observed both within the pack ice region (e.g. Ensor, 1989; Ribic *et al.*, 1991; Thiele *et al.*, 2002; 2005; Thiele and Gill, 1999; van Franeker, 1992) and in the open ocean (Friedlaender *et al.*, 2006; Kasamatsu *et al.*, 1988; 2000; Murase *et al.*, 2002; Thiele *et al.*, 2000).

The Antarctic minke whale is currently the most abundant baleen whale species in the Southern Ocean, and is likely to be a major consumer of krill. During the austral summer, several hundred thousand Antarctic minke whales inhabit the Southern Ocean (Branch, 2006), although Antarctic minke whale abundance estimates are currently under major review (IWC, 2009; Zerbini *et al.*, 2008). Estimates of annual circumpolar krill consumption by Antarctic minke whales are important to understand the role of minke whales in marine ecosystems, including interactions with potential competitors (e.g. Ainley *et al.*, 2006). Estimates of krill consumption by minke whales range between 35.5 (± 6.2) million tonnes per year (Armstrong and Siegfried, 1991) and 75 million tonnes per year (Everson, 2000). However, they are based on historic Antarctic minke whale abundance estimates. Understanding how the changing environment affects minke whales and their prey is important to map changes in whale abundance and trends.

Several studies have reported regional trends in sea surface temperature and sea ice extent attributed to climate change in the Southern Ocean in the second half of the 20th century. This is especially true for the Bellingshausen-Amundsen Seas sector, with a marked increase in sea surface temperature (Meredith and King, 2005) and a strongly negative trend in sea ice extent (Stammerjohn *et al.*, 2008; Zwally *et al.*, 2002). The environmental variability may underlie long-term changes in Antarctic minke whale density. For a better understanding of these long-term changes the physical environment associated with Antarctic minke whale density dynamics needs to be characterised.

From large-scale independent studies (e.g. Kasamatsu *et al.*, 1988; 2000; Murase *et al.*, 2002; Thiele *et al.*, 2000), it is not clear which environmental variables determine the circumantarctic variability in Antarctic minke whale summer distribution and density. Only recently, studies on Antarctic minke whale distribution have been conducted at a smaller scale, and these indicate potentially complex spatial relationships between Antarctic minke whales and their prey (Friedlaender *et al.*, 2006; 2009).

The International Whaling Commission (IWC) has conducted visual cetacean surveys in the Southern Ocean for almost 30 years under the IDCR (International Decade of Cetacean Research) and SOWER (Southern Ocean Whale and Ecosystem Research) programmes. These have resulted

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in three circumpolar sets of surveys, which were specifically designed for the visual detection of cetaceans, with an emphasis on Antarctic minke whales and the environment. This is in contrast with multidisciplinary surveys, such as the CCAMLR 2000 (Commission for the Conservation of Antarctic Marine Living Resources – Reilly *et al.*, 2004) and SO GLOBEC surveys (Southern Ocean Global Ocean Ecosystem Dynamics – Friedlaender *et al.*, 2006; Thiele *et al.*, 2004), which targeted specific study areas.

The IWC/IDCR-SOWER dataset is thus the only circumantarctic whale sightings dataset for the Southern Ocean that allows for a long-term large-scale analysis of spatio-temporal variability in minke whale density. To determine the environmental drivers of whale density, the data were analysed with the spatial modelling methodology developed by Hedley *et al.* (1999), and simple generalised additive models (GAMs) (Wood, 2006). Input variables were derived from remote sensing data that are related to transition zones in the Southern Ocean. These zones are characterised by their enhanced productivity, such as the marginal ice zone (e.g. Arrigo *et al.*, 1998; Moore and Abbott, 2000; Smith and Nelson, 1986) and frontal zones (e.g. Moore and Abbott, 2000). Bathymetric variables, sea surface temperature, chlorophyll a concentration and latitude were also considered as inputs for the spatial models.

With this analysis, predictive spatial models were developed for Antarctic minke whale summer density in open waters of the Southern Ocean at the regional scale, which is defined as the area surveyed during a specific season. In recent years, improved models have been developed to estimate Antarctic minke whale summer abundance in the Southern Ocean (recently developed models are presented in Bravington and Hedley (2009), Cooke (2009) and Okamura and Kitakado (2009)). However, the models presented in this paper were not used for derivation of summer abundance estimates. Instead, the aim of the models was to identify aspects of the environment that underlie Antarctic minke whale density distribution at the regional scale, and to characterise the various relationships between minke whale density and the environment. Furthermore, whether these relationships held at the circumantarctic scale was also investigated.

MATERIALS AND METHODS

Study area and effort

The IWC/IDCR-SOWER programme has completed three circumpolar (CP) sets of cetacean sighting surveys in the Southern Ocean, namely CPI (1978/79–1983/84), CPII (1985/86–1990/91) and CPIII (1991/92–2003/04). The IWC has divided the Southern Ocean into six Management Areas (Fig. 1) (Donovan, 1991; Mackintosh, 1942), and Table 1 shows general information about the surveys analysed in this study in the context of the Management Areas. Coverage of most surveys was restricted to one Management Area, and some surveys covered sections of two Management Areas. Almost all open waters within the full latitudinal range from below 60°S to the sea ice edge were surveyed in CPIII. In contrast, the surveyed strata covered only about 65% and 81% of the ranges in CPI and CPII, respectively (Branch and Butterworth, 2001), with northern boundaries of the surveyed strata often at latitudes south of 60°S. During each survey, 2–4 vessels covered the open waters of the Southern Ocean, thereby excluding the pack ice region and polynyas (enclosed or semi-enclosed areas of open water) within this region. The surveys varied in timing and duration, but were always conducted during austral summer, within a period from the end of December to the beginning of March of each season.

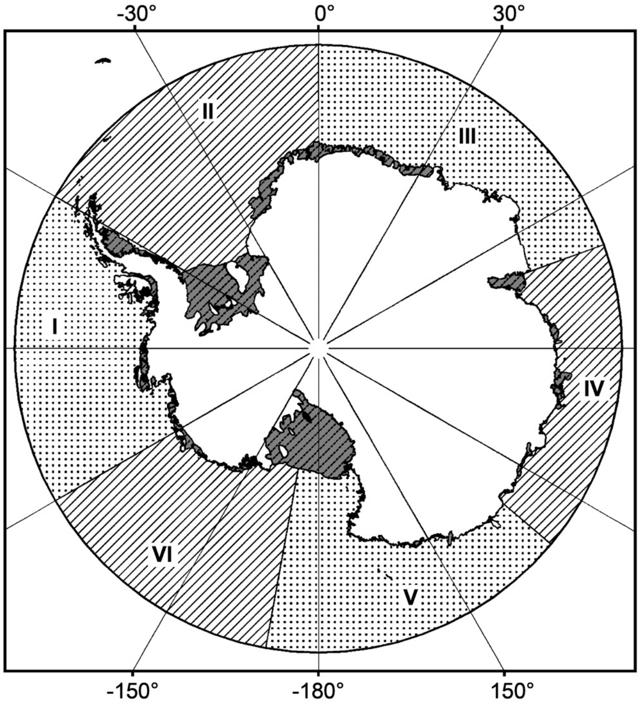

Fig. 1. IWC Management Areas in the Southern Ocean (Mackintosh, 1942; Donovan, 1991). Ice shelves are represented by the grey striped areas. See Branch and Butterworth (2001) and Branch (2006) for detailed maps of the strata surveyed during the IDCR/SOWER programme.

Primary search effort, i.e. effort made when a vessel is in searching mode, was exclusively in closing mode for the surveys conducted between 1978/79 and 1984/85 and alternated between effort in closing mode and Independent Observer (IO) mode for surveys since 1985/86. In IO mode, the vessel stays on the track line after a sighting, with the two observer teams on the primary and secondary platforms on full search effort. Meanwhile, the observers on the upper bridge track and identify the sighting. In contrast, in closing mode the survey vessel leaves the track line and approaches the sighted group(s) of whales for better school size estimation and species identification (Branch and Butterworth, 2001). See Branch and Butterworth (2001) and Branch (2006) for a more detailed description of the IWC/IDCR-SOWER surveys, including maps of the surveyed strata.

The first surveys (1978/79–1980/81) were not considered because of the lack of environmental data from the satellite record needed to develop spatial models. Thus, spatial models were developed with line transect data from the 1981/82–2004/05 surveys. Total survey area ranged from 0.690 million km^2 (2001/02 survey) to 3.305 million km^2 (1985/86 survey). The lowest level of primary effort was 2,842km (2000/2001 survey), while a maximum of 15,645km primary effort was obtained during the survey in 1985/86. Table 1 summarises Antarctic minke whale

Table 1

Survey and Antarctic minke whale sighting information, grouped per IWC Management Area, south of 60°S. Sighting information refers to sightings made during primary effort and Independent Observer (IO) modes. Schools and sightings are standardised per unit primary effort and are given before truncation.

IWC Area[1]	Survey season	Survey period	Area size (10^6 km^2)	Primary effort (km)	IO effort (km)	Number of schools	Schools/ effort	Number of whales	Whales/ effort
Area I	1982/83	01 Jan.–18 Feb. 1983	1.099	8,938	n/a	616	0.069	1,546	0.173
(120–60°W)	1989/90	28 Dec. 1989–15 Feb. 1990	1.473	10,192	5,635	608	0.060	1,208	0.119
	1993/94	29 Dec. 1993–13 Feb. 1994	2.290	9,002	4,601	314	0.035	608	0.068
	1999/2000	12 Jan. 1999–14 Feb. 2000	0.776	3,409	1,887	53	0.016	95	0.028
Area II	1981/82	26 Dec. 1981–08 Feb. 1982	1.078	11,503	n/a	505	0.044	1,418	0.123
(60°W–0)	1986/87	25 Dec. 1986–09 Feb. 1987	1.699	13,503	6,988	791	0.059	2,621	0.194
	1996/97	13 Jan.–17 Feb. 1997	1.479	6,235	3,303	214	0.034	404	0.065
	1997/98	16 Jan.–15 Feb. 1998	1.053	5,699	3,133	199	0.035	370	0.065
Area III	1987/88	20 Dec. 1987–27 Jan. 1988	1.645	8,204	4,314	365	0.044	807	0.098
(0–70°E)	1992/93	25 Dec. 1992–02 Feb. 1993	1.527	10,126	5,298	388	0.038	870	0.086
	1994/95	12 Jan.–27 Feb. 1995	1.470	8,017	4,201	277	0.035	498	0.062
	2004/05	10 Jan.–27 Feb. 2005	0.720	4,843	2,318	162	0.033	333	0.069
Area IV	1984/85	28 Dec.1984–21 Feb. 1985	1.105	11,436	n/a	370	0.032	904	0.079
(70–130°E)	1988/89	28 Dec. 1988–12 Feb. 1989	1.622	12,957	4,767	476	0.037	1,361	0.105
	1998/99	20 Jan.–23 Feb. 1999	1.329	7,288	3,933	186	0.026	432	0.059
Area V	1985/86	22 Dec. 1985–20 Feb. 1986	3.305	15,645	8,101	1,184	0.076	2,752	0.176
(130°E–170°W)	1991/92	27 Dec. 1991–12 Feb. 1992	1.522	6,872	3,834	637	0.093	1,491	0.217
	2001/02	25 Dec. 2001–13 Feb. 2002	0.690	3,397	1,879	136	0.040	392	0.115
	2002/03	22 Dec. 2002–26 Feb. 2003	1.653	7,332	3,892	265	0.036	580	0.079
	2003/04	21 Dec. 2002–1 Mar. 2003	1.446	7,333	3,845	704	0.096	2,136	0.291
Area VI	1983/84	03 Jan.–18 Feb. 1984	2.516	7,701	n/a	194	0.025	431	0.056
(170–120°W)	1990/91	02 Jan.–13 Feb. 1991	1.912	6,734	4,020	187	0.028	357	0.053
	1995/96	10 Jan.–24 Feb. 1996	1.531	6,298	3,222	227	0.036	379	0.060
	2000/01	08 Jan.–22 Feb. 2001	1.553	6,046	2,842	207	0.034	490	0.081

[1] In this table, as in subsequent tables, only the Management Areas were listed that were predominantly surveyed during a season. During most seasons, (part of) only one Management Area was surveyed. Three surveys were conducted in two Management Areas, namely the 1999/2000 survey (80–55°W, Areas I + II), 1994/95 survey (40–80°E, Areas III + IV) and 1995/96 survey (140–110°W, Areas VI + I).

sightings data under primary effort. The number of Antarctic minke whale schools per km ranged from 0.016 (Area I, 1999/2000 survey) to 0.096 (Area V, 2003/04 survey). The number of sighted Antarctic minke whales per km ranged from 0.028 (Area I, 1999/2000 survey) to 0.291 (Area V, 2003/04 survey).

Whale sightings and detection probabilities

Following recommendations in Branch and Ensor (2001), Branch and Butterworth (2001) and Branch (2006), sightings coded as 04, 91 and 92 (all classified as 'definitely minke whale') and 39 ('like minke whale') were extracted from the DESS (IWC Database-Estimation Software System) V3.52 database package (Strindberg and Burt, 2004), under the assumption that these sightings represented Antarctic minke whales. Dwarf minke whales, so far an unnamed subspecies of the common minke whale (*Balaenoptera acutorostrata*), also inhabit the Southern Ocean, and may be confused with Antarctic minke whales during shipboard surveys. However, probably less than 1% of minke whales in the Southern Ocean are dwarf minke whales (Zerbini *et al.*, 2008). Sightings used for this analysis were obtained in both closing and IO mode.

Some whale schools were sighted two or three times from different platforms during the survey and recorded as duplicates or triplicates, respectively. Each duplicate/triplicate was marked as either 'definite', 'possible', 'remotely possible' or 'uncertain'. Only the first sighting of a duplicate/triplicate marked as 'definite' was included. All other duplicates/triplicates were treated as distinct schools (Branch and Butterworth, 2001). Only sightings with activity codes considered suitable as defined in Table 3 of Branch (2006) were included in this analysis. Radial distances and angles were smeared using Method II of Buckland and Anganuzzi (1988). Selected sightings were further filtered by truncation of perpendicular distances at 1.5 nautical miles (nmi), after smearing (Branch and Butterworth, 2001).

Detection probabilities were estimated using Mark Recapture Distance Sampling (MRDS) methods implemented in Distance V5.0 release 2 (Thomas *et al.*, 2006) and the MRDS package (V1.2.9) of Program R, V2.9.2 (R Development Core Team, 2008), which is part of Distance.

An MRDS detection function can be written as (Laake and Borchers, 2004):

$$p.(x, \underline{z}) = p.(0, \underline{z})g.(x, \underline{z}) \tag{1}$$

where: $p.(x, \underline{z})$ = the probability that at least one of the observers detects a whale group at perpendicular distance x from the track line, given the vector of $\underline{z}$ sighting covariates (school size, sea state, etc);

$p.(0, \underline{z})$ = the probability that at least one of the observers detects a whale group on the track line (with perpendicular distance $x = 0$), given the covariate vector $\underline{z}$. The mark recapture (MR) component of the MRDS model is needed to estimate this probability;

$g.(x, \underline{z})$ = the probability that at least one of the observers detects a whale group at perpendicular distance x from the track line, given the covariate vector $\underline{z}$ and under the assumption that $g.(0, \underline{z}) = 1$. The distance sampling (DS) component of the MRDS model is needed to estimate this probability.

$p.(x, \underline{z})$ is derived from the individual detection functions in the following way (Laake and Borchers, 2004):

$$p.(x, \underline{z}) = p_1(x, \underline{z}) + p_2(x, \underline{z})\,[1 - p_{1|2}(x, \underline{z})] \qquad (2)$$

where: $p_j(x, \underline{z})$ = the probability that observer j detects a whale group at perpendicular distance x from the track line, given the covariate vector $\underline{z}$, for $j = 1$ or 2;
$p_{1|2}(x, \underline{z})$ = the conditional probability that observer 1 detects a whale group at perpendicular distance x from the track line, given that observer 2 detects the animal, for covariate vector $\underline{z}$.

To model the DS component, the half-normal and hazard-rate key functions without any adjustment terms were considered (see Buckland *et al.* [2001] for the formulae of these functions). The MR component as implemented in the MRDS package is the logistic model:

$$p_{j|3-j}(x, \underline{z}) = \frac{\exp(\beta_0 + \beta_1 z_1 + \ldots + \beta_q z_q)}{1 + \exp(\beta_0 + \beta_1 z_1 + \ldots + \beta_q z_q)} \qquad (3)$$

where: $p_{j|3-j}(x, \underline{z})$ = the conditional probability that observer j detects a whale group at perpendicular distance x from the track line, given that observer ($3-j$) also detects the group, for sighting covariates $z_1 \ldots, z_q$; $\beta_0, \ldots, \beta_q$ = parameters to be estimated, with q = total number of covariates.

School size, sightability and sea state were considered as covariates for the detection-function models. All covariates were fitted as factor variables, with five levels for school size (i.e. 1, 2, 3–4, 5–9, 10+), four levels for sightability (2, 3, 4 and 5) and two levels for sea state (0 = Beaufort 0–2; 1 = Beaufort 3+) (Bravington and Hedley, 2009; Okamura and Kitakado, 2009). Model selection was based on Akaike's Information Criterion (AIC) (Akaike, 1973).

Only Antarctic minke whale sightings collected during double platform effort in IO mode were used to model MR detection functions with the assumption of 'point independence'. This means that the individual detection probabilities $p_1(x, \underline{z})$ and $p_2(x, \underline{z})$ are independent at $x = 0$, but not necessarily elsewhere (Laake and Borchers, 2004). The $p.(0, \underline{z})$ values were only estimated for surveys since the 1985/86 season, which collected IO data, but not previously. Models for $p.(x, \underline{z})$ were fitted using all IO data pooled over the following Area(s): Areas I + II, Areas III + IV + VI and Area V. Pooling was necessary to meet the recommendation of having at least 60 duplicate sightings, which is desirable for a good detection-function model (Buckland *et al.*, 2001; Hedley *et al.*, 2001). Detection-function models were fitted per vessel when sample size was appropriate.

The estimated $p.(0, \underline{z})$ values were smaller than 1 for all surveys conducted since 1985/86. Therefore, the $p.(0, \underline{z}) = 1$ assumption was also relaxed for the surveys between 1981/82 and 1984/85, for which IO data were not available. For these surveys, $g.(x, \underline{z})$ values were estimated by fitting detection functions to data collected under closing mode. As every vessel collected more than 60 sightings during each survey, detection-function models for $g.(x, \underline{z})$ were fitted per vessel and season. Values of $p.(0, \underline{z})$ were predicted with the detection-function models fitted to IO data in the same Areas. For instance, the detection-function model based on IO data pooled over Areas I + II was used to predict $p.(0, \underline{z})$ values for the 1982/83 survey, which was conducted in Area I. Estimates of $p.(x, \underline{z})$ for the early surveys were then derived from the individual components using equation (1). In this way, although IO data were not available for these surveys, sightings and covariate information collected during these surveys were used to determine the shape of the detection function.

Remote sensing data

The IWC/IDCR-SOWER surveys were specifically designed to detect cetaceans and relatively few non-biotic data were collected when compared to cruises under multi-disciplinary programmes such as SO GLOBEC and CCAMLR 2000. No observations were made on krill during the IWC/IDCR-SOWER cruises and *in situ* biotic data are not available. Instead, remote sensing datasets were used for the derivation of potential environmental covariates needed to study the relationships between Antarctic minke whale density and their environment. Ocean depth and continental shelf break locations were obtained from the General Bathymetric Chart of the Oceans (GEBCO) dataset, at one lat-lon minute resolution (IOC *et al.*, 2003). Sea ice concentrations were estimated from weekly passive microwave remote sensing data, derived from measurements obtained by the Scanning Multichannel Microwave Radiometer (SMMR) onboard the Nimbus-7 satellite and by the Special Sensor Microwave Imagers (SSM/I) onboard Defense Meteorological Satellite Program (DMSP) satellites F8, F11 and F13. Version 2 of the sea ice concentration data were used, released in September 2007, which had a 0.2° × 0.2° resolution (Cavalieri *et al.*, 1996, updated 2006). Weekly 0.083° × 0.083° gridded chlorophyll a concentration data were derived from the NASA Sea-viewing Wide Field-of-view Sensor (SeaWiFS) dataset (*http://oceancolor.gsfc.nasa.gov/SeaWiFS*). For sea surface temperature, Optimum Interpolation version 2 Sea Surface Temperature (hereafter called OISST) data (Reynolds *et al.*, 2002; Reynolds and Smith, 1994) were used, provided on an approximately 7 day interval one-degree latitude-longitude grid (*http://www.cdc.noaa.gov/data/gridded/data.noaa.oisst.v2.html*). Frontal zone locations were obtained from two sources: firstly, positions were used of the Southern Antarctic Circumpolar Current Front (SACCF) and the Southern Boundary of the Antarctic Circumpolar Current (SBACC) as identified by Orsi *et al.* (1995), based on long-term datasets; secondly, sea surface velocities (SSV), a proxy for frontal zone location, were derived from absolute geostrophic velocities from AVISO (Archiving, Validation and Interpretation of Satellite Oceanographic data) on a weekly 1/3° × 1/3° Mercator grid based on altimetry instruments onboard the Topex/Poseidon, Jason-1, ERS and ENVISAT satellites.

Spatial models and potential covariates

Antarctic minke whale sightings were used in spatial models based on line transect data using GAMs from Wood (2006), as implemented in the R software library *mgcv (*V1.5–5). The count method developed by Hedley *et al.* (1999) was applied for which the transect line was divided into equal segments of ten nautical miles.

The number of Antarctic minke whales per segment area, N_i, was obtained using the following Horvitz-Thompson-like (Horvitz and Thompson, 1952) estimator:

$$\hat{N}_i = \Sigma_j \frac{n_{i,j}}{\hat{p}(x, \underline{z})_{i,j}} \tag{4}$$

where: $n_{i,j}$ = the number of minke whales within group j in segment i;
$\hat{p}.(x, \underline{z})_{i,j}$ = the estimated probability that at least one of the observers detects the jth group in segment i, at perpendicular distance x from the track line, given the covariate vector $\underline{z}$.

$\hat{N}$ was then used as the response variable for GAMs that assumed a logarithmic link-function and a Tweedie error distribution. Tweedie distributions are characterised by a variance that is proportional to the power θ of the mean (Peel *et al.*, 2008). Within the package *mgcv* (Wood, 2006), the best value of θ was selected where $1<\theta<2$, based on the best possible fit according to standard diagnostic plots. Furthermore, the quasi-Poisson and simple Poisson error distributions were considered, which are special cases of the more general Tweedie distribution (Peel *et al.*, 2008).

The following GAM-model (Hedley *et al.*, 1999) was used with the natural logarithm of the segment area as an offset variable:

$$E(\hat{N}_i) = \exp\left[\ln(A_i) + \theta_0 + \Sigma_r f_r(k_{i,r})\right] \tag{5}$$

where: A_i = segment area, equal to 2 l_i w (l_i = segment length, with w = 1.5 nmi);
θ_0 = intercept;
$k_{i,r}$ = value of covariate r for segment i;
f_r = smoothed function ('smoother') of covariate r.

Two different smoother function types were considered, namely isotropic smoothers and tensor product smoothers.

Potential covariates used in the spatial models were: closest distance to the sea ice edge, defined at 15% sea ice concentration (Tynan and Thiele, 2003), bathymetric depth and nearest distance to the continental shelf break, defined as the 1000m depth contour, SSV and closest distances to the SACCF and SBACC, OISST, chlorophyll a, latitude and longitude (latter two covariates both in degrees). The GAMs were fitted independently by survey year. Although the package *mgcv* can be used for automated model selection (Wood, 2008), a somewhat *ad hoc* selection procedure was used, as the primary aim was to identify important whale density – environment relationships with this study, instead of maximising explained deviance. Also, covariate interaction terms were not considered in this study. Model selection was based on minimisation of the Generalised Cross Validation (GCV) score, while excluding GAMs that generated extreme minke whale density values.

To avoid overfitting, the degree of covariate smoothing was constrained by setting the argument gamma to 1.4 within the function 'gam' of package *mgcv* (Wood, 2006, p.256). Forward selection was used as a selection procedure: in each step, covariates were considered which had correlation coefficients smaller than 0.7 with the covariates that were already selected in the previous steps. In each step, the covariate was selected for which inclusion showed the largest increase in explained deviance. A new covariate was only retained if it was significant, lowered the GCV score, and increased the amount of explained deviance by at least 4% (Southwell *et al.*, 2008).

Predicted density maps

Spatial models were used to generate Antarctic minke whale density surfaces for each Area and year, in regions encompassed by the surveyed strata. Density maps were used to examine the predictions of the selected models, e.g. to identify extreme predicted density values, if present. Antarctic minke whale densities were only predicted for the surveyed strata, which were all in open waters of the Southern Ocean. Predicted density maps on a 0.2-degree latitude-longitude grid were plotted with ESRI ArcMap V9.2 (ESRI, 2006).

In order to compare the results between different surveys, whale density, $\hat{D}_v$, was defined as $\hat{N}_v/A_v$, the number of Antarctic minke whales per km^2 for grid cell v. The segment area per grid cell, A_v, was calculated using the South Pole Lambert Azimuthal Equal Area polar projection within ArcMap. As surveys within a specific Area took place over weeks throughout the year, covariate values were estimated for the middle date of the overlapping survey period for surveys conducted within the same Area.

RESULTS

Whale sightings and detection probabilities

Tables 2 and 3 summarise the selected detection-function models and derived detection probability estimates (also Figs 2 and 3). To illustrate the model selection process, Tables 4 and 5 list the detection-function model fits of the models that were successfully fitted. The $\bar{g}.(x)$ estimates for the surveys between 1981/82 and 1984/85 ranged from 0.392 (SE = 0.048, vessel K27, 1983/84 survey) to 0.576 (SE = 0.022, vessel SM2, 1982/83 survey). For these surveys, sea state data were only available for the 1984/85 survey. School size was the only sighting covariate apart from perpendicular distance that was frequently included in the models (Table 2), even though sightability and sea state were also considered as sighting covariates in some of the surveys (Table 4). The estimated $\bar{p}.(0)$ values for surveys conducted

Table 2

Summary of selected detection function models and derived $\hat{\bar{g}}.(x)$ estimates for surveys between 1981/82 and 1984/85. $\hat{\bar{g}}.(x)$ is the estimated average detection probability derived from the detection function model which assumed $g(0) = 1$. Detection function models were fitted per survey year and vessel. Abbreviations: hn = half-normal model, hr = hazard-rate model, x = perpendicular distance, s = school size.

Survey season	Area	Vessel	Number of sightings	Selected model	$\hat{\bar{g}}.(x)$ ± SE
1981/82	II	SM1	268	hn ($x + s$)	0.480 ± 0.021
		SM2	198	hn ($x + s$)	0.455 ± 0.022
1982/83	I	SM1	179	hn ($x + s$)	0.558 ± 0.032
		SM2	393	hn ($x + s$)	0.576 ± 0.022
1983/84	VI	SM1	120	hr ($x + s$)	0.492 ± 0.054
		SM2	165	hn (x)	0.410 ± 0.019
		K27	95	hr ($x + s$)	0.392 ± 0.048
1984/85	IV	SM1	73	hn (x)	0.438 ± 0.035
		SM2	162	hr ($x + s$)	0.565 ± 0.057
		K27	79	hn ($x + s$)	0.565 ± 0.047

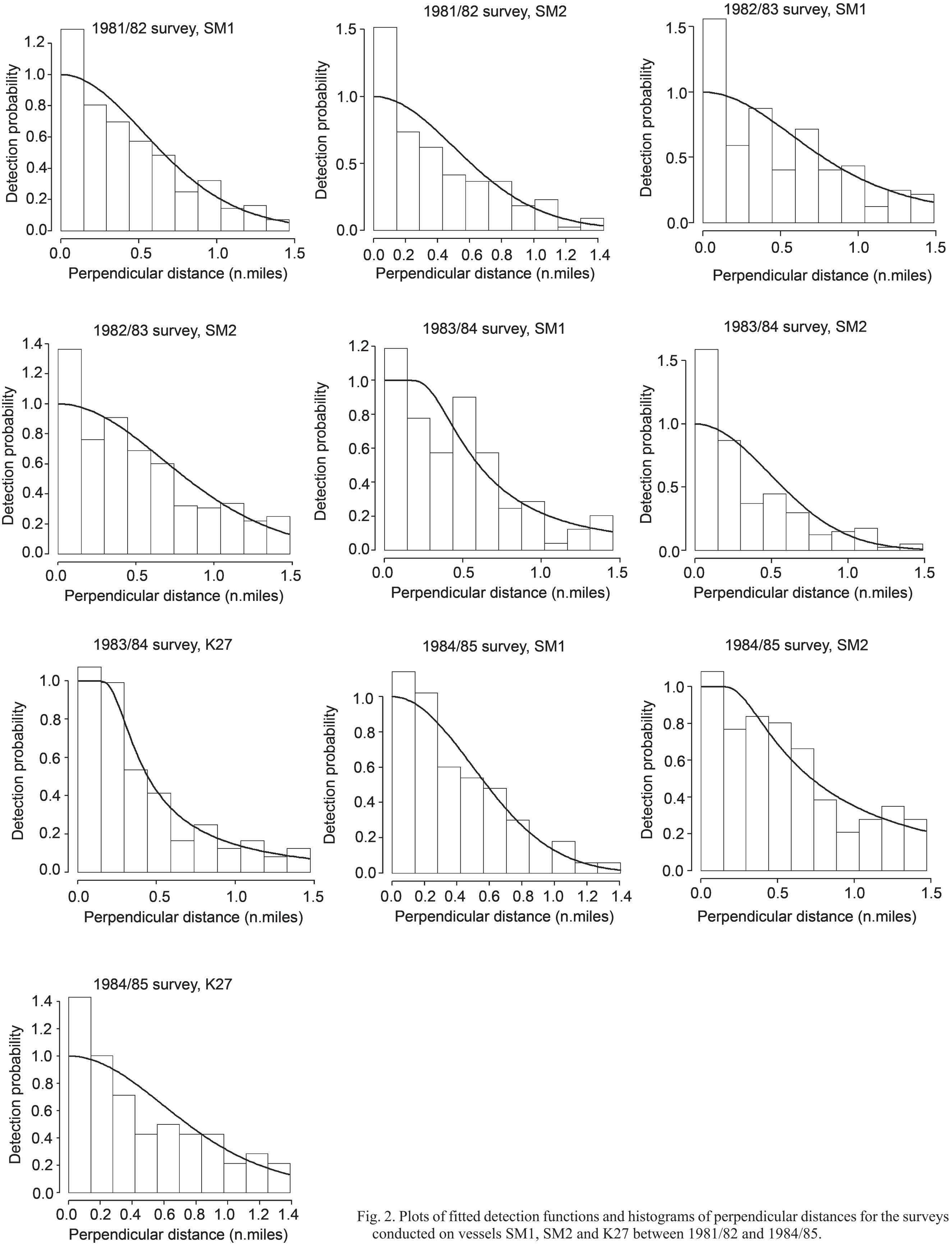

Fig. 2. Plots of fitted detection functions and histograms of perpendicular distances for the surveys conducted on vessels SM1, SM2 and K27 between 1981/82 and 1984/85.

between 1985/86 and 2003/04 ranged from 0.561 (SE = 0.027, vessels SM1 + K27, Area V) to 0.724 (SE = 0.031, vessel SM1, Areas III+IV+VI). Estimated $\overline{p}.(x)$ values ranged from 0.182 (SE = 0.021, vessel SM2, Area V) to 0.338 (SE = 0.019, vessels SM1 + K27, Areas I + II). Group size was always selected in the models (Table 3). The MR component of some models included sea state as well, but sightability never improved model fit (Table 5).

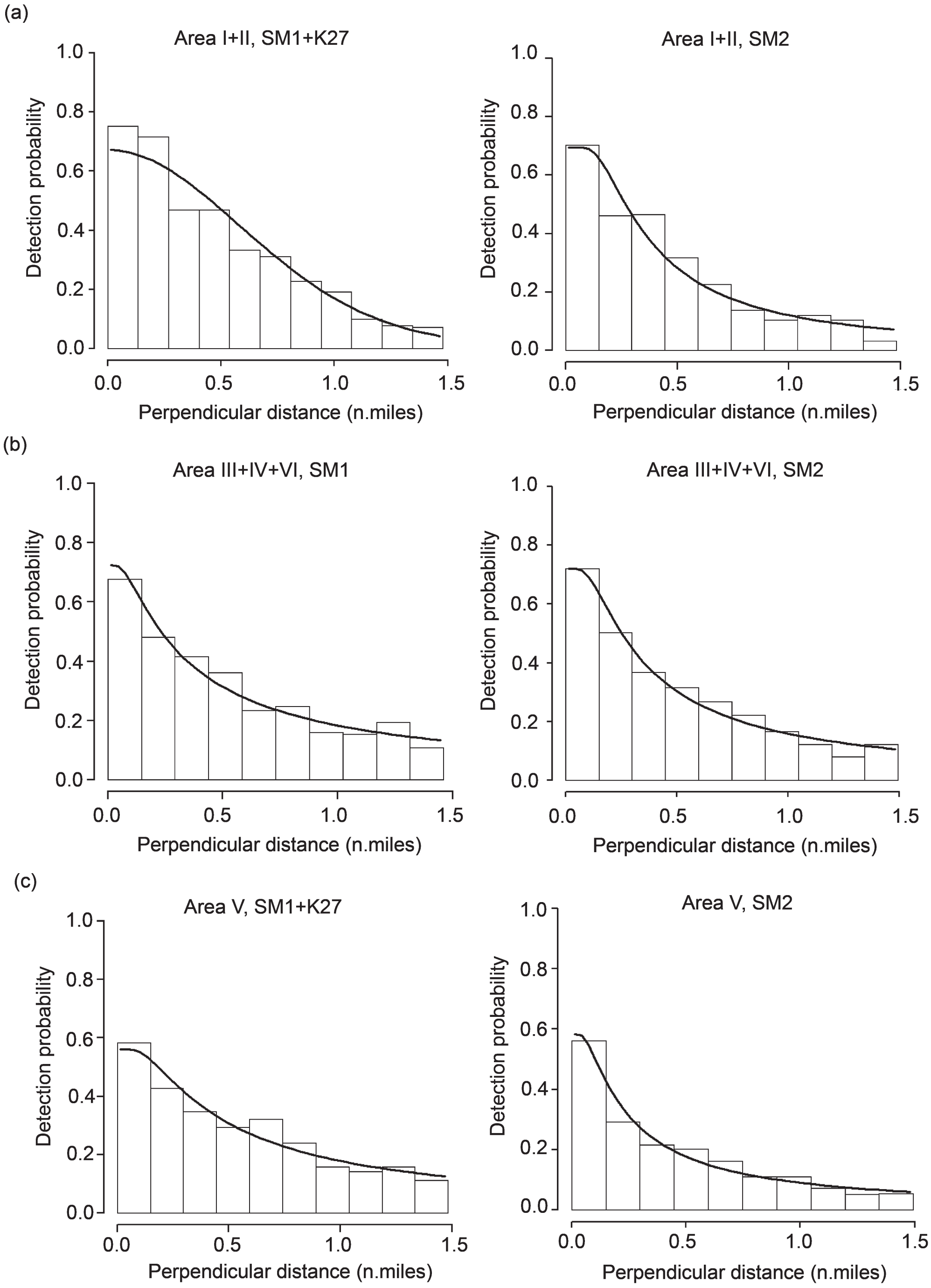

Fig. 3. Plots of fitted detection functions and histograms of perpendicular distances for the surveys conducted on vessels SM1, SM2 and K27 between 1985/86 and 2004/05. Detection function models were fitted with independent observer (IO) sightings data from all surveys conducted in the following (sets of) Area(s): (a) Areas I+II; (b) Areas III, IV and VI; (c) Area V.

Table 3

Summary of selected detection function models and derived detection probability estimates for surveys between 1985/86 and 2003/04. Detection function models were fitted with Independent Observer (IO) sightings data from all surveys conducted in the following (sets of) Area(s): (a) Areas I + II; (b) Areas III, IV and VI; and (c) Area V. $\hat{p}.(0)$ is the estimated average probability of sighting an Antarctic minke whale group on the survey line, derived from the mark recapture (MR) model. All MR models assumed point independence. $\hat{g}.(x)$ is the estimated average detection probability derived from the distance sampling (DS) model which assumed $g(0) = 1$. $\hat{p}.(x)$ is the estimated average detection probability from the mark recapture distance sampling (MRDS) model. Abbreviations: hn = half-normal model, hr = hazard-rate model, x = perpendicular distance, s = school size, ss = sea state.

Area	Vessel	Number of duplicate sightings	Selected model	$\hat{p}.(0) \pm SE$	$\hat{g}.(x) \pm$ SE	$\hat{p}.(x) \pm$ SE
I + II	SM1 + K27	119	hn (DS: $x + s$, MR: $x + s$)	0.672 ± 0.030	0.503 ± 0.017	0.338 ± 0.019
	SM2	135	hr (DS: $x + s$, MR: $x + s$)	0.696 ± 0.029	0.384 ± 0.028	0.267 ± 0.023
III + IV + VI	SM1	127	hr (DS: $x + s$, MR: $x + s + ss$)	0.724 ± 0.031	0.418 ± 0.045	0.303 ± 0.036
	SM2	167	hr (DS: x, MR: $x + s$)	0.721 ± 0.025	0.400 ± 0.034	0.289 ± 0.027
V	SM1 + K27	234	hr (DS: $x + s$, MR: $x + s + ss$)	0.561 ± 0.027	0.496 ± 0.034	0.278 ± 0.024
	SM2	152	hr (DS: $x + s$, MR: $x + s + ss$)	0.584 ± 0.031	0.313 ± 0.031	0.182 ± 0.021

Table 4

Detection-function model fits with AIC and ΔAIC for the surveys conducted between 1981/82 and 1984/85. Abbreviations: hn = half-normal model, hr = hazard-rate model, x = perpendicular distance, s = school size, sg = sightability, ss = sea state. Selected models are in bold. Only models with good fits are listed.

Survey season	Area	Vessel	Model	AIC	ΔAIC
1981/82	II	SM1	**hn (x+s)**	**60.8**	**0**
			hn (x+sg)	73.1	12.3
			hn (x)	74.9	14.1
		SM2	**hn (x+s)**	**22.6**	**0**
			hn (x)	28.8	6.2
			hn (x+sg)	30.5	7.9
			hn (x+s+sg)	21.0	8.4
1982/83	I	SM1	**hn (x+s)**	**79.8**	**0**
			hn (x+s+sg)	81.9	2.1
			hn (x)	94.6	14.8
			hn (x+sg)	94.7	14.9
		SM2	**hn ($x + s$)**	**194.2**	**0**
			hn ($x + sg$)	197.0	2.8
			hn ($x + s + sg$)	199.6	5.4
			hn (x)	204.2	10.0
1983/84	VI	SM1	**hr ($x + s$)**	**38.8**	**0**
			hr (x)	39.4	0.6
			hn (x)	40.5	1.7
			hr ($x + sg$)	41.2	2.4
			hr ($x + s$)	41.7	2.9
		SM2	**hn (x)**	**– 0.14**	**0**
			hn ($x + sg$)	1.81	2.0
			hn ($x + s$)	1.86	2.0
		K27	**hr ($x + s$)**	**5.1**	**0**
			hr ($x + s + sg$)	9.0	3.9
			hr ($x + s$)	11.7	6.6
			hr (x)	12.2	7.1
			hn (x)	21.6	16.5
1984/85	IV	SM1	**hn (x)**	**1.5**	**0**
			hn ($x + s$)	2.1	0.6
			hr (x)	3.1	1.6
			hn ($x + sg$)	3.4	1.9
			hn ($x + ss$)	3.5	2.0
		SM2	**hr ($x + s$)**	**78.9**	**0**
			hr (x)	94.1	15.2
			hn (x)	95.6	16.7
			hr ($x + ss$)	95.8	16.9
			hr ($x + sg$)	96.1	17.2
		K27	**hn ($x + s$)**	**29.3**	**0**
			hn (x)	31.0	1.7
			hn ($x + ss$)	31.9	2.6
			hn ($x + sg$)	32.3	3.0

Spatial models and selected covariates

To illustrate goodness-of-fit, Fig. 4 shows standard diagnostic plots for a fitted GAM using the gam.check function in package *mgcv*. Plots correspond to data collected during the 1981/82 survey and show patterns common to the majority of models fitted in this study. For instance, the QQ-plot (upper left panel) has a convex shape and the histogram of residuals (lower left panel) is right-skewed. Nevertheless, the distribution of predicted Antarctic minke whale density for the 1981/82 survey corresponded broadly with the sightings distribution (Fig. 5). The moderate model fit is the result of the high proportion of segments for which no schools were sighted: this proportion was often in excess of 70% for the various survey years. Methods specifically devised for zero-inflated data (R package *COZIGAM* 2.0–2, Liu and Chan, 2009) could not improve the results, due to non-convergence issues during the iteration process of model fitting.

GAM model descriptions are given in Table 6. It was not possible to select a good model, based on spatial covariates which were the main focus of this analysis, for the 1995/96 and 2001/02 surveys. Seven out of ten potential covariates were included at least once in the selected GAMs; only SSV, chlorophyll a concentration and latitude were never selected.

Table 5

Detection-function model fits with AIC and ΔAIC for the surveys conducted between 1985/86 and 2003/04. Abbreviations: hn = half-normal model, hr = hazard-rate model, DS = Distance Sampling model, MR = Mark Recapture model, x = perpendicular distance, s = school size, sg = sightability, ss = sea state, v = vessel. Selected models are in bold. Only models with good fits are listed.

Area	Vessel	Model	AIC	ΔAIC
I+II	SM1+K27	**hn (DS: $x + s$, MR: $x + s$)**	**1,242.9**	**0**
		hn (DS: $x + s + ss$, MR: $x + s$)	1,245.9	3.0
		hn (DS: $x + s + sg$, MR: $x + s$)	1,248.0	5.1
		hn (DS: $x + sg$, MR: $x + s$)	1,250.1	7.2
		hn (DS: $x + ss$, MR: $x + s$)	1,251.5	8.6
		hn (DS: x, MR: $x + s$)	1,255.9	13
		hn (DS: x, MR: $x + s + ss$)	1,257.0	14.1
		hn (DS: x, MR: $x + s + v$)	1,257.7	14.8
		hn (DS: x, MR: $x + s + sg$)	1,259.2	16.3
		hr (DS: x, MR: $x + s$)	1,259.4	16.5
		hn (DS: x, MR: $x + ss$)	1,291.6	48.7
		hn (DS: x, MR: x)	1,291.7	48.8
		hn (DS: x, MR: $x + v$)	1,292.6	49.7
		hn (DS: x, MR: $x + sg$)	1,296.1	53.2
	SM2	**hr (DS: $x + s$, MR: $x + s$)**	**1,176.9**	**0**
		hr (DS: $x + sg$, MR: $x + s$)	1,180.2	3.3
		hr (DS: x, MR: $x + s$)	1,180.3	3.4
		hr (DS: $x + ss$, MR: $x + s$)	1,182.3	5.4
		hn (DS: x, MR: $x + s$)	1,191.1	14.2
		hn (DS: x, MR: $x + s + ss$)	1,191.1	14.2
		hn (DS: x, MR: x)	1,201.1	24.2
		hn (DS: x, MR: $x + ss$)	1,202.0	25.1
III+IV+VI	SM1	**hr (DS: $x + s$, MR: $x + s + ss$)**	**1,188.4**	**0**
		hr (DS: x, MR: $x + s + ss$)	1,191.7	3.3
		hr (DS: $x + sg$, MR: $x + s + ss$)	1,193.0	4.6
		hr (DS: $x + ss$, MR: $x + s + ss$)	1,193.2	4.8
		hn (DS: x, MR: $x + s + ss$)	1,206.3	17.9
		hn (DS: x, MR: $x + s$)	1,213.3	24.9
		hn (DS: x, MR: $x + s + sg$)	1,215.3	26.9
		hn (DS: x, MR: $x + ss$)	1,216.0	27.6
		hn (DS: x, MR: x)	1,222.8	34.4
		hn (DS: x, MR: $x + sg$)	1,224.2	35.8
III+IV+VI	SM2	**hr (DS: x, MR: $x + s$)**	**1,588.4**	**0**
		hr (DS: $x + s$, MR: $x + s$)	1,588.7	0.3
		hr (DS: $x + sg$, MR: $x + s$)	1,590.4	2.0
		hr (DS: $x + ss$, MR: $x + s$)	1,590.4	2.0
		hn (DS: x, MR: $x + s$)	1,614.3	25.9
		hn (DS: x, MR: $x + s + ss$)	1,615.3	26.9
		hn (DS: x, MR: $x + ss$)	1,618.9	30.5
		hn (DS: x, MR: $x + s + sg$)	1,621.1	32.7
		hn (DS: x, MR: x)	1,624.8	36.4
		hn (DS: x, MR: $x + sg$)	1,631.1	42.7
V	SM1 + K27	**hr (DS: $x + s$, MR: $x + s + ss$)**	**2,373.6**	**0**
		hr (DS: x, MR: $x + s + ss$)	2,380.6	7.0
		hr (DS: $x + sg$, MR: $x + s + ss$)	2,391.2	17.6
		hr (DS: $x + ss$, MR: $x + s + ss$)	2,392.2	18.6
		hn (DS: x, MR: $x + s + ss$)	2,396.3	22.7
		hn (DS: x, MR: $x + ss$)	2,445.3	71.7
		hn (DS: x, MR: $x + s$)	2,447.3	73.7
		hn (DS: x, MR: $x + s + sg$)	2,449.9	76.3
		hn (DS: x, MR: x)	2,466.6	93.0
		hn (DS: x, MR: $x + sg$)	2,468.1	94.5
	SM2	**hr (DS: $x + s$, MR: $x + s + ss$)**	**1,291.9**	**0**
		hr (DS: $x + sg$, MR: $x + s + ss$)	1,294.3	2.4
		hr (DS: x, MR: $x + s + ss$)	1,296.9	5.0
		hr (DS: $x + ss$, MR: $x + s + ss$)	1,298.5	6.6
		hn (DS: x, MR: $x + s + ss$)	1,339.0	47.1
		hn (DS: x, MR: $x + s$)	1,342.3	50.4
		hn (DS: x, MR: $x + ss$)	1,361.9	70.0
		hn (DS: x, MR: x)	1,365.4	73.5

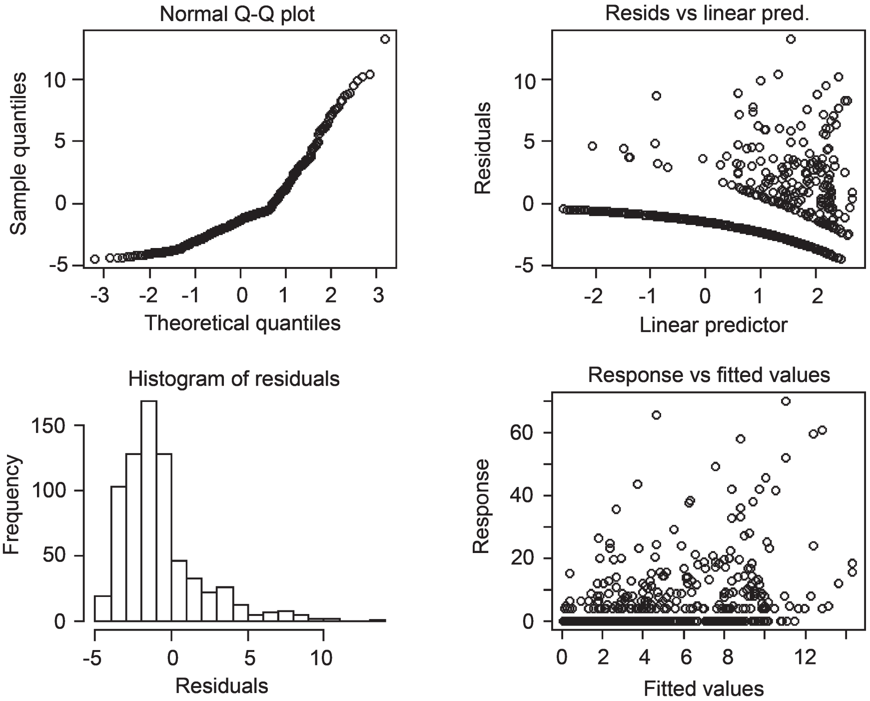

Fig. 4. Standard diagnostic plots for the model based on the 1981/82 survey.

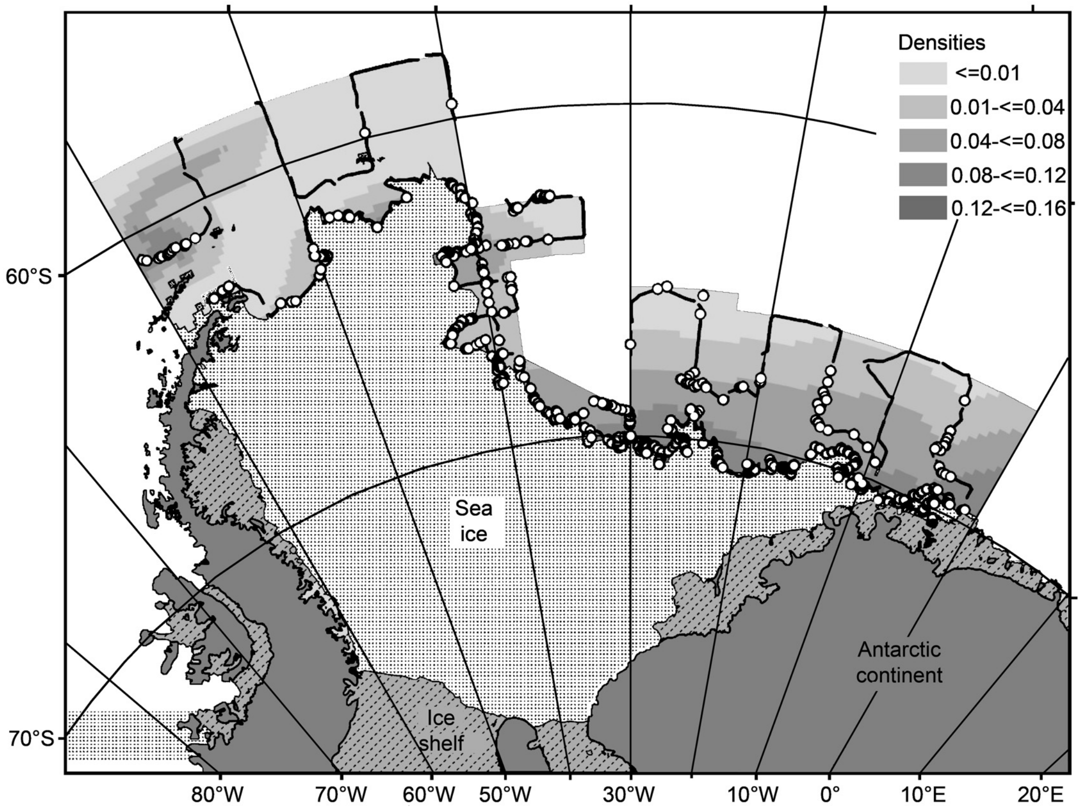

Fig. 5. Prediction plot of Antarctic minke whale density in the Weddell Sea sector (Area II) for the 1981/82 survey. Density, expressed in number of whales per km^2, was only predicted for surveyed strata. Sightings are represented by circles; survey effort is displayed by thick solid lines. The overlapping period for surveys conducted in Area II was 16 January – 8 February.

Of the environmental covariates, closest distance to the continental shelf break (1000m-dist), sea ice edge (icedist) and SACCF (SACCFdist) were most often included in the models. Table 7 shows selected model output. Explained deviances ranged from 14.9% to 35.1%, with a mean explained deviance of 25.3%.

Table 7 highlights the highly variable nature of the relationships between whale density and the environment. Firstly, none of the covariates showed a consistent qualitative relationship with its effect on Antarctic minke whale density. However, three covariates (1,000m-dist, icedist and OISST) had a predominantly negative relationship with density. No

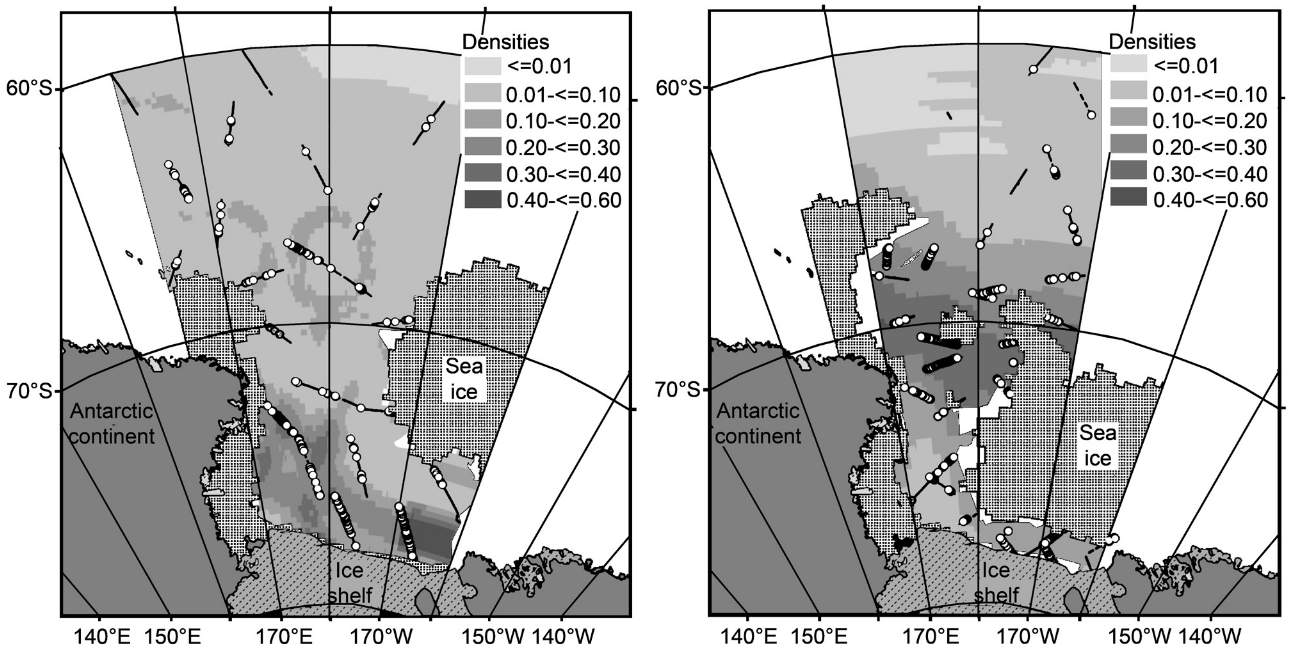

Fig. 6. Prediction plots of Antarctic minke whale density in the Ross Sea sector (Area V) for the 1985/86 survey (a) and 2003/04 survey (b). Density, expressed in number of whales per km^2, was only predicted for surveyed strata. Sightings in independent observer (IO) mode are represented by circles; survey effort in IO mode is displayed by thick solid lines. The overlapping period for surveys conducted in Area V was 27 December – 8 February.

dominant qualitative relationships were found for longitude, depth, SACCFdist or SBACCdist. Secondly, the selected models for every Management Area had variable sets of covariates. None of the covariates were selected in all surveys conducted in the same Management Area. Icedist was most often selected in models based on surveys in the Weddell Sea sector (Area II), a sector characterised by strong seasonal ice melt. Furthermore, icedist was non-significant for all models based on surveys in regions within the Bellingshausen/Amundsen Seas (Area I) and Indian Ocean sector (Area III). Areas I and III were characterised by relatively small sea ice coverage throughout the survey period. 1000m-dist was most often selected in models based on surveys conducted in Area III.

Table 6

Descriptions of selected models per area and survey year. Numbers between brackets in the 'selected model' column refer to the covariate-specific number of degrees of freedom. Numbers between brackets in the error distribution column refer to the selected θ-value for the Tweedie error distribution. Abbreviations of the smoothers: s = isotropic smoother, te = tensor product smoother. Abbreviations of the covariates: *icedist* = closest distance to the sea ice edge (defined at 15% sea ice concentration), *OISST* = Optimally Interpolated Sea Surface Temperature, *1000m-dist* = closest distance to the continental shelf edge (defined at 1000m depth), *SACCFdist* = closest distance to the Southern Antarctic Circumpolar Current Front (SACCF), *SBACCdist* = closest distance to the Southern Boundary of the Antarctic Circumpolar Current (SBACC). Model descriptions are given as fitted with the R software library *mgcv* (V1.5–5). All models included an offset variable which consisted of the natural logarithm of the segment area.

Area	Survey season	Selected model	Error distribution
I	1982/83	s(*longitude*, 2.6) + s(*1000m-dist*, 8.4)	Tweedie (1.3)
	1989/90	s(*OISST*, 3.0) + s(*SACCFdist*, 4.8)	Tweedie (1.4)
	1993/94	s(*longitude*, 8.7) + s(*1000m-dist*, 2.0)	Tweedie (1.2)
	1999/2000	s(*longitude*, 4.5) + s(*1000m-dist*, 1.0)	Tweedie (1.3)
II	1981/82	s(*icedist*, 3.0) + s(*SACCFdist*, 7.8)	Tweedie (1.1)
	1986/87	s(*longitude*, 7.2) + s(*depth*, 4.0)	Tweedie (1.3)
	1996/97	s(*longitude*, 4.0) + s(*icedist*, 3.0)	Tweedie (1.1)
	1997/98	s(*icedist*, 2.1) + s(*1000m-dist*, 4.0)	quasi-Poisson
III	1987/88	s(*longitude*, 8.4) + te(*1000m-dist*, 1.0)	Tweedie (1.1)
	1992/93	s(*longitude*, 4.0) + s(*1000m-dist*, 4.9)	Tweedie (1.1)
	1994/95	s(*OISST*, 6.1) + s(*1000m-dist*, 1.0) + te(*SACCFdist*, 1.8)	quasi-Poisson
	2004/05	s(*OISST*, 1.0) + s(*depth*, 4.0)	Tweedie (1.3)
IV	1984/85	s(*longitude*, 8.0) + te(*OISST*, 2.2) + s(*SBACCdist*, 5.0)	Tweedie (1.1)
	1988/89	s(*longitude*, 4.0) + s(*icedist*, 2.0)	Tweedie (1.3)
	1998/99	s(*longitude*, 4.0) + s(*1000m-dist*, 1.6)	Tweedie (1.3)
V	1985/86	s(*depth*, 4.0) + s(*1000m-dist*, 4.0)	Tweedie (1.2)
	1991/92	s(*1000m-dist*, 1.0) + s(*SACCFdist*, 7.0)	Tweedie (1.3)
	2002/03	s(*longitude*, 6.3) + s(*icedist*, 1.0)	Tweedie (1.1)
	2003/04	s(*OISST*, 4.0) + s(*SACCFdist*, 2.7)	Tweedie (1.2)
VI	1983/84	s(*longitude*, 2.5) + s(*1000m-dist*, 7.4)	Tweedie (1.2)
	1990/91	s(*icedist*, 2.0) + te(*SACCFdist*, 3.4)	quasi-Poisson
	2000/2001	s(*longitude*, 8.4) + s(*icedist*, 1.4)	quasi-Poisson

Table 7

Model output for the various surveys, grouped per IWC Area. The covariate columns show the relationships between a specific covariate and the effect of the specific covariate on Antarctic minke whale density. Abbreviations of the covariates: *icedist* = closest distance to the sea ice edge (defined at 15% sea ice concentration), *OISST* = Optimally Interpolated Sea Surface Temperature, *1000m-dist* = closest distance to the continental shelf edge (defined at 1,000m depth), *SACCFdist* = closest distance to the Southern Antarctic Circumpolar Current Front (SACCF), *SBACCdist* = closest distance to the Southern Boundary of the Antarctic Circumpolar Current (SBACC). Legend for the relationship characterisations: — = negative, + = positive, ∪ = minimum effect on density in middle of covariate range, ∩ = maximum effect on density in middle of covariate range, NL = complex non-linear relationship.

			Covariates						
IWC Area	Survey season	Explained deviance (%)	*Longitude*	*Icedist*	*OISST*	*Depth*	*1000m-dist*	*SACCF-dist*	*SBACC-dist*
Area I	1982/83	21.5	∩				—		
(120–60°W)	1989/90	22.0			—			∪	
	1993/94	30.5	NL				—		
	1999/2000	32.8	+				—		
Area II	1981/82	27.3		—				NL	
(60°W–0)	1986/87	26.4	NL			—			
	1996/97	23.7	—	∪					
	1997/98	35.1		—			+		
Area III	1987/88	33.4	NL				—		
(0–70°E)	1992/93	31.2	—				—		
	1994/95	33.5			—		—	—	
	2004/05	30.8			—	NL			
Area IV	1984/85	17.0	NL		—				NL
(70–130°E)	1988/89	28.2	∪	—					
	1998/99	20.9	NL				—		
Area V	1985/86	19.5				—	∩		
(130°E–170°W)	1991/92	14.9					—	NL	
	2002/03	17.4	NL	—					
	2003/04	24.8			—			∩	
Area VI	1983/84	23.6	—				NL		
(170–120°W)	1990/91	15.5		—				∪	
	2000/2001	27.3	NL	—					

Density distributions

The Antarctic minke whale density distribution plots generated with the spatial models showed changes in whale density distribution throughout the years. As an example, Fig. 6 shows the predicted density distributions within the Ross Sea sector (165°E–170°W) for the 1985/86 and 2003/04 surveys. For both surveys, relatively high minke whale densities were predicted on or near the continental shelf. However, minke whale densities higher than 0.2 whale per km^2 were exclusively predicted below 72°S for the 1985/86 survey (Fig. 6a), whereas these densities were predicted within the 68°–72°S band for the 2003/04 survey (Fig. 6b). These results suggest an important spatial and temporal heterogeneity in Antarctic minke whale density and distribution.

DISCUSSION

Detection probabilities

Detection probability estimates as reported by Bravington and Hedley (2009) were closest to independent estimates reported by Burt *et al.* (2009), based on Buckland-Turnock (BT) mode experiments conducted during 2005/06–2007/08 (IWC, 2009). Therefore, the detection probability estimates in this study were compared with those reported by Bravington and Hedley (2009); the estimates in Burt *et al.* (2009) were derived from a different dataset. As $\bar{p}.(0)$ estimates in Bravington and Hedley (2009) were only provided for the individual platforms, the estimates for $\bar{p}.(x)$ were compared with each other (Table 8). For the majority of CPII sightings, $\bar{p}.(x)$ estimates reported by the two studies were similar. Furthermore, $\bar{p}.(x)$ estimates were also similar for the two largest classes of CPIII sightings. These two classes contained only sightings of one-animal schools, and had sightability values of 3 and 4+, respectively. For almost all other classes of CPIII sightings, $\bar{p}.(x)$ estimates in this study were lower than those reported by Bravington and Hedley (2009). The exception was sightings of individual whales seen with sightability 2, which had a higher $\bar{p}.(x)$ estimate in this study.

The discrepancies in $\bar{p}.(x)$ estimates for various classes may be partly attributed to the different ways in which the two studies pooled IO sightings data. Furthermore, Bravington and Hedley (2009) developed a more sophisticated method for estimating detection probabilities, which takes school size errors into account. The possibility that discrepancies in $\bar{p}.(x)$ estimates could affect presented model output was assessed by comparing the output of the models presented in this paper with models in which the $\bar{p}.(x)$ estimates reported by Bravington and Hedley (2009) were incorporated. It was found that the model output in terms of covariate inclusion and the qualitative nature of covariate- whale density relationships remained the same. However, explained deviance was often somewhat lower for the models that incorporated the $\bar{p}.(x)$ estimates reported by Bravington and Hedley (2009). The aim of this study was to examine the relationships between whale density and the environment; the detection probability estimates were not used for whale abundance estimation. Therefore, the detection probability estimates reported in this paper are sufficient for the purpose of this study.

Table 8

Comparison of estimates $\overline{p}.(x)$ for in this study, $\hat{p}.(x)_{BE}$, with those reported by Bravington and Hedley (2009), $\hat{p}.(x)_{BR}$. $\hat{p}.(x)_{BR}$ is defined as $\widehat{ESW}_{BR}$ / 1.5 (truncation distance = 1.5 nmi), with $\widehat{ESW}_{BR}$ = estimated effective strip half-width as reported in Bravington and Hedley (2009). CP = circumpolar set, n = number of sightings in specific class. $\hat{p}.(x)_{DIFF} = \hat{p}.(x)_{BE}$ minus $\hat{p}.(x)_{BR}$. ESW_{BR} estimates are given for classes defined by sea state for CPII surveys, and for classes defined by sightability for CPIII surveys.

Sea state	Sightability	School size	n	$\hat{p}.(x)_{BE}$	$\widehat{ESW}_{BR}$	$\hat{p}.(x)_{BR}$	$\hat{p}.(x)_{DIFF}$
CPII							
0–2		1	90	0.24	0.33	0.22	+0.02
		2	27	0.38	0.69	0.46	–0.08
		3–4	14	0.48	0.89	0.59	–0.11
		5–9	7	0.47	1.03	0.69	–0.22
		10+	3	0.71	1.30	0.87	–0.16
3+		1	812	0.23	0.29	0.19	+0.04
		2	323	0.35	0.46	0.31	+0.04
		3–4	208	0.43	0.65	0.43	0
		5–9	73	0.44	0.69	0.46	–0.02
		10+	25	0.64	1.04	0.69	–0.05
CPIII							
	4+	1	513	0.29	0.52	0.35	–0.06
		2	179	0.38	0.78	0.52	–0.14
		3–4	98	0.43	0.99	0.66	–0.23
		5–9	43	0.46	1.02	0.68	–0.22
		10+	17	0.50	1.38	0.92	–0.42
	3	1	521	0.24	0.41	0.27	–0.03
		2	176	0.33	0.64	0.43	–0.10
		3–4	121	0.40	0.85	0.57	–0.17
		5–9	44	0.42	0.91	0.61	–0.19
		10+	21	0.51	1.33	0.89	–0.38
	2	1	86	0.23	0.16	0.11	+0.12
		2	30	0.28	0.62	0.41	–0.13
		3–4	10	0.30	0.76	0.51	–0.21
		5–9	2	0.37	0.81	0.54	–0.17
		10+	1	0.63	0.98	0.65	–0.02

Exclusion of covariates in the GAMs

Most covariates considered for model selection were retained by the best models in various combinations (Table 6). Only SSV, chlorophyll a concentration and latitude were never selected in the best models. For the first two covariates, this may have been due to limitations of the available remote sensing datasets: SSV data were not available for a wide band along the sea ice edge, which made it harder to detect a signal across the survey region, if indeed there was any signal present; and chlorophyll a data were missing in a large proportion of the weekly grids due to cloud cover. The chlorophyll a range was also very small for some Areas (e.g. Area IV), which made it hard to detect any signal if present. Thus, it is not clear if a better spatial coverage of this covariate would improve the explanatory value of the models. Latitude was often highly correlated with other covariates, especially with icedist and OISST, and thus was often dropped in later steps of the model selection process.

Relationships with the environment

Covariates related to transition zones, such as 1,000m-dist, icedist and SACCFdist, were most often selected in the models. As transition zones often show enhanced productivity, the expected effect of these covariates on whale density would be smaller or more negative at greater distances to the boundaries of the zones (Kasamatsu *et al.*, 2000; Tynan, 1998). In agreement, the covariate-density effect relationships for 1,000m-dist and icedist were predominantly negative. This suggested that Antarctic minke whale density tended to be higher in regions closer to the continental shelf break and/or sea ice edge, often in colder waters (as icedist and OISST were often highly correlated, a selected model never included both icedist and OISST, with icedist having a clearer signal in more models). However, the covariate-density effect relationship for SACCFdist was often difficult to interpret, suggesting that the Antarctic Circumpolar Current may not be as important for Antarctic minke whales as it has been reported to be for larger baleen whales (Tynan, 1998).

This study suggests that relationships between minke whales and their environment are best explored at a regional scale; spatial models did not show consistent relationships between the covariates and their effects on density at the circumantarctic scale. Circumantarctic relationships between minke whale density and their environment may be non-significant, while those relationships are significant at a regional scale.

Even within Management Areas, it was not possible to detect consistent qualitative relationships between minke whale density and environment over the various survey years. This in part may be explained by the changing ice-related boundaries of the surveys between years and hence differences in survey regions. Another possible reason may be that only a limited number of environmental variables could be considered for this study. Other aspects of the environment that interact with the selected covariates, for which data were not available, may have changed throughout the years. In conjunction with this, the IWC/IDCR-SOWER surveys did not cover the pack ice region. Changes in the extent and heterogeneity of the pack ice may influence the Antarctic minke whale distribution in the pack ice region (Thiele *et al.*, 2005). The pack ice quantity and quality may affect the minke whale density distribution in open waters close to the sea ice edge as well. For instance, in years when the pack ice is more diverse in quality, shows more cracks, or encloses polynyas relatively in the proximity of the sea ice edge, Antarctic minke whales may move more easily into the pack ice region. In years when the pack ice close to the sea ice edge is more solid, the whales may be restricted in their movements into the pack ice region and stay in open waters close to the sea ice edge. In those years, the relationship between closest distance to the sea ice edge and its effect on Antarctic minke whale density in open waters may be (more) negative. In order to have a better understanding of the relationship between minke whale density and its environment in the various sectors of the Southern Ocean, more aerial and shipboard surveys within the pack ice region are needed, ideally in combination with shipboard surveys in open waters in the same sector of the Southern Ocean (Hedley *et al.*, 2007; Kelly *et al.*, 2009).

Performance and application of spatial models

Most spatial models for Antarctic minke whale density had moderate value for explained deviance. This was in part the result of the conservative selection method used in this study. The flexibility of the GAMs potentially leads to overfitting of the data (Forney, 2000; Hastie *et al.*, 2005). While overfitting is not critical for prediction purposes, it did not improve the ability to describe the physical environment underlying minke whale distribution, which was the main objective of this analysis. In order to prevent overfitting, a covariate was only selected if it contributed at least 4% to the explained deviance of the model. Alternatively, Principal Components Analysis can be used to reduce the number of intercorrelated variables, and then the principal components can be interpreted as synthetic climatic covariates (Grosbois *et al.*, 2008). However, this interpretation necessarily provides less fine-scale resolution when explaining the specific relationships whale-environment, and may not work well for covariate data sets with poor spatial resolution.

The performance of the models used in this study was probably also limited by the nature of the available environmental datasets from which covariates were derived. At this spatial scale, only remote sensing data and long-term frontal positions could be considered as covariate input for our models. Explained deviance of the models would probably increase if covariates could be included that more accurately reflect the environment, such as *in situ* data or remote sensing data at a higher resolution. For instance, explained deviances were 63.1% and higher for spatial models of baleen whales near the Western Antarctic Peninsula that included covariates derived from *in situ* chlorophyll a and acoustic zooplankton data (Friedlaender *et al.*, 2006). In order to obtain a better understanding of the relationship between whale density and the environment, more localised surveys can be conducted during which whale sightings data will be collected simultaneously with *in situ* non-biotic and biotic (prey) data.

Nevertheless, given the limited possibilities for including environmental information in our models, model performance was satisfactory. Furthermore, models could be developed for surveys under considerably different environmental conditions, such as sea ice distribution and coverage, for the same time period (Fig. 6). The predicted density maps (Figs 5 and 6) show both spatial and temporal variability in Antarctic minke whale density. Further investigation is planned on the temporal variability in density at a regional scale across the Southern Ocean by focusing on regional environmental features that were not captured by the models. Examples are regional sea ice extent during the survey and the degree of seasonal change therein. A better understanding of the temporal variability in whale density is needed for any scenario analysis of Antarctic minke whale density in the Southern Ocean under various climate regimes.

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Increasing numbers of ship strikes in the Canary Islands: proposals for immediate action to reduce risk of vessel-whale collisions

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ABSTRACT

The Canary Islands, known for their extraordinarily high cetacean species diversity, have witnessed a rapid expansion in fast and high speed ferry traffic during the past few years. At the same time, ship strikes have been increasingly reported. 556 cetacean carcasses, found ashore, or reported, in the Canary Islands between 1991 and 2007, were examined. 59 strandings (10.6%) were found to involve vessel-whale collisions, the great majority of strandings (58%) occurred on Tenerife. Species most affected were sperm whales (*Physeter macrocephalus*, *n* = 24, 41%), pygmy sperm whales (*Kogia breviceps*, *n* = 10, 17%), Cuvier's beaked whales (*Ziphius cavirostris*, *n* = 7, 12%), short-finned pilot whales (*Globicephala macrorhynchus*, *n* = 6, 10%) and at least three baleen whale species (*n* = 9, 15%). Twenty six animals (44%, *n* = 42) were either calves or juveniles, and one was a newborn. The temporal distribution of strandings indicates that lethal strikes have increased in recent years. Most ship strikes, assumingly by large and fast moving vessels, probably resulted in the death of the animals, as indicated by severe injuries such as huge slashes, cuts, broken vertebrae or animals separated into halves. Given these numbers and the widely accepted fact that only a portion of ship strikes will be recorded due to under-reporting and carcasses drifting away or sinking, ship strikes appear to be a major threat to cetaceans in the Canary Islands, especially to sperm whales. Moreover, the issue is a matter of human safety, as crew and passengers are at risk of being harmed, too. In this situation, a number of measures to mitigate the risk of ship strikes are recommended as a matter of high priority. These include the placement of dedicated look-outs on fast moving vessels, the shift of ferry transects where feasible, a speed limitation for local high-risk areas where cetacean abundance is notably high, the introduction of an obligatory reporting system of vessel-whale collisions and the conduction of detailed studies dealing with this pressing issue.

KEY WORDS: CETACEANS; SHIP STRIKES; CANARY ISLANDS; NORTHERN HEMISPHERE; MEDITERRANEAN SEA; FAST FERRY TRAFFIC, MITIGATION; SPERM WHALE; PYGMY SPERM WHALE; CUVIER'S BEAKED WHALE; SHORT FINNED PILOT WHALE

INTRODUCTION

The worldwide number of collisions increased markedly from the 1950s onwards, which corresponds to the period of time when ships customarily began to reach maximum speeds of 14–15 knots or more (IWC, 2008; Laist *et al.*, 2001). During recent decades, with the rapid development of shipping traffic on a global scale, the situation in some parts of the world has become so critical that the issue by now is on the Agenda of the International Maritime Organisation (IMO, 2007; 2009).

Cetacean species affected include both large whales and small cetaceans such as dolphins and beaked whales (see review by Van Waerebeek *et al.*, 2007). However, certain species are especially vulnerable, namely those ones which swim slowly and stay at the surface for longer periods of time, for example right whales (*Eubalaena spp.*) and sperm whales (*Physeter macrocephalus*). Collisions with whales can also pose a threat to human safety, which is highlighted by the fact that considerable damage to ships has been reported (IWC, 2008; Laist *et al.*, 2001), as well as instances where sailors and ferry passengers have been hurt, including a case of human fatality in the Canary Islands (de Stephanis and Urquiola, 2006).

Although relatively little is known about the geographical distribution of collision cases on a global scale, a number of hot spots have been identified where ship strikes may affect the status of cetacean populations (ACCOBAMS, 2005; Pesante *et al.*, 2002). These include the east coast of the USA (Douglas *et al.*, 2008; Knowlton and Kraus, 2001), the northern Mediterranean Sea (Panigada *et al.*, 2006), the Strait of Gibraltar (de Stephanis and Urquiola, 2006), the Western Pacific (IMO, 2007) and the Canary Islands (de Stephanis and Urquiola, 2006; Ritter, 2010). These areas are characterised by a substantial overlap between high levels of shipping traffic and a known high density of cetaceans.

Where known, the types of vessels involved in collisions include a great variety of watercraft comprising large ships such as tankers, cargo or cruise ships, but also whale watching vessels, navy ships, yachts, hydrofoils and others (Jensen and Silber, 2004; Laist *et al.*, 2001; Ritter, 2009; Van Waerebeek *et al.*, 2007). Large high speed craft (HSC) have become a major concern, because they travel regularly at speeds of up to 35–40 knots, and collisions appear to be increasing (Ritter, 2010; Weinrich, 2004). These craft typically incorporate modern hull shapes like wave-piercing catamarans or trimarans.

Not surprisingly, fatality rates and severity of injury to whales struck by boats are related to size and speed of vessels. According to Laist *et al.* (2001), 89% of accounts in which the whale was seriously injured or killed occurred at speeds of 14 knots or more. Moreover, most lethal and serious injuries were caused by large ships of 80m length or more. Thus, speed appears to be a central factor with regards to collisions.

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Table 1

Details of vessel-whale collision cases in the Canary Islands (1991-2007). Legend: TF = Tenerife, GC = Gran Canaria, LG = La Gomera, LZ = Lanzarote, LP = La Palma, FV = Fuerteventura, H = El Hierro, n.n. = not determined, MoD = Moderately decomposed, AD = Advanced decomposition. M = Male, F = Female.

Date	Species	Code	Island	Length (cm)	Sex	Condition	Age class	Notes
07/07/91	Sperm whale	Pm.070791	TF	n.n.	F	Fresh	Calf	Huge cuts. Collision with jet-foil (Company Trasmediterranea).
07/07/91	Sperm whale	Pm.070791	TF	n.n.	F	Fresh	Adult	Huge cuts. Collision with jet-foil (Company Trasmediterranea).
26/02/92	Short-finned pilot whale	Gm.260292	TF	340	F	MoD	Juvenile	Found floating on 22/02/92 with a large dorsal cut.
28/02/92	Undetermined	–	FV	1,200	–	–	–	Impact with ferry *Princesa Teguise*. Described as large cetacean of >12 m. Passengers: 1 injury and 18 with contusions.
30/05/92	Cuvier's beaked whale	Zc.300592	TF	550	M	MoD	Juvenile	Clear cut which separated the caudal peduncle from body. Cookie cutter marks and other shark bites.
12/07/95	Sperm whale	Pm.120795	TF	n.n.	–	Fresh	Calf	Only head of animal was found.
09/04/96	Sperm whale	Pm.090496a	GC	1,010	F	–	Adult	Ferry *Armas*.
09/04/96	Sperm whale	Pm.090496b	GC	680	M	–	Calf	Ferry *Armas*.
04/05/99	*Balaenopteridae*	B.040599	GC	n.n.	–	–	–	Collision observed by fishermen.
10/06/99	Short-finned pilot whale	Gm.100699	TF	n.n.	–	–	–	Collision with ferry *Gomera Jet*.
00/07/99	Fin whale	Bp.000799	TF	n.n.	–	–	Adult	Male of more than 20m. Press report in *La Gaceta* (18/09/99): *'¿Por qué mueren las ballenas?'*.
04/08/99	Sperm whale	Pm.040899	TF	n.n.	–	–	–	Head separated from body. Buried by technicians from Tenerife Council (Servicio de Recuperación Fauna).
06/08/99	Sperm whale	Pm.060899	TF	1,050	F	Fresh	Adult	Deep mediodorsal cut. Found floating and brought into harbour.
10/09/99	*Balaenopteridae*	B.100999	LG	n.n.	–	–	–	Rorqual tropical with a deep cut. Body was hauled off.
06/10/99	Bryde's whale	Be.061099	GC	1,200	F	MoD	Adult	Hematoms found all over the body.
20/01/00	*Balaenopteridae*	B.200100	LG	n.n.	–	–	–	Reported by passenger of ferry *Gomera Jet*.
09/06/00	Cuvier's beaked whale	Zc.090600	TF	n.n.	F	Fresh	Juvenile	Cut at the level of dorsal fin.
06/04/00	Sperm whale	Pm.060400	LZ	n.n.	M	MoD	Calf	Two cuts on head typical for propeller strikes.
12/06/00	Sperm whale	Pm.120600	TF	n.n.	–	Fresh	Juvenile	Head separated from body. Many plastic items found in stomach.
21/08/01	Sperm whale	Pm.210801	TF	600	F	Fresh	Calf	Large wound on posterior third of body: 600cm.
23/09/01	Sperm whale	Pm.230901	TF	n.n.	–	Fresh	Calf	Length of the head (which was separated from the body): 135cm.
24/09/01	Sperm whale	Pm.240901	TF	790	M	AD	–	Deep lateral cut lefthand side from lower jaw to dorsal fin.
07/02/02	Pygmy sperm whale	Kb.070202	TF	240	M	AD	Juvenile	Deep cuts mediodorsal and caudal.
18/04/02	Short-finned pilot whale	Gm.180402	TF	167	F	AD	Calf	Politraumatised on the skull, jaws, ribs and vertebrae, but without external marks.
21/06/02	Cuvier's beaked whale	Zc.210602	TF	525	M	AD	Adult	Medio-lateral cut at the height of the dorsal fin.
02/04/03	Short-finned pilot whale	Gm.020403	TF	1,60(+)	–	AD	Adult	Support from technicians of the 'Servicio de Fauna del Cabildo de Tenerife'. Only first third of body appeared.
28/04/03	Pygmy sperm whale	Kb.280403	TF	250	M	AD	Juvenile	Body cut at two locations: (1) at the height of the lung; (2) at the height of reproductive organs.
30/06/03	Pygmy sperm whale	Kb.300603	TF	238	M	AD	Juvenile	Deep cut from pectoral flipper to the vertebral column.
02/07/03	Pygmy sperm whale	K.020703	LP	300	–	AD	Adult	Deep sagittal cut.
05/07/03	Sperm whale	Pm.050703	TF	490	M	Fresh	Calf	Two traversing cuts: (1) from head to behind the blowhole; (2) deep cut close to dorsal fin.
11/10/03	Sperm whale	Pm.111003	H	953	M	AD	Juvenile	Deep dorsal cut (mid body).
14/11/03	Gervais' beaked whale	Me.141103	TF	282+	M	AD	Adult	Body cut off behind the genital area. Has been floating several days.
25/11/03	Sperm whale	Pm.251103	GC	1,200	–	–	–	Referenced in the press media.
15/04/04	Sei whale	Bb.150404	GC	n.n.	F	AD	Juvenile	Body cut into halves behind the dorsal fin.
06/05/04	Cuvier's beaked whale	Zc.060504	TF	n.n.		MoD	Adult	Animal cut at the onset of dorsal fin.
21/06/04	Pygmy sperm whale	Kb.210604	TF	188	M	AD	Juvenile	Appeared the day before at La Caleta, then drifted to harbour of Güimar. Partially sectioned in front of dorsal fin.
12/08/04	Sperm whale	Pm.120804	LG	n.n.	–	AD	Juvenile	Body cut in front of pectoral fin. Animal brought quickly to dumping site.
01/10/04	Sperm whale	Pm.011004	TF	1,050	F	AD	Adult	Cut at the height of cervical vertebrae.
31/12/04	Cuvier's beaked whale	Zc.311204	TF	620	M	AD	Adult	Hauled off by Guardia Civil but then resighted. Cut at the height of digestive apparatus.
15/02/05	Sperm whale	Pm.150205	TF	500	M	AD	Calf	Deep cuts at level of thorax. Numerous shark bites.
11/05/05	Sperm whale	Pm.110505	FV	686	F	Fresh	Calf	Numerous propeller cuts.
25/05/05	Balaenopteridae	B.250505	LG	1,000	–	AD	Juvenile	First seen floating off Tenerife, stranded on 22 May on La Gomera.
29/06/05	Short-finned pilot whale	Gm.290605	TF	115	M	AD	Calf	Floating body was accompanied by bottlenose dolphins up to the harbour of Alcalá. Head cut off.
20/07/05	Indeterminado	I.200705	FV	n.n.	–	–	–	Referenced in the press media. Probable collision with jet-foil.
27/09/05	Pygmy sperm whale	Kb.270905	GC	285	F	Fresh	–	Referenced in the press media/internet.
31/03/06	Pygmy sperm whale	Kb.310306	LG	280	F	Fresh	Juvenile	Found floating off LG. Full necropsy by veterenarians of the Las Palmas University. Hematoms present. No obvious markings.

Table 1 *continued*

Date	Species	Code	Island	Length (cm)	Sex	Condition	Age class	Notes
18/04/06	Pygmy sperm whale	Kb.180406	TF	274	F	AD	Adult	Foetus of 37 cm length. Skull destroyed.
27/04/06	Sperm whale	Pm.270406	TF	460	F	Fresh	Calf	Appeared 28/05/06 at Las Maretas. Longitudinal mediodorsal cut.
04/06/06	Cuvier's beaked whale	Zc.040606	LG	490+	M	AD	Adult	Deep cut which separated the tail stock.
05/07/06	Cuvier's beaked whale	Zc.050706	TF	400+	F	AD	–	Animal was observed 4 days floating in the area. No shark bites. Last third of body cut off at the level of genitals.
25/02/07	Fin whale	Bp.250207	GC	1,700	–	MoD	Juvenile	Animal wedged on the bow of monohull ferry (Company Trasemediterranea).
06/04/07	Pygmy sperm whale	Kb.060407	TF	275 (282)	F	SD	Adult	Dorsal and mediodorsal cuts of 15–30cm length and up to 12cm deep. Orca attack?
16/05/07	Sperm whale	Pm.160507	TF	325 (+)	M	SD	Calf	Animal cut at the level of the anus. Numerous shark bites.
04/06/07	Short-finned pilot whale	Gm.010607	TF	100 (+)	F	AD	Newborn	Animal cut at the end of the genital opening. Curved cuts 25–30cm length. Shark bites. Clearly visible foetal folds on right side.
20/03/07	Sei whale	Bb.200307	GC	1390	F	MoD	Adult	Fractured thoracic vertebrae. Hematoms (anterior region right side).
00/07/07	Sperm whale	Pm.000707	GC	n.n.	–	AD	–	Only part of the first third appeared.
20/06/07	Pygmy sperm whale	Kb.200607	GC	170 (+)	–	AD	–	Curved mediodorsal cuts. Stomach contents present.
08/07/07	Sperm whale	Pm.080707	H	n.n.	–	AD	–	Deep cut at the head. No skull present. Stomach contents present.
16/07/07	Sperm whale	Pm.160707	GC	1,300	–	AD	–	Deep cut at the level of cervical vertebrae. Head separated from body at the stranding site.

In this paper collision cases in the Canary Islands from 1991–2007, identified through the investigation of dead animals, are summarised. Ship strikes are related to the high density of fast and high speed inter-island traffic in the archipelago and the urgent need to introduce mitigation measures so as to preserve the integrity of the natural populations and to conserve the extraordinarily high cetacean species diversity found in the Canary Islands are discussed.

METHODS

This study investigated cetaceans which stranded between 1 January 1991 and 31 December 2007 on the coasts of the Canary Islands or were found floating dead at sea. Moreover, reports from eye witnesses, as well as those in the press and the internet, were analysed and included, as long as descriptions unambiguously pointed to a vessel-whale collision.

Direct investigation of carcasses included the determination of species and the state of decomposition. Sex and age class were identified as far as possible. External measurements, date and locality of the carcass were noted, and photographs were taken wherever feasible. Each stranding was assigned a unique ID code. All cases were entered into a database. Five categories were used for the state of decomposition: 1 = Fresh; 2 = Little decomposition; 3 = Moderate decomposition; 4 = Advanced decomposition; and 5 = Indeterminate (ECS, 1991). For the determination of age classes, the following length-based categories were used: 1 = Adult; 2 = Juvenile; 3 = Calf; and 4 = Newborn (compare Ritter, 2003). Carcasses were searched for indications of collisions with vessels. A collision event was identified if one or more of the following observations were noted: lesions including deep parallel cuts, usually dorsal, indicative of propeller strikes; large and/or deep slashes, sometimes cutting off large portions of the body; massive blunt trauma: broken bones such as vertebrae; jaws; etc.; or animals wedged on the bow of a vessel.

RESULTS

From 1991 until 2007, 556 cetacean carcasses were found stranded on the shoreline of the seven main Canary Islands, or were reported floating dead at sea. 59 animals, representing 10.6% of strandings, showed signs of collisions or were reported as being hit by a ship. The latter was the case nine times, whereas 50 animals were directly investigated by the first author and members of the Canarian Cetacean Stranding Network. One animal was found on the bow of a large vessel (see Table 1). Other sources of mortality included natural (54%), naval exercises (5%), interaction with fisheries (4%) and death related to waste (1%). In 141 animals (26%) the cause of death could not be determined.

The species primarily involved were sperm whales (*Physeter macrocephalus*, *n* = 24, 41%), pygmy sperm whales (*Kogia breviceps*, *n* = 10, 17%), Cuvier's beaked whales (*Ziphius cavirostris*, *n* = 7, 12%), short-finned pilot whales (*Globicephala macrorhynchus*, *n* = 6, 10%) and one True's beaked whale (*Mesoplodon europaeus*; see Fig. 1). At least three baleen whale species (*n* = 9, 15%) were found after being hit by a vessel: two fin whales (*Balaenoptera physalus*), two Bryde's whales (*B. brydei*) and one sei whale (*B. borealis*). Four balaenopterid whales could not be identified to the species level, and in another two genus and species remained unknown.

58% of cetaceans thought hit by vessels were found on Tenerife (*n* = 24) and 20% on Gran Canaria (*n* = 12). On La Gomera, six animals (10%) were encountered and three on Fuerteventura (5%). El Hierro accounted for two strandings, La Palma and Lanzarote one each. Some of the stranding locations are shown in Fig. 1.

Most animals were either juveniles (*n* = 13, 22%) or calves (*n* = 13, 22%). 15 animals (25%) were adults and one was a newborn. However, in almost one third of all strandings the age class remained indeterminate. Of those animals, where

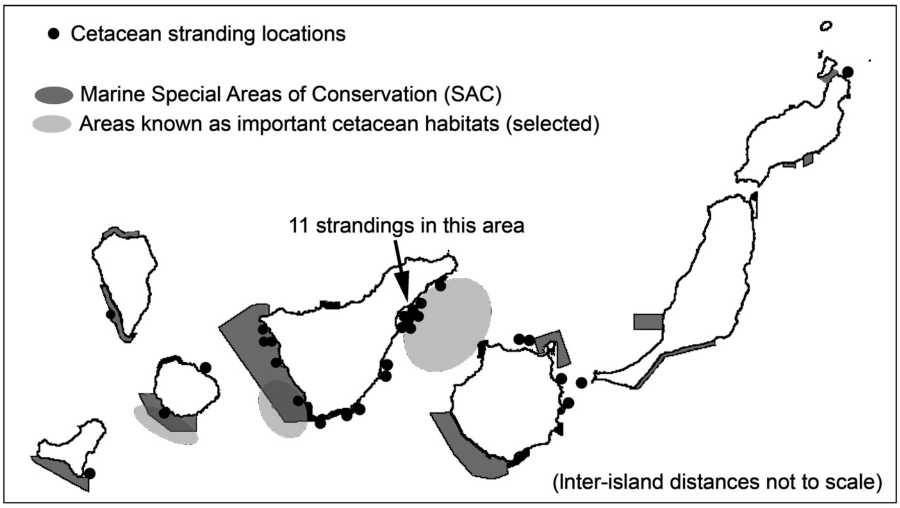


Fig. 1. Stranding locations of cetaceans showing signs of ship strikes, Canary Islands 1991–2007.

the sex could be determined (n = 36), 19 (53%) were females, and 17 (47%) were males. For 23 carcasses, the sex was not identifiable. For sperm whales, it was found that 8 animals were female, 7 were male and in 9 animals the sex could not be determined. 11 (46%) sperm whales were calves, 3 were juveniles, 4 were adults and in 6 animals the age class was not determined. Details on all strandings, together with remarks on the types of injuries encountered, are presented in Table 1.

DISCUSSION

The rate of strandings showing evidence of ship strike appears to have increased over the data collection period and indicates that the number of collisions has been at a consistently high level since 1999 (see Fig. 2). From 1991–98 the number of ship strikes recorded varied from 0 to 3, with an average of 1 per year. From 1999–2007, this number ranges from 3 to 9, averaging 6.4 per year. The effect of increased sighting effort can be ruled out as the Canary Island Cetacean Stranding network has not changed its mode of operation since it was established in 1991.

This study found that almost 11% of cetaceans stranded or found dead in the Canary Islands showed signs of collisions with vessels. Other studies have found similar percentages. Laist *et al.* (2001) reported ship strikes as possible or known cause of death in 16 out of 127 strandings (13%) on the French coast from 1972–1998, in 14 out of 407 strandings along the US Atlantic (1976–1993), and in 11 out of 55 strandings (20%) on the coast of South Africa from 1963–1998. In the Mediterranean Sea, Panigada *et al.* (2006) found that 16% (46 of 287) of cetacean deaths were caused by vessels. However, all of these areas are at least an order of magnitude larger than the spatial area described here.

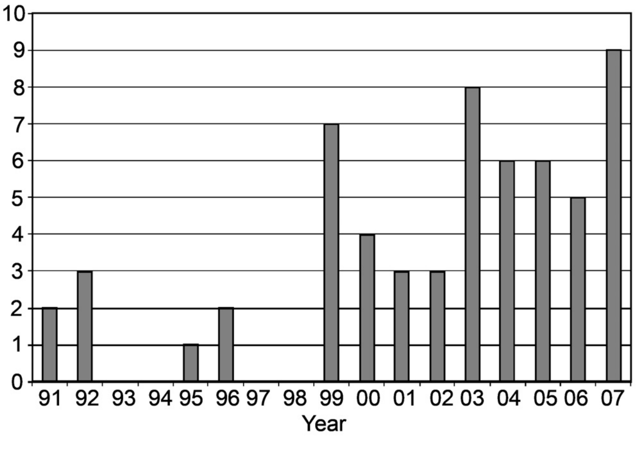


Fig. 2. Temporal distribution of vessel whale collisions in the Canary Islands 1991–2007 (n = 59).

As previously reported (Laist *et al.*, 2001; Van Waerebeek *et al.*, 2007), a variety of different cetacean species, including both large and small cetaceans, were affected by vessel collisions. Nonetheless, the numbers presented here are based exclusively on strandings and animals found floating dead at sea. To date, no single case has been corroborated by ferry operators, despite several witness reports from, for example, tourists and fishermen (Aguilar *et al.*, 2000; Ritter, unpubl. data; see also Table 1). As pointed out by Weinrich (2004), intentionally not reporting collisions may entail the attempt to avoid the implication of industrial involvement in vessel-whale collisions. Thus, the true numbers of ship strikes remain largely unknown. Official numbers provided by the Canarian Government vary from three to seven ship strikes per year from 2000–08, with a total of 42 cases in the same period (Gobierno de Canarias, 2009). These numbers are based on data provided by different Canarian research groups, including the data presented in this paper. It presumably is an underestimation, not least because collisions may go unnoticed, animals hit may sink to the seafloor or simply drift away (ACCOBAMS, 2005; Laist *et al.*, 2001). Therefore, to date it has not been possible to calculate any collision risk or conduct sound modelling for Canarian waters, despite the relatively predictable numbers concerning ferry traffic (see below).

A high percentage of juveniles and calves being hit by vessels has been observed before (Laist *et al.*, 2001; Lammers *et al.*, 2007; Panigada *et al.*, 2006). This could be explained by a greater naivety of younger animals towards ships, or less experience. Most ship strikes (41%) involved sperm whales. This number is unprecedented, as elsewhere other cetacean species are more commonly affected. In Jensen and Silber's (2004) large whale ship strike database, 5% of strandings were sperm whales. 4.8% of ship strikes in the Mediterranean Sea were reported to involve sperm whales (ACCOBAMS, 2005). Also, in the Strait of Gibraltar, where sperm whales are partially resident (Cañadas *et al.*, 2005), 'only' two collisions have been reported from 2001 until 2005 (de Stephanis and Urquiola, 2006). To our knowledge, there is no other area where sperm whales are at an especially high risk of being hit by vessels. Thus, sperm whales in the Canaries apparently are more vulnerable than elsewhere.

André *et al.* (1997) found little or no behavioural reactions of sperm whales in the Canaries after the playback of artificial sound, which was explained by a loss of sensitivity to low frequencies or habituation processes. This could explain at least partly the elevated percentage of strikes. More generally, it may be difficult for whales to detect ship noise due to a variety of different biological and physical factors (ACCOBAMS, 2005), although this will affect all species similarly. Whales also may be unaware of ships because they are distracted or asleep. This may be especially true for the sperm whales which only recently were found to show apparent bi-hemispheric sleep and may not react to approaching vessels at all (Miller *et al.*, 2008). Apparently, ship strikes have increased since the introduction of fast and high speed ferries in the Canaries. Hence, the high density of ferry traffic in the Canaries may also play a central role. Several million people (tourists and locals) travel from one island to the other every year (Rodrigez *et al.*, 2005), therefore ferry traffic is an important transport medium within the archipelago. There are several types of ferries operating between the islands to date, including one 'normal' traditional monohull and a number of different fast ferries (travelling at approx. 25 knots) as well as numerous high speed crafts (HSC, reaching maximum velocities of 40 knots, see Ritter, 2010), including the largest ferry trimaran in the world. The large catamarans are so called wave-piercing vessels and strongly dominate the inter-island traffic in the Canaries today. As pointed out by Ritter (2010), there is a concentration of HSC ferry traffic in the southwest of Tenerife (>11,000 transects per year) and between Tenerife and Gran Canaria (6,760 transects per year). The latter area is known for its high abundance of sperm whales (André, 1998). This might explain why so many sperm whales are hit by ships, and why the majority of cetaceans become stranded/washed ashore on Tenerife (see Fig. 1).

The temporal distribution of strandings indicates that the number of collisions has been at a consistently high level since 1999 (see Fig. 3). In the same year, a regular high speed craft service was introduced in the Canaries (Rodrigez *et al.*, 2005) and within the first weeks of the operation, a number of ship strikes were documented (Aguilar *et al.*, 2000). A hydrofoil operating between Tenerife and Gran Canaria in 1999 collided with a whale, which caused numerous injured passengers and one fatality (de Stephanis and Urquiola, 2006). It is not always clear if a collision took place ante or post mortem. In many animals, the symptoms (e.g. hematoma) unambiguously pointed to an ante-mortem strike, and other animals were subsequently necropsied at the University of Las Palmas in detail. The great majority of these were identified as being hit while still alive (Gobierno de Canarias, 2009).

Commercial, fast and HSC ferries today are almost the only means to travel between the islands at sea. This is illustrated in Fig. 3, which represents an overview over the inter-island ferry transects, and the types of ferries operating on each transect. Ritter (2010) calculated that there were around 29,000 transects between the islands and almost 1.5 million kilometres were covered in 2007, the vast majority by fast and high speed ferries. As can be seen from Fig. 3, there is a considerable overlap with important cetacean habitats, as well as with Special Areas of Conservation under the EU Habitat Directive (see Fig. 1). Based on several cetacean studies conducted in the Canary Islands, Ritter (2010) also identified (small scale) high risk areas for vessel whale collisions, located between the islands of Tenerife and Gran Canaria as well as between La Gomera and Tenerife.

It was found that the major proportion of animals (58%) came ashore on Tenerife. Strikingly, 14 of 21 sperm whales (66%) were found on the coast of this island, and one should question the reason for this accumulation. In one of the most detailed studies on sperm whales in the archipelago, André (1998) identified the region between Tenerife and Gran

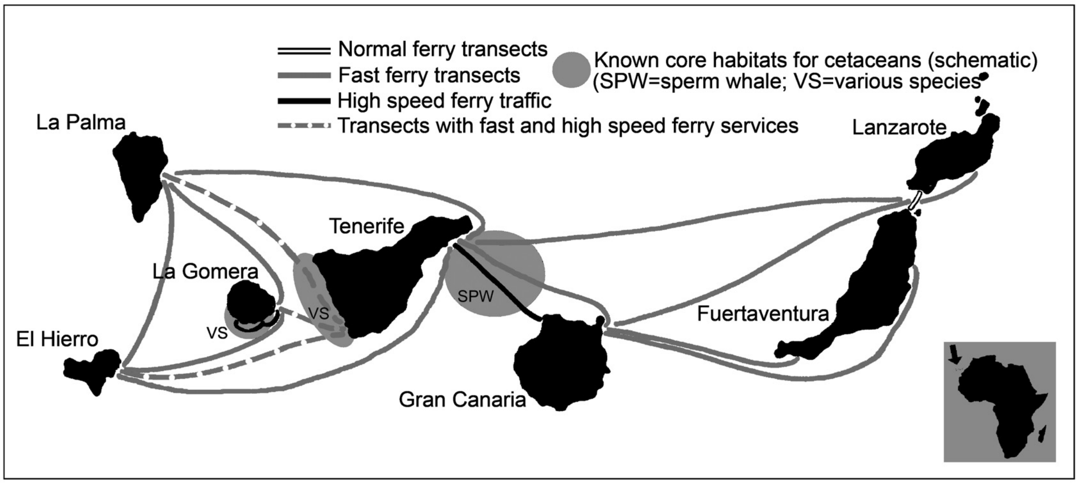


Fig. 3. Ferry transects in the Canary Islands in 2007. Adapted from Ritter (2007).

Canaria as a prime habitat for this species, where the animals were seen most regularly. This area clearly overlaps with HSC ferry transects (see Fig. 3), and for this reason was also identified as a high risk area by Ritter (2010, see above). Ritter (2010) also pointed out that if a sperm whale was hit in this area, one would expect the carcass to appear somewhere west or southwest to this region due to the prevailing south-westerly direction of the Canaries current. Most likely such a carcass therefore would strand on Tenerife.

Furthermore, some types of trauma (large whales cut in half, large longitudinal slashes, see Fig. 4) leave almost no other conclusion than that the animal was killed by a large vessel. Sometimes animals are caught on top of the bulb of monohull vessels, which was the case with one whale during this study. In any case, bulbous bows will not be capable of separating large proportions from a whale's body, as is expected from the sharp-edged wave-piercing hulls of catamarans customarily used in the Canary Islands, as witnessed several times by ferry passengers and fishermen (Aguilar *et al.*, 2000; see also Table 1). HSC were reported to have caused 43% of ship strikes in the Mediterranean Sea (Panigada, 2006). Weinrich (2004), in reviewing collision cases with ferries on a global scale, found that 46% involved ferries travelling at speeds >30 knots. Hence, it is suspected that wave piercing HSC play a major role in the magnitude of collision numbers in the Canary Islands.

Although to date a huge knowledge gap exists, especially concerning true numbers of vessel-whale collisions, it can be stated that a minimum of 1–3 sperm whales are hit per year (see Table 1). It is not possible to determine (although it is suspected) that this affects the population, as to date there exist no population estimates for most cetacean species in the archipelago. Unfortunately it is still unknown whether the sperm whales form a 'resident' population or are part of a wider unit (see Whitehead, 2003).

In light of the numbers presented here, the Canary Islands can be acknowledged as a hot spot for vessel-whale collisions. This situation certainly is a matter of concern and poses a risk to humans and cetaceans alike. There is an urgent need for mitigative action to avoid ship strikes, to achieve more transparency in reporting and to obtain more reliability for recorded numbers of collisions, in the interest of cetacean conservation.

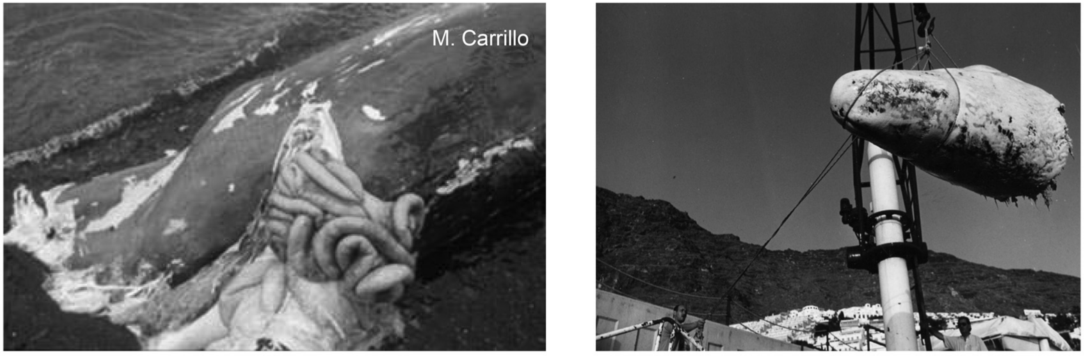
CONCLUSIONS

Several measures have been discussed to mitigate the risk of vessel-whale collisions, such as a reduction in speed, placing dedicated observers onboard, the shift of shipping lanes, remote sensing of cetaceans via night vision, laser, sonar or infrared techniques and passive acoustic monitoring systems, among others (ACCOBAMS, 2005; IWC, 2008).

While technical measures up to now mostly have failed to prove their efficacy (ACCOBAMS, 2005) or are extremely expensive to install, a number of measures are relatively easy to realise in the short term. First, and most obviously, reducing speed will have an instant effect. High speed limits the time frame to take evasive navigational action once a whale is seen. For example, detecting a whale in the ship's path 600m away at a speed of 40 knots leaves a vessel's captain a reaction time of 30 seconds before a whale potentially is hit. Vanderlaan and Taggart (2007), reviewing


(a) Sperm whale with large dorsal cut
Pm-050703 (see Table 1)

(b) Sperm whale calf missing caudal peduncle
Pm-160507 (see Table 1)


(c) Cuvier's beaked whale remains
Zc-090600 (see Table 1)

(d) Sperm whale head
Pm-120795 (see Table 1)

Fig. 4. Examples of injuries found in cetaceans hit by ships in the Canary Islands. All images copyright Manuel Carrillo.

collisions listed in Laist *et al.* (2001), found that at 15 knots 80% of collisions were fatal to the whales. At speeds of 11.8 and 8.6 knots the percentage of fatal collisions dropped to 50% and 20%, respectively. A speed limitation was introduced in Hawaii for the new 'super ferry' which operated 2007–09. Also, on the US East Coast vessels of 65ft and above are asked to slow down as they enter certain right whale habitats. Speed reduction has also been used to lower the risk of collision with marine mammals other than cetaceans (Calleson and Frohlich, 2007), although problems with compliance will often remain.

Dedicated observers onboard vessels have proven to be an effective means to detect whales (ACCOBAMS, 2005; Weinrich, 2004), which under high speed conditions is a crucial aspect. In Hawaii, the newly introduced HSC ferry has two full time look-outs (IWC, 2008).

Therefore, under the current state of knowledge, and re-iterating some of the recommendations by Ritter (2010), the following measures should to be taken immediately as high priority action in the Canary Islands:

(1) The placement of dedicated onboard observers (look-outs) on fast and high speed ferries operating in known core habitats (i.e. between Tenerife and Gran Canaria/La Gomera, respectively), as well as experimental onboard application of technical mitigation measures to test the feasibility and effectiveness of such measures for fast and HSC ferries.

(2) The introduction of a speed reduction on an experimental basis in zones identified as local high risk-areas (see Ritter, 2010) so as to assess a comparative collision risk.

(3) The introduction of a mandatory reporting scheme for collisions, thereby making use of the database being developed by the IWC Vessel Strike Data Standardisation Group (Van Waerebeek and Leaper, 2007).

To address knowledge gaps, a Canarian-wide quantification of both cetacean densities and shipping traffic should be conducted to enable modelling of collision risks. It should be stressed that the current situation is very favourable for research being conducted on board ferries, not least because ferry operators may be accepting observers, as indicated by De Stephanis and Urquiola (2006). In this way, the Canaries can be turned into a centre for investigating ways to avoid ship strikes. The ultimate goal must be to protect the integrity of the Canarian cetacean populations on the grounds of precaution and sustainability and to develop an effective policy to manage shipping traffic so as to secure both human and animal safety.

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Quantification of ferry traffic in the Canary Islands (Spain) and its implications for collisions with cetaceans

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ABSTRACT

The Canary Islands, known for their high cetacean species diversity, have witnessed a rapid expansion of fast ferry traffic during the past few years. At the same time, ship strikes have been repeatedly documented. In this paper an overview of the inter-island ferry traffic in the archipelago is given. Ferry types in use (normal, fast and high speed vessels) are described, and the transects on which they operate are identified. To quantify the extent of the inter-island ferry traffic, three parameters were determined: (1) the actual transects from the different ports on the islands; (2) the number of journeys made per week on each transect; and (3) the length of each transect. Resulting numbers indicate that normal ferries travel approx. 66,000km, fast ferries travel approx. 570,000km and high speed ferries travel approx. 845,000km between islands each year. Fast and high speed ferry traffic is concentrated in the western islands. Areas of high risk for ship strikes within the archipelago are identified by comparing the location of transects with known areas of high cetacean abundance. It is argued that the Canary Islands are a hot spot for vessel-whale collisions and that a policy to counteract this situation is urgently needed.

KEYWORDS: CETACEANS; SHIP STRIKES; CANARY ISLANDS; NORTHERN HEMISPHERE; EUROPE; SPERM WHALES; WHALEWATCHING

INTRODUCTION

Collisions between vessels and cetaceans globally are an issue of growing concern. Since large ships reached travelling speeds of greater than 14 knots around the 1950s, collisions with vessels have increased and today affect a rising number of cetacean populations (Laist *et al.*, 2001). Different types of vessels have been reported to collide with whales, including container ships, ferries, whale-watching boats and military vessels (Jensen and Silber, 2004; Laist *et al.*, 2001; Van Waerebeek *et al.*, 2007).

Resident coastal populations appear to be especially vulnerable to ship strikes, but seasonally abundant cetaceans, migration corridors for larger whales as well as animals living on the high seas may all be affected (Pesante *et al.*, 2002). The problem appears to be of special concern in geographical areas where there exists an overlap between a high amount of maritime traffic, both commercial and non-commercial, and a high abundance of cetaceans (ACCOBAMS, 2005; de Stephanis and Urquiola, 2006; IWC, 2006; Panigada, 2006; Pesante *et al.*, 2002).

The Canary Islands (NE Atlantic Ocean, Spain), are a major European tourist destination with several million tourists visiting annually. With 29 identified species the islands are renowned for their high cetacean species diversity and have witnessed a rapid expansion of fast and high speed ferry traffic during the past few years (Aguilar *et al.*, 2000; de Stephanis and Urquiola, 2006). In an ever growing number of ferry transects, which connect most of the seven islands in the archipelago with each other, ‘normal’ ferries have been replaced by fast moving vessels of different sizes. At the same time, ship strikes have been repeatedly documented and also appear to have increased in numbers (de Stephanis and Urquiola, 2006; Carrillo and Ritter, 2010).

In 2005, the IWC set up the Ship Strike Working Group (SSWG) under its Conservation Committee to deal with this issue. One goal of the SSWG is to assess the problem on a global scale, including the identification of ‘high risk areas’, where either a higher number of collisions have been reported or there is an elevated likelihood of such events occurring, for the reasons mentioned above (IWC, 2006). Up to now, only a small number of high risk areas have been described and/or identified, mainly due to the fact that the real number of collisions in a given area is rarely known, even when collisions are regularly reported (ACCOBAMS, 2005; Laist *et al.*, 2001; Panigada *et al.*, 2006). Moreover, a quantitative assessment of collision risk is hard to achieve as long as the actual amount of ship traffic (e.g. expressed as the number of transects of certain types of vessels, travel distances and the frequency of transects) and the number and distribution of cetaceans are not known (ACCOBAMS, 2005; IWC, 2006). In this paper, this knowledge gap is addressed by quantifying the extent of inter-island ferry traffic in the Canary Islands to create a basis for further assessments. A description of the different types of fast ferries operating in the Canary Islands is included.

METHODS

In the Canarian archipelago, ferries connect most of the seven islands with each other. Transects were identified by searching the internet for regular schedules of the three known ferry companies operating in 2007. Hard copy schedules were collected on La Gomera and Tenerife, and travel agencies were interviewed about available schedules. The timetables for each inter-island connection were then analysed for the number of transects made per day and per week.

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A distinction was made between ferries moving at speeds of 15–20 knots (termed normal ferries), ferries with travel speeds of 21–29 knots (fast ferries) and ferries travelling at speeds of 30 knots or more, (high speed ferries). Three (in part overlapping) transect categories were distinguished accordingly.

To quantify the total extent of the inter-island ferry traffic, three parameters were determined: (1) the actual transects to and from the different ports on the islands linked by ferries; (2) the number of travels made on each transect (per day, per week and per year); and (3) the length of each transect. For a technical description of ferry types, information was taken from the websites of the operators.

The lengths of the transects were measured using the distance measuring application (‘ruler function’) of internet based Google Earth Software. The shortest possible distance between two harbours was taken as the (minimum) length of the transect, in some cases being a straight line from port to port. Otherwise the transect was assumed to lie as close as possible to the direct straight line.

The total distance travelled by all ferries operating on the same transect (both ways) was then calculated by multiplying the length of the transect (in km) with the number of transects travelled per day, per week and per year. The number of transects per week was determined and the number of transects per year was calculated by multiplying the number of transects per week by 52. Finally, the total amount of inter-island ferry traffic in the archipelago was estimated by adding those numbers previously calculated for each of the transects.

In addition, the literature on abundance and distribution of cetaceans in the Canaries was searched so as to make out small areas of high cetacean abundance and Special Areas of Conservation (SAC) under the European Union Habitat Directive. Where these overlapped with ferry traffic concentrations, primary and secondary high risk areas for ship strikes were identified. Primary high risk areas are here defined as areas with known high cetacean abundance which receive the highest number of transects (>2,000) per year. Secondary high risk areas are areas with known high cetacean abundance (i.e. habitats where concentrations of several cetacean species have been found) and/or a considerable concentration of ferry traffic (>1,000 transects/year). The location of high risk areas was then plotted on a map.

RESULTS

The estimates of distance travelled presented here are based on a synthesis of five internet schedules, three hard copy schedules, and supplementary information from two travel agencies. Fifteen ferry transects were identified, frequented by three operators. All transects are given in Tables 1 and 2 and they are graphically represented in Figure 1.

Ferry types

One normal ferry is operating in the Canary Islands. It is a regular monohull ship (Fig. 2a) which travels at speeds of around 17 knots (see Table 1). There are four fast ferries operating in the Canaries, run by one operator. These are large monohull ships (length 132–143m, see Fig. 2f) which can accommodate up to 1,350 passengers and 300 cars while travelling 23–25 knots (see Table 1).

High speed ferries of four different types are run by two operators in the Canary Islands: large wave-piercing catamarans, a large wave-piercing trimaran and a smaller wave-piercing catamaran (all taking passengers and cars) as well as smaller wave piercing catamarans for passengers only. The large catamarans have lengths of approx. 95m and a capacity of up to 891 passengers and 271 cars (Fig. 2b). Travel speed is around 38 knots. The trimaran ferry (see Fig. 2c), said to be the largest car ferry existing (length 127m, capacity 1,291 passengers/341 cars), has a travel speed of approximately 40 knots. The smaller catamaran car ferry (66m in length, see Fig. 2d) takes up to 436 passengers and 96 cars and travels at a speed of 30 knots. Likewise, the smaller catamaran passenger ferry (length 40m, see Fig. 2e) travels at around 30 knots and has a capacity of 348 passengers. An overview of ferries and their technical data is given in Table 1.

Normal ferry traffic

The normal ferry connects the harbours of Playa Blanca (Lanzarote) and Corralejo (Fuerteventura, see Fig. 1). This transect is 14km long. The number of transects is 94 per week (4,888/year = 1,269km, see Table 2a). The minimum estimate of total distance travelled by normal ferries thus is 1,269km per week (65,988km per year, see Table 2a).

Fast ferry traffic

Twelve transects are frequented by fast ferries which are run by one operator. Fast ferries travel on all transects shown

Table 1

Ferry types operating in the Canary Islands (for abbreviations see Table 2).

No.	Ferry type	Length	Capacity	Travel speed	Transects
1	Large catamaran high speed ferry	95m	871 passengers 271 cars	38kn	LC-VV, LC-SS, SC-AG
2	Large trimaran high speed ferry	118m	1,290 passengers 280 cars	35–40kn	LC-SS, LC-SCLP
3	Large monohull fast ferry	132–143m	1,200–1,500 passengers 300 cars	23–24.5kn	LC-SS, SS-VV, SCLP-VV, LC-SCLP, LC-VV, SS-SCLP, SC-SCLP, SC-AR, SC-LPGC, SC-VV, LPGC-AR, LPGC-MO, LPGC-PR
4	Small catamaran high speed ferry	66m	436 passengers 96 cars	30kn	PB-CO
5	Small catamaran high speed ferry (passengers only)	40m	348 passengers	30kn	LC-VGR
6	Large Monohull normal ferry	78m	700 passengers 120 cars	17kn	PB-CO

Table 2

Ferry traffic in the Canary Islands: length, frequency of ferry transects and distances travelled in 2007.

Ferry line	Operator	Transect	Length (km)	Transects/d	Transects/wk	Transects/yr	Total km/d	Total km/week	Total km/year
(a) Normal ferry transects									
LZ-FV	ARMAS	PB-CO	14	10–14	94	4,888	70–98	1,269	65,988
Total								**1,269**	**65,988**
(b) Fast ferry transects									
TF-LG	ARMAS	LC-SS	39	1–4	36	1,872	39–156	1,404	73,008
LG-LP	ARMAS	SS-SCLP	96	0–2	6	312	0–192	576	29,952
LG-EH	ARMAS	SS-VV	86	0–1	2	104	0–86	172	8,944
GC-TF	ARMAS	LPGC-SC	97	1–3	26	1,352	97–291	2,522	131,144
GC-LZ	ARMAS	LPGC-AR	206	0–1	6	312	0–312	1,236	64,272
GC-FV	ARMAS	LPGC-MO	105	2	14	728	210	1,470	76,440
GC-FV	ARMAS	LPGC-PR	191	0–1	4	208	0–191	764	39,728
TF-LP	ARMAS	SC-SCLP	144	0–1	2	104	0–144	288	14,976
TF-LZ	ARMAS	SC-AR	272	0–1	4	208	0–272	1,088	56,576
TF-LP	ARMAS	LC-SCLP	125	0–1	4	208	0–125	500	26,000
TF-EH	ARMAS	SC-VV	197	0–1	4	208	0–197	788	40,976
EH-LP	ARMAS	SCLP-VV	103	0–1	2	104	0–103	206	10,712
Total			**1,661**	**4–19**	**110**	**5,720**	**556–2,279**	**11,014**	**572,728**
(c) High speed ferry transects									
TF-LG	OLSEN	LC-SS	39	8	56	2,912	312	2,184	113,568
	Garajonay Expres	LC-SS	39	6	42	2,184	234	1,638	85,176
	Garajonay Expres	SS-VGR	28	6	42	2,184	168	1,176	61,152
TF-LP	OLSEN	LC-SCLP	125	2	14	728	250	1,750	91,000
TF-EH	OLSEN	LC-VV	120	2	12	624	240	1,440	74,880
TF-GC	OLSEN	SC-AG	66	12–16	104	5,408	792–1,056	6,864	356,928
LZ-FV	OLSEN	PB-CO	14	10–14	90	4,680	135–189	1,215	63,180
Total				**76**	**360**	**18,720**	**3,376**	**16,267**	**845,884**

Abbreviations: Islands (from W to E): EH = El Hierro; FV = Fuerteventura; GC = Gran Canaria; LG = La Gomera; LP = La Palma; LZ = Lanzarote; TF = Tenerife. Ports (from W to E): VV = Valverde/El Hierro; SCLP = Santa Cruz/La Palma; VGR = Valle Gran Rey/La Gomera; SS = San Sebastian/La Gomera; LC = Los Christianos/Tenerife; SC = Santa Cruz/Tenerife; AG = Agaete/Gran Canaria; LPGC = Las Palmas/Gran Canaria; MO = Morrojable/ Fuerteventura; PR = Puerto Rosario/Fuerteventura; CO = Corralejo/Fuerteventura; PB = Playa Blanca/Lanzarote; AR = Arrecife/Lanzarote.

in Fig. 1 except on the transects between Lanzarote and Fuerteventura, Lanzarote and Gran Canaria, between Tenerife and Agaete on Gran Canaria and along the South coast of La Gomera.

The number of transects varies from two per week (104/year, transect SS-VV) up to 36 per week (1,872/year, transect LC-SS). Transect length varies between 39km (transect LC-SS) and 272km (SC-AR). An overview is given in Table 2b.

Distances travelled on one transect ranged from 172km per week (8,944km/year, transect SS-VV) to 2,552km per week (131,144km/week, transect SC-LPGC). The minimum estimation of total distance travelled by fast ferries was 11,014km per week (572,728km/year, see Table 2b).

High speed ferry traffic

Six transects are frequented by high speed ferries (see Fig. 1): between Los Christianos (Tenerife) and San Sebastian (La Gomera), San Sebastian and Valle Gran Rey (La Gomera), Valverde (El Hierro) and Santa Cruz (La Palma);

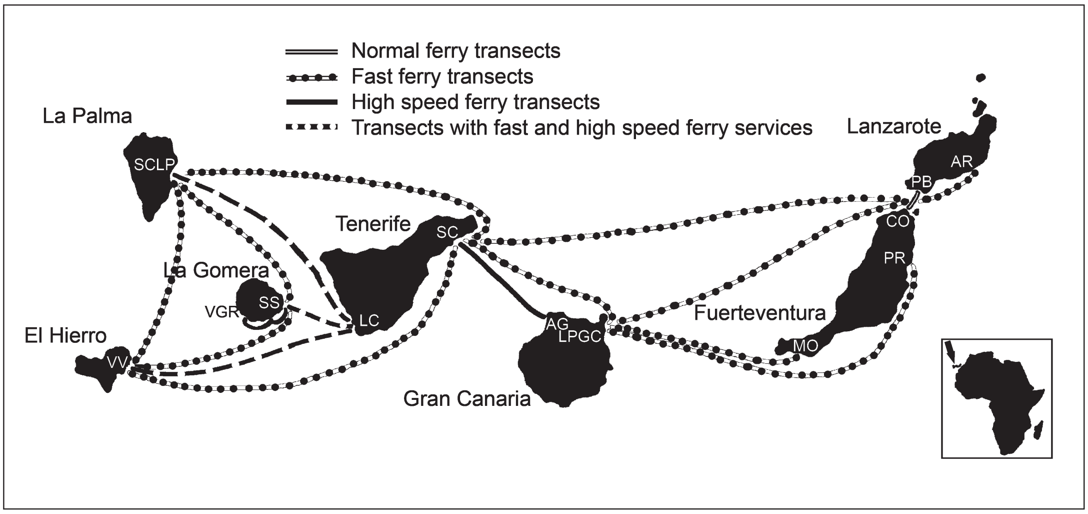

Fig. 1. Inter-island ferry transects in the Canary Islands in 2007.

(a) Normal ferry

(b) Large catamaran

(c) Large trimaran

(d) Smaller catamaran (passengers and cars)

(e) Smaller catarmaran

(f) Fast ferry

Fig. 2. Ferry types operating in the Canary Islands (2007). Photographs (a), (c), (d) and (f) taken from operator websites.

between San Sebastian (La Gomera) and Santa Cruz (La Palma); between Santa Cruz (Tenerife) and Agaete (Gran Canaria) and between Play Blanca (Lanzarote) and Corralejo (Fuerteventura). Thus, the greater part of the high speed ferry traffic is concentrated in the western part of the archipelago, mainly around Tenerife and neighbouring islands.

The number of transects ranged from 12 per week (624/year, transect LC-VV) and 104 per week (5,408km/year, transect SC-AG). Transect length varied between 14km (transect PB-CO) and 125km (transect LC-VV). An overview is given in Table 2c.

Distances travelled on one transect ranged from 1,176km per week (61,152/year, transect SS-VGR) and 6,864 per week (356,928/year, transect SC-AG). The minimum estimation of total distance travelled by all high speed ferries was 16,267km per week (845,884km/year, see Table 2c).

Overlap with known cetacean habitats

The Canary Islands are known for their extraordinary cetacean species diversity. Twenty nine species have been identified so far. Due to the fact that coastal bottlenose dolphin, rough-toothed dolphin, (Martin *et al.*, 1995; Mayr and Ritter, 2005; Ritter, 2003) pelagic pilot whale and dolphin populations are found (Heimlich-Boran, 1993; Ritter, 2003), it can be assumed that ferries may come across cetaceans virtually everywhere in the archipelago. However, certain areas have been investigated and/or are subject to whalewatching activities and thus the presence and distribution of cetaceans is known in more detail (Fig. 3). Areas with high cetacean abundance are: the waters south and southwest of the Islands of Tenerife, La Gomera, Gran Canaria and Fuerteventura as well as the channels between Tenerife and La Gomera and Gran Canaria respectively (Heimlich-Boran, 1993; Martin *et al.*, 1995; Mayr and Ritter, 2005; Ritter, 2003; Urquiola *et al.*, 1997). Some of these were already declared as Special Areas of Conservation (SACs, see Fig. 3) under the EU Habitat Directive (Carrillo, 2003; Ritter, 2003). There exists considerable overlap between these areas and a large part of the ferry operations:

(1) the region between Tenerife and Gran Canaria, which is a prime habitat for sperm whales (André, 1998). This area receives a total of 6,760 ferry transects every year, 80% thereof made by high speed ferries and 20% made by fast ferries;

(2) the waters around La Gomera and Tenerife, which are inhabited by a variety of cetaceans, especially the lee (southwest) sides of the islands, where calmer waters favour their observation and oceanographic features contribute to a high productivity (Carrillo, 2003; Ritter, 2001; 2003). The whole area receives 11,128 transects per year, 72% made by high speed ferries and 28% by fast ferries.

(a) In the Southwest of Tenerife, declared as a SAC and a proposed 'Marine Park for Cetaceans' (Gobierno de Canarias, 2002), the highest concentration of ferry traffic occurs. This area receives a total of 8,944 ferry transects per annum, 65% made by high speed ferries and 35% by fast ferries.

(b) In the South and Southwest of La Gomera, declared as a SAC, one of the highest species diversity areas (related to its size) in Europe was found (Ritter, 2003). The smaller catamaran passenger high speed ferry accounts for 2,184 transects per year.

High risk areas

By relating the available information on abundance and distribution of cetaceans to the ferry transects, four primary high risk areas were identified (see Fig. 4):

(1) the channel between Tenerife and La Gomera – due to a known high density of several cetacean species and an extreme concentration of ferry traffic (172 transects/week, 8,944 transects/year; 65% by high speed ferries and 35% by fast ferries);

(2) the waters south and southwest to La Gomera – due to a known high density of several cetacean species and a considerable concentration of ferry traffic (42 transects/week, 2,184 transects/year; 100% high speed ferries);

(3) the channel between Tenerife and Gran Canaria and the area around the harbour of Las Palmas – due to a known high density of sperm whales (and probably other cetaceans) and a considerable concentration of ferry traffic (130 transects/week, 6,760 transects/year; 80% by high speed ferries and 20% by fast ferries);

(4) the area between Lanzarote and Fuerteventura – due to an extreme concentration of ferry traffic (184 transects/week, 9,568/year; 51% by the normal ferry and 49% by high speed ferries) while only deficient data on cetacean abundance/distribution are available.

Additionally, there is a considerable spatial concentration of ferry traffic around the main ferry harbours on different islands (besides the harbours lying within the primary high risk areas described above). Although little is known about cetacean abundance and distribution here, two areas were identified as secondary high risk areas due to the fact that they are the start and end points of a high number of ferry transects. These areas are found off the harbours of:

(5) Santa Cruz de La Palma: 26 transects per week/1,352 per year (69% by high speed and 31% by fast ferries); and

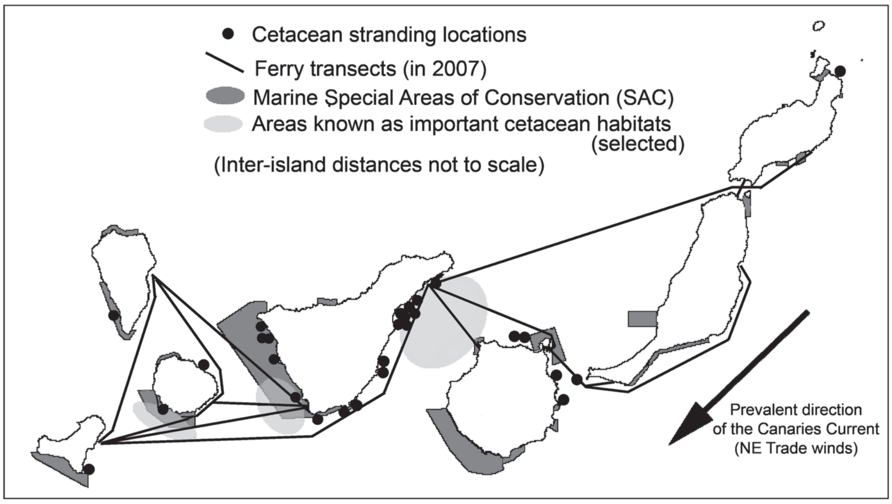

Fig. 3. Schematic map of Special Areas of Conservation (SACs) and important cetacean habitats in the Canary Islands (from Boehlke, 2006, modified). Black dots indicate strandings of cetaceans with obvious signs of ship strike injuries.

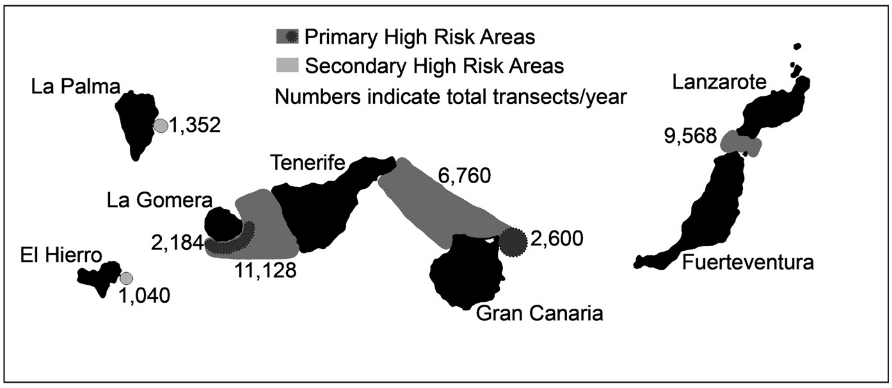

Fig. 4. Primary and secondary high risk areas for ship strikes in the Canary Islands. Dark grey areas are frequented by numbers of transects as indicated.

(6) Valverde (El Hierro): 20 transects per week/1,040 per year (60% by high speed and 40% by fast ferries)

The primary and secondary high risk areas for ship strikes are illustrated in Fig. 4.

DISCUSSION

This quantification of the ferry traffic in the Canary Islands has brought to light a huge amount of inter-island ferry traffic. A distance of 65,988km is travelled by normal ferries together with 572,728km travelled by fast ferries and 845,884 travelled by high speed ferries each year add up to more than 1.48 million kilometres. The number of transect may actually not be as high as calculated due to bad weather conditions or technical malfunction of the ferries. However, the transect distances where set as straight lines, which represents a minimum estimation of the distances travelled. Ferries in reality might take different routes between ports, thereby considerably diverging from the direct line. Thus, it can be assumed that the real distances travelled are probably higher than the minimum estimations made in this paper. The resulting numbers clearly signify an enormous concentration of ferry traffic within a comparably small area. Although almost all islands are connected with fast ferries, there is a prominence of fast and high speed ferry traffic in the western part of the Canarian archipelago, especially between Tenerife and its surrounding islands. In fact, the large catamaran and trimaran high speed ferries are exclusively operating between the western islands (see Fig. 1).

Ferry schedules change regularly, sometimes at short notice, so the calculations made here constitute a 'snapshot' of ferry traffic in spring 2007. However, there is a general trend towards more fast and high speed ferries. Tregenza *et al.* (2000) counted 4,624 ferry transects between Tenerife and La Gomera (transect LC-SS) in 2000. Today, that number has reached 6,968, representing an over 50% increase. Hence, it can be assumed that the amount of ferry traffic likely will increase further or stay at the same level in the future.

Likewise, this investigation only dealt with inter-island ferry traffic. There are several additional ferry lines connecting the Canaries with mainland Spain and Madeira. If the high quantity of commercial (fishing, merchant, whale watching, etc.) and non commercial (sailing, big game fishing, motor yachting, etc.) vessel traffic that can be found in the Canary Islands is noted, the archipelago as a whole must be considered as a high risk area for ship strikes.

The amount of ferry traffic alone appears to be a major threat to cetaceans in the archipelago and ship strikes have regularly been reported. From 1985 until 2005, 37 whales were reported to have been hit by ships, and 30 of these (81%) occurred after the introduction of fast ferries in 1999 (de Stephanis and Urquiola, 2006). The first whales were hit only weeks after the start of operation of the first high-speed ferry (Aguilar *et al.*, 2000). The species involved is predominantly the sperm whales, but baleen whales, pygmy sperm whales, Cuvier's beaked whales and other beaked and short-finned pilot whales were also found (de Stephanis and Urquiola, 2006). Carrillo and Ritter (2010) found that of a total of 556 cetaceans stranded between 1996 and 2007, 59 (11%) involved animals being hit by a vessel. They also documented that 41% of stranded animals showing ship strike related injuries were sperm whales. Numbers given by the local government say that the percentage of sperm whales hit by vessels is as high as 52% (Gobierno de Canarias, 2009). Sperm whales thus appear especially vulnerable. They are known to stay for prolonged periods at the surface while recovering from deep and long dives (Watwood *et al.*, 2006). Moreover, they may have bi-hemispheric sleep (Miller *et al.*, 2008). Recognition of ship strikes mainly comes through strandings of carcasses or dead animals found floating at sea which show clear signs of collisions. In other cases, lesions typical for ship strikes have been identified through post mortem examinations. The reported numbers of whales hit per year between 2000 and 2008 varied from 3–7 according to official numbers (Gobierno de Canarias, 2009). Yet, this probably is an underestimate of the true numbers due to the fact that dead animals may drift offshore or sink and thus are not found. Reporting by ferry operators does not occur.

At a finer scale, a considerable overlap between ferry transects and prime cetacean habitats has been identified. Within the primary high risk areas one would expect a higher frequency of ship strikes than elsewhere in the archipelago, due to a high concentration of ferry traffic, a high density of cetaceans, or both. De Stephanis and Urquiola (2006) showed, that the largest portion of stranded animals hit by ships were found on the coasts of Tenerife. Carrillo and Ritter (2010) also found that a large portion of the animals that showed clear signs of ship strike related injuries stranded on the coast of Tenerife (see Fig. 2). This is exactly what one would expect to happen to animals hit between Tenerife and Gran Canaria since the Canaries current flows in a southeasterly direction and thus transports carcasses towards Tenerife's shoreline. A similarly high number of stranded animals were found on the South-west coast of Tenerife within one of the zones identified as high risk areas (see Fig. 3). Tregenza *et al.* (2000), with a simple model of collision risk, calculated that each pilot whale off Tenerife is at risk of 1.7 ship strikes per year. Near collision events regularly occur (pers. obs.).

Cetaceans may have already have learned to avoid certain high risk areas where they frequently and predictably encounter vessel traffic. This may also apply to the primary high risk area between Fuerteventura and Lanzarote and the areas around the largest harbours in the Canaries (Santa Cruz on Tenerife and Las Palmas on Gran Canaria). Off Southwest Tenerife, where besides the highest number of ferry transects a large amount of whalewatching takes place (10–15,000 trips per year as for 2002, see Servidio *et al.*, 2003), the situation is taken to extremes, in that cetaceans constantly live under the pressure of avoiding whalewatching vessels or ferries. Off La Gomera, where a high species diversity is also found (Ritter, 2003), the high speed ferry connecting Tenerife and El Hierro (transect LC-VV) has been seen to pass through the SAC of La Gomera although the transect is usually much farther offshore (Ritter, unpublished data).

The true extent of the problem still remains unclear. Ferry captains do not in general report collisions, although there have been reports by tourists travelling on high speed ferries and other vessels (for example Aguilar *et al.*, 2000; Ritter, unpublished data). To date, a carcass is identified as a victim of a ship strike if it is either found floating at sea or washed ashore. Stranded cetaceans are examined in detail by one of the Canarian specialist groups, who try to determine whether a ship strike was involved.

There are many different types of ferries operating in the archipelago. However, it is not even known if high-speed ferries have a higher collision risk than normal and fast ferries, or if the larger high-speed ferries collide more often than smaller ones. Depending on their construction features and sizes these vessels have differing manoeuvrabilities and presumably different abilities to avoid collisions. The Canaries Government reported 42 ship strike cases between 2000 and 2008 out of a total of 54 documented since 1985. Thus, 78% of registered ship strikes in the Canary Islands occurred after the introduction of regular fast and high speed ferry traffic (Gobierno de Canarias, 2009). Panigada (2006) found, however, that since their introduction in 1996 in the Mediterranean Sea, 43% of ship strikes involved fast ferries. Moreover, Weinrich (2004) found that all collisions of large vessels with cetaceans at a speed greater than 18 knots were fatal. Likewise, Laist *et al.* (2001) recognised that the most severe injuries in cetaceans were observed after collisions with vessel travelling faster than 14 knots. Jensen and Silber (2004) reported that relatively large and relatively fast moving vessels were most often involved in ship strikes. Hence, vessel speed and vessel size are crucial (see also Vanderlaan and Taggart, 2007).

It must be stressed that the current situation indicated that research must be conducted onboard ferries. Such research is urgently needed, e.g. to study the responsive behaviour of the animals to fast approaching ships, something that probably can be assessed by onboard observers (Capoulade, 2002; Ritter, 2007). Another important issue is the actual effect that ship strikes have on local cetacean populations (see also Tregenza *et al.*, 2000; Weinrich, 2004).

To address these issues, it is vital that effective communication between the ferry operators and the Canaries administration is established. Up to now, although dialogue has begun, there have been no substantial advances towards more transparency. It is therefore recommended (see also Carrillo and Ritter, 2010) to act on a precautionary ground and:

(1) install an obligatory reporting system making use of the IWC ship strike database, see *http://www.iwcoffice.org/sci_com/shipstrikes.htm*;

(2) implement shifts of transects away from primary high risk areas and/or speed restrictions;

(3) install onboard observers on ferries operating in primary high risk areas;

(4) implement research projects assessing the actual number of collision or near-collision events, preferably by placing researchers on board of the ferries; and

(5) develop a general strategy integrating different available mitigation measures.

Onboard observers appear to be an effective measure to lower collision risk (ACCOBAMS, 2005), and one Canarian ferry operator is already accepting such observers (de Stephanis and Urquiola, 2006). Other possible mitigation measures have been proposed, such as a Whale Anti Collision System (WACS, see Andre *et al.*, 2002). However, they are not very likely to be implemented in the short term. There has already been an attempt to modify certain transects (de Stephanis and Urquiola, 2006), but as long as monitoring and enforcement does not occur, these efforts will not be fruitful.

Finally, ship strikes may not only involve large or medium-sized whales but also dolphins (apart from being dangerous for other marine wildlife living more or less close to the surface), as indicated by a large number of dolphins showing propeller wounds (Van Waerebeek *et al.*, 2007; Ritter, unpublished data). It should also be noted that ship strikes also present a human safety issue. During a collision event, not only might the vessel be damaged, but also passengers may be hurt, or even killed. As an example, in a collision of a jet foil (which was afterwards taken out of operation), between Tenerife and Gran Canaria in 1999, one passenger was killed (de Stephanis and Urquiola, 2006) and many were injured. In light of this, an effective policy to manage ferry traffic so as to secure both human and animal safety appears an urgent matter.

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Exposure of humpback whales to unregulated whalewatching activities in their main reproductive area in New Caledonia

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ABSTRACT

Whale- and dolphin-watching activities are demonstrating a strong growth worldwide, raising concern of their potential impacts on cetacean populations and emphasising the need for management. Humpback whales recently have become the focus of an important tourism industry in the South Pacific, particularly in New Caledonia, where operators focus on a small population of humpback whales on their main breeding ground. Despite considerable growth since it began in 1995, the industry remains unregulated. Between 2005 and 2007, a study was conducted to assess the impact of whalewatching activities on the behaviour of humpback whales in New Caledonia. All data were collected from a land-based research station using a theodolite. Results show that 54% of all humpback whale groups sighted were exposed to whalewatching boats. Each group was watched simultaneously by an average of 2.5 boats. More than three boats were present within 300m of a group of whales 30% of the time. The length of time a group of whales was observed in the presence of boats each day was an average of one hour and 52 minutes but exceeded two hours 37% of the time. On average, each boat spent 52 minutes with the same group of whales. The closest point of approach was less than 100m for 86% of groups with a calf and 55% of non-calf groups. These results indicate that humpback whales are exposed to whalewatching boats in New Caledonia at a level exceeding the limits commonly recommended by management measures worldwide. Such exposure could be particularly problematic for mother-calf pairs, more vulnerable to threats. The strong site fidelity of individuals on this breeding ground raises concern of potential cumulative impacts. Management measures should be implemented to regulate whalewatching activities and ensure the conservation of this small, endangered population of humpback whales.

KEYWORDS: WHALEWATCHING; HUMPBACK WHALE; MANAGEMENT; CONSERVATION; PACIFIC OCEAN; SOUTHERN HEMISPHERE

INTRODUCTION

Whale- and dolphin-watching activities (hereafter referred to as whalewatching) have been expanding around the world, involving 119 countries and approximately 13 million participants each year (O'Connor *et al.*, 2009). This activity contributes substantially to the local economies of many countries, states and territories (Hoyt, 2001; O'Connor *et al.*, 2009) and plays an important role in increasing public awareness of the need for conservation of cetacean populations (IFAW *et al.*, 1997).

The increasing growth in whalewatching activities has led to concerns within the scientific community as to whether the presence of numerous boats and their operation around the animals may have an effect on their behaviour and survival. Several studies have shown that whalewatching activities can induce short-term behavioural changes in many of the species exposed (e.g. Baker and Herman, 1989; Corkeron, 1995; Scheidat *et al.*, 2004; Sousa-Lima *et al.*, 2002; Stockin *et al.*, 2008; Williams *et al.*, 2002) and therefore may represent a threat to some populations (e.g. Bejder *et al.*, 2006). Many countries have regulated approaches to whales and dolphins (Carlson, 2004) as managing the development of whalewatching and minimising the risk of adverse impacts is essential to ensure the conservation of cetacean species (IWC, 2000).

In the South Pacific Islands region, the whalewatching industry has demonstrated a remarkable growth of 45% per annum since 1998 (Economists at Large, 2008). Humpback whales (*Megaptera novaeangliae*), migrating every winter from Antarctica to their tropical breeding grounds, attract thousands of tourists and represent an important part of this development (Economists at Large, 2008; Orams, 1999; Schaffar and Garrigue, 2007). New Caledonia is one of the South Pacific Islands where humpback whales can be observed during the austral winter. Commercial humpback whalewatching activities focus on the southern lagoon of New Caledonia, an area identified as the main breeding ground for this population (Garrigue *et al.*, 2001). Since its start in 1995, whalewatching has grown at an average annual rate of 40% and is now a well-established industry with 26 commercial tour boats (Schaffar *et al.*, 2009a). Despite this considerable growth, whalewatching activities have yet to be regulated in New Caledonia.

Humpback whales wintering in New Caledonian waters could be particularly vulnerable to this unregulated tourism industry. The species has not yet recovered from decades of whaling operations in the Southern Ocean (Clapham *et al.*, 2009) and the New Caledonian humpback whale population remains one of the smallest in the South Pacific Islands region with only 472 individuals (South Pacific Whale Research Consortium, 2006). Moreover, strong site fidelity (Garrigue *et al.*, 2002) combined with demographic and reproductive isolation (Garrigue *et al.*, 2004), suggests a risk of cumulative exposure over the years (Schaffar and Garrigue, 2006).

Given the development of whalewatching in New Caledonia and the characteristics of the humpback whale population, this activity may have reached its maximum carrying capacity. A study was therefore initiated in 2005 in

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order to assess the potential effects of recreational and commercial whalewatching boats on the behaviour of humpback whales, recommend management measures for the conservation of this population and determine carrying capacity. In this paper information is provided on the level of exposure of humpback whales to whalewatching activities in the southern lagoon of New Caledonia based on numbers of boats viewing whales, length of encounters and minimum distance of approach.

METHODS

Study site and period of research

All observations were made from Cap Ndoua, a lookout point located 189m above sea level and overlooking the area where the majority of interactions between boats and whales occur within the southern lagoon (Fig. 1). Observations were restricted to days with no rain and a wind speed less than 15 knots.

Observations were conducted in 2005, 2006 and 2007 by a team of three researchers from early morning (around 7am) to mid-afternoon (around 3pm) during the main period of presence of humpback whales in the southern lagoon (mid-July to mid-September).

Data collection

A Sokkia Set 5 theodolite was used to monitor the movement and behaviour of humpback whales in the absence and presence of boats. The theodolite was connected to a laptop computer running the tracking program Cyclopes (Kniest and Paton, 2001) and used to transform the vertical and horizontal coordinates from the theodolite readings into GPS points and to record other behavioural and fix data.

To test the maximum distance at which whales' movement and behaviour could be tracked reliably, data collected simultaneously from the land-based station and during boat-based surveys on the same group of whales were compared. On clear days and with a wind speed less than five knots, groups could be tracked reliably up to eight nautical miles from the lookout point. Therefore, the maximum distance at which humpback whales were tracked was set at eight nautical miles (Fig. 1) but varied with weather conditions and wind speed.

Due to the small numbers of humpback whales within the New Caledonian population (estimated at 472, CV=0.18; South Pacific Whale Research Consortium, 2006) the sighting rate within the study area remains relatively low with an average of only 1.8 groups per day. These characteristics reduce the likelihood of re-sampling the same group multiple times per day (pseudo-replication) and the choice of which group to track. When more than one group was within sight of the land-based station, the group closest to shore was tracked to increase the probability of tracking the same group with boats afterwards.

Each group of whales was tracked for a minimum of 20 minutes with at least five surfacing bouts. The whales' position was fixed with the theodolite once every minute and was taken on the first whale to surface after that time elapsed. A group of whales was defined as one or more whales within 100m of each other, generally moving in the same direction in a coordinated manner (Mobley and Herman, 1985; Whitehead, 1983). Group type was recorded at the start of each tracking session and four categories were used: singleton, pair, groups of three adults or more, and mother-calf (i.e. alone or with other adult whales). A calf was defined as an animal in close proximity to another whale, visually estimated to be less than 30% of the length of the accompanying animal. All surface behaviours, such as blows, breaches, and tail slaps, were continuously recorded. Between each recording of the whales' position, the position

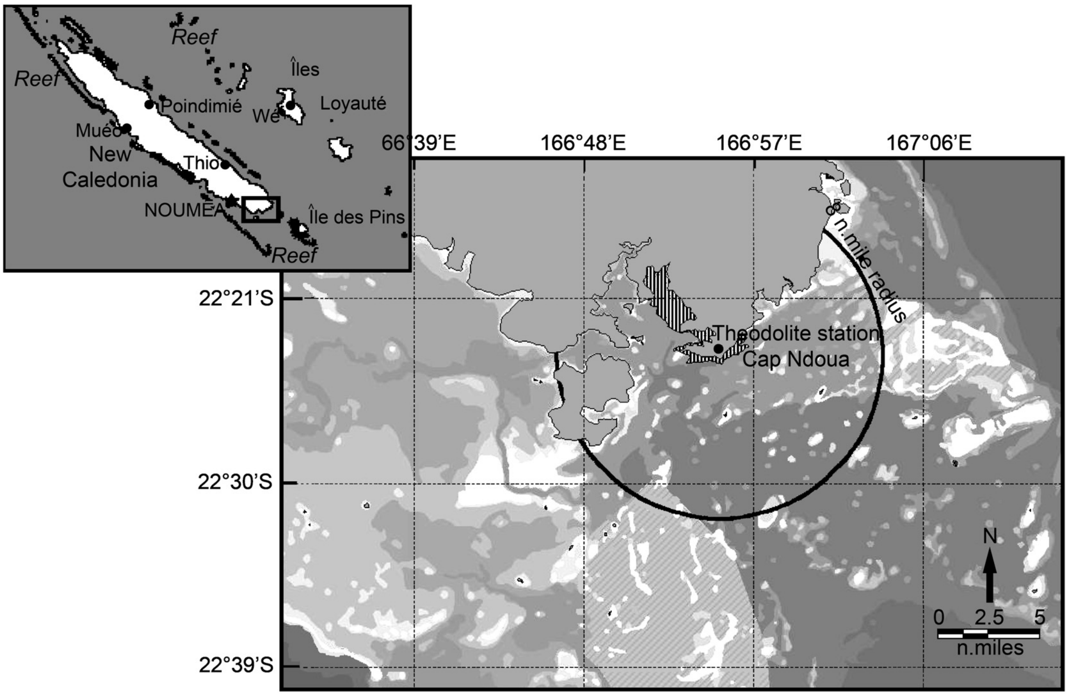

Fig. 1. Observation site and study area within a 8 n.mile radius from Cap Ndoua. The striped area represents the blind area from the shore station.

of all whalewatching boats within a 1,000m radius of the whales was also recorded. Each whalewatching boat was individually identified and recorded as either commercial or recreational. Another track was started when conditions changed, i.e. if boats arrived within 1,000m of whales that had been observed without boats up to that point, if all boats left the whales or if group composition changed (i.e. affiliation or disaffiliation of individuals).

After a track was completed, the number and identities of all boats with the group of whales was recorded every 15 minutes, while searching or tracking other groups. This information was compiled with the data obtained from tracking sessions of whales in the presence of boats in order to assess as accurately as possible the level of exposure of humpback whales to whalewatching boats. Data on the length of whalewatch encounters were also collected for some groups that could not be tracked with the theodolite.

Data analysis

The level of exposure of humpback whales to whalewatching boats was assessed using the following variables: number of boats viewing whales; length of encounters; and minimum distance of approach. These variables were calculated using all data collected on boats within 300m of a group of whales as this is the most common distance used worldwide to define the whalewatch zone (Carlson, 2004; IFAW, 2008).

The length of encounters corresponds to the time spent by each boat with the same group of whales. The cumulative time during which a group of whales was observed per day was also calculated and refers to the total amount of time a group was watched by boats. Both theodolite data and information gathered outside tracking sessions were used to assess these variables.

Only theodolite data were used to determine the distance of approach of whales by boats and the number of boats with whales. For each whale position recorded, the distance of each boat to a group was first calculated, from which the minimum distance of approach was determined. The amount of time boats were present at different distances to the animals was then calculated.

The number of boats with whales refers to the total number of whalewatch boats, either commercial or recreational, within 300m of a group of whales.

The level of exposure to whalewatching activities was compared between groups with and without a calf and between the three years of this study. The amount of time spent with whales by recreational versus commercial whalewatching boats was also compared. The mean number of boats watching whales was assessed by day of the week and time of day. Histograms were generated for each variable to assess normality before conducting an analysis of variance (ANOVA). Where *post hoc* tests were required, LSD analysis was used. A value of $p < 0.05$ was used for significance.

RESULTS

Research effort and sample size

Data were collected over three field seasons from 2005 to 2007 (Table 1). Over the 146 days of observation, 275 groups of humpback whales were sighted within the study area. Of these, 154 were tracked using the theodolite during 171.4hr (Table 2). Data collected on groups that could not be tracked with the theodolite provided information on the length of encounters for another 50 groups.

Groups of whales were tracked for an average of 1.1hr (±0.8hr, range = 0.3 – 5.1hr, *n* = 154). The majority of groups tracked were singletons (41%, *n* = 63) and pairs (33%, *n* = 51) (Fig. 2).

Table 1

Research effort by year showing the number of days and hours of observation in the field and the total number of hours spent tracking whales.

Year	Dates	Number of days (and hours) of observation	Number of hours tracking whales
2005	14 Jul.–4 Sep.	42 (236)	47.9
2006	18 Jul.–17 Sep.	53 (329)	58.4
2007	12 Jul.–19 Sep.	51 (308)	65.1
Total		**146 (873)**	**171.4**

Table 2

Number of humpback whale groups tracked from the shore station using the theodolite.

Year	Number of groups	Groups tracked with boats	Groups tracked without boats	Groups tracked with and without boats
2005	33	16	11	6
2006	59	13	30	16
2007	62	13	30	19
Total	**154**	**42**	**71**	**41**

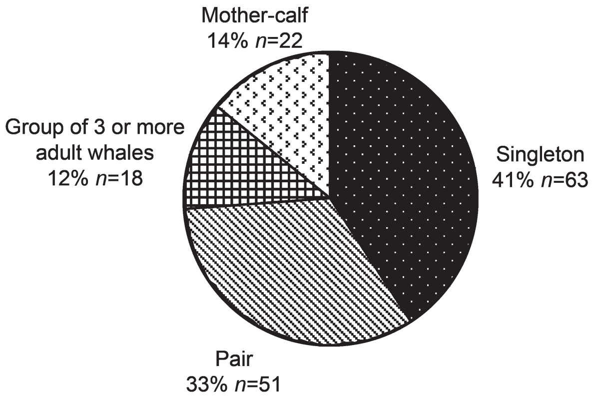

Fig. 2. Percentage of groups tracked per group type (*n*=154).

Exposure to whalewatching boats

During the observations, a total of 148 groups of humpback whales were exposed to whalewatching boats, which represents 54% of all groups sighted within the study area (*n* = 275). Five hundred and fifteen occurrences of boats watching whales were observed, 31% recreational (*n* = 160) and 69% commercial (*n* = 355).

Each boat spent an average of 52min (±42.5min, range = 1min – 3.8hr, *n* = 515) with a group of whales. Observation time per boat exceeded 30min 31% of the time (*n* = 157) and 1hr 65% of the time (*n* = 332) (Fig. 3), with 13 occasions where boats stayed with the same group for over three hours. Boats spent more time with adult whales (54min ±44.7, range = 1min – 3.8hr, *n* = 432) than with groups containing a calf (42min ±26.5, range = 5min – 2.01hr, *n* = 83) ($F = 6.260$, $p < 0.05$). Boats spent more than 30min with mother-

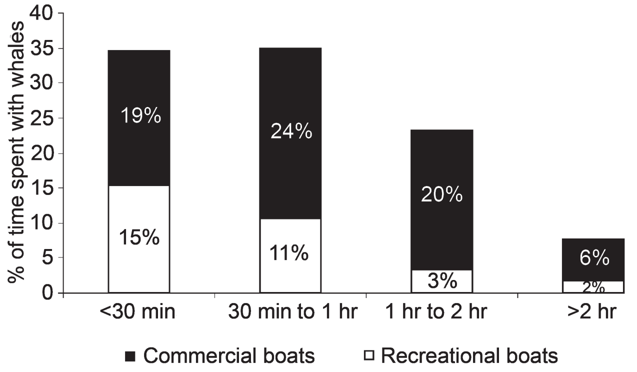

Fig. 3. Percentage of time spent with whales by commercial and recreational whalewatching boats.

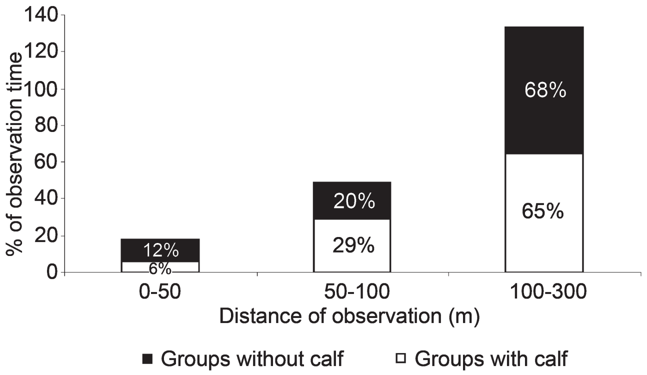

Fig. 5. Percentage of observation time with whalewatching boats present at different distances to groups with and without a calf.

calf groups 57% of the time (n = 47). Recreational boats spent significantly less time with whales than commercial whalewatching boats ($F = 12.726, p < 0.01$) (Fig. 3), with an average observation time of respectively 43 min (±42.2min, range = 3min – 3.8hr, n = 160) and 57min (±42min, range = 1min – 3.8hr, n = 355).

Each group of whales was accompanied by boats for an average cumulative time of 1hr and 52 min each day (±1.13hr, range = 15min – 5.8hr, n = 131). Whales were observed by boats for over 2hr 37% (n = 49) of the time, and sometimes up to over five hours a day. There were no significant differences in the cumulative observation time depending on the presence of a calf in the group ($F = 0.009$, $p > 0.05$).

Groups of humpback whales were simultaneously watched (i.e. within 300m) by an average of 2.5 boats (±2.2, range = 1 – 15, n = 75) over the length of a tracking session. Over the three field seasons, the maximum number of boats simultaneously observing a group of whales was 15. There were more than three boats with whales 30% of the time (n = 23) and over five boats 16% of the time (n = 12). The average number of boats with whales was significantly higher at weekends (3.5 ± 2.8, range = 1 – 15, n = 30) than during weekdays (1.7 ± 1.03, range = 1 – 7, n = 45) (F = 177.975, $p < 0.01$). A time specific analysis showed that the number of boats varied significantly throughout the day ($F = 30.796, p < 0.01$), with a peak between 10am and noon ($p < 0.01$) (Fig. 4). Boats were present in lower numbers with mother-calf groups (1.7 ± 1.3, range = 1 – 7, n =15) than with non-calf groups (2.6 ± 2.3, range = 1 – 15, n = 60) ($F = 18.848, p < 0.01$).

Out of all groups tracked in the presence of boats (n = 83), the closest point of approach by boats was less than 100m for 86% of groups with a calf (n = 13) and 55% of non-calf groups (n = 38). Boats were present within 100m of non-calf groups during 32% (n = 12.7hr) of observation time and 35% (n = 3.4hr) for groups containing a calf (Fig. 5). Although the closest point of approach for groups with a calf was on average closer (67.7m ± 55.7, range = 4.4 – 236.5m, n = 15) than that of groups without a calf (137.3m ± 139.4, range = 2.8 – 738.6m, n = 68), this difference was not statistically significant ($F = 3.584, p > 0.05$).

There were no significant differences in the observation time per boat ($F = 2.119$, $p > 0.05$), the cumulative observation time for each group ($F = 0.298, p > 0.05$), the number of boats within 300m of whales ($F = 2.345$, $p > 0.05$), and in the minimum distance of approach ($F = 0.887, p > 0.05$) between the three years of this study.

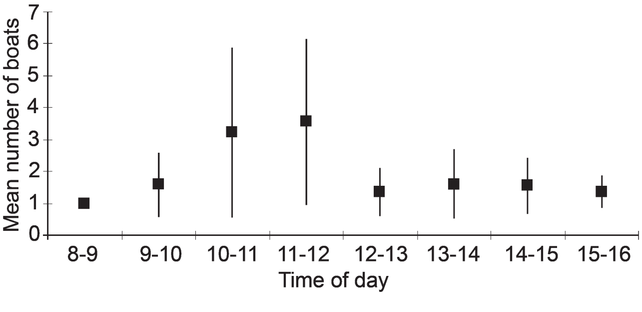

Fig. 4. Mean number of whalewatching boats within 300m of whales and standard error per time of day.

DISCUSSION

The results of this assessment show that the small population of humpback whales wintering in the southern lagoon of New Caledonia is exposed to numerous whalewatching boats for several hours everyday. The risk of long-term deleterious effects on this population is high, especially when one considers management measures in place around the world.

An analysis of 58 whalewatching codes of conduct and regulations showed that the most common observation time allowable for boats was 30 minutes (Garrod and Fennell, 2004). During our surveys, whalewatching boats spent on average almost twice that time with the same whales. Observation time exceeded 30min 65% of the time. Restrictions on the cumulative duration of whalewatch encounters (total amount of time a group of whales is in the presence of boats within a day) are rare within the literature. Only one example has been found in the Caribbean where the cumulative observation time per group of whales is limited to 30 minutes (Carlson, 2004). Such restriction can be particularly difficult to implement and enforce as it strongly relies on communication between observers of a specific group of whales throughout the day. Due to the low number of humpback whale groups present in the whalewatch area each day and the large numbers of commercial whalewatching boats, the cumulative duration of encounters is particularly crucial in New Caledonia and often exceeds two hours.

Regarding the number of boats simultaneously watching a group of whales, almost half of the management measures reviewed by Garrod and Fennell (2004) suggest no more than one boat at a time, 30% specified two, while 20% recommended three boats. In the Pacific Islands region, existing guidelines and regulations consistently recommend a maximum of three boats or less simultaneously watching a group of whales (IFAW *et al.*, 2008). The observations conducted in this study have shown that the number of boats with whales is regularly higher than three, especially on weekends when the demand for whalewatch trips is the highest.

The results show that boats most frequently watch whales from a distance of between 100 and 300m. The minimum distance recommended to approach a group of whales is generally between 50 and 100m in other areas (Carlson, 2004; Garrod and Fennell, 2004; IFAW *et al.*, 2008). Humpback whales in New Caledonia are approached at distances closer than 50m during 18% of the total observation time.

Specific restrictions regarding approaches of mother-calf groups often are implemented to provide extra protection to young whales, considered to be more vulnerable to threats. In many countries, watching mother-calf groups is strictly forbidden (Carlson, 2004; Garrod and Fennell, 2004). When allowed, the minimum approach distance recommended for groups with calves is often greater than for groups without a calf and most commonly is limited to 100m or more (Carlson, 2004; IFAW *et al*., 2008). This study shows that whalewatching boats approach within 100m of groups with a calf 35% of the time. Although whalewatching boats tend to spend less time with groups with calf, observation time was over 30 minutes 57% of the time and the cumulative length of encounters was not different from other group types. Mothers and calves could be particularly vulnerable to such exposure as it may interfere with nursing or other social behaviour essential to their survival.

The number of boats with whales, the length of encounters and the distance at which mother-calf groups are approached are often beyond the limits generally recommended or enforced worldwide. Only around a hundred humpback whales visit the southern lagoon every year and the majority of individuals are exposed to whalewatching activities. The level of exposure is likely due to the large number of whalewatching boats, combined with the lack of management measures. Furthermore, the high level of exposure to whalewatching activities is probably the cause of significant behavioural changes demonstrated in the presence of boats (Schaffar *et al.*, 2009b). Although the level of individual exposure is currently unknown, the strong site fidelity of humpback whales observed in the southern lagoon of New Caledonia (Garrigue *et al.*, 2002) raises the question of the impact of cumulative exposure of a small number of animals to a high level of whalewatching activity. Minimising the level of exposure of humpback whales to whalewatching activities in the southern lagoon of New Caledonia is therefore essential.

In 2007, guidelines on how to approach and observe humpback whales were produced by New Caledonian whalewatch tour operators. For mother-calf pairs, a minimum approach distance of 100m and a maximum observation time of half an hour were recommended. It also suggested a limited number of five boats simultaneously watching the same group of whales. The results presented in this paper show that the voluntary guidelines were often breached and did not result in a significant change in the level of exposure during that year. These guidelines therefore are unlikely to provide accurate protection to humpback whales from the impact of whalewatching activities in New Caledonia.

The results of this assessment provide valuable information that can assist the development of an informed management plan. The lack of compliance with voluntary guidelines indicates that self-regulatory measures are insufficient to ensure the conservation of humpback whales in New Caledonia, which is not an uncommon occurrence in the whalewatch industry (Constantine and Bejder, 2008). Regulations are therefore required and will need to include enforcement measures. The results of the present study also show that specific efforts should be made to limit approaches to groups containing a calf to a minimum of at least 100m. The number of boats operating in the whalewatch area appears to be a major problem and cannot be considered sustainable for the small and endangered population of humpback whales wintering in New Caledonia. As commercial whalewatching boats represent 69% of all approaches to whales, a licensing scheme limiting their number should urgently be implemented. Other measures, such as two-tiered approach distances, also need to be considered for recreational vessels. The recent listing of the southern lagoon of New Caledonia as a World Heritage site undoubtedly offers the framework to implement effective management of whalewatching and to ensure the conservation of one of the country's most emblematic species.

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Mark-recapture estimates of seasonal abundance and survivorship for bottlenose dolphins (*Tursiops truncatus*) near Charleston, South Carolina, USA

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ABSTRACT

The stock structure of western North Atlantic bottlenose dolphins (*Tursiops truncatus*) is complex, with seasonally migratory stocks often overlapping with year-round resident stocks. High rates of exchange between northernmost sites have been documented but movement and seasonal fluctuation in abundance among sites along the southern portion of the US Atlantic coast is not well understood. To better understand seasonal abundance, a three-year mark-recapture study of bottlenose dolphins in coastal and estuarine waters near Charleston, South Carolina, USA was conducted. A robust design was employed in order to minimise bias and more precisely determine seasonal estimates of abundance and concurrently examine temporary immigration/emigration and survivorship. Systematic boat-based surveys were carried out (n = 192) from January 2004 to December 2006. The entire study area was surveyed one week per month; an additional survey was conducted in the months in which seasonal abundance was estimated: January (winter), April (spring), July (summer) and October (autumn). Standard photo-identification techniques were used to accumulate sightings of 521 distinctively marked dolphins, 65% of which were sighted more than once. Pollock's robust design was applied using *MARK* and the ensuing abundance estimates were adjusted for the seasonal proportion of unmarked dolphins (ranging from 0.27 to 0.40) in the population. Estimates ranged from 364 (95% CI = 305–442) in January 2004 to 910 (95% CI = 819–1018) in October 2006. Summer abundance estimates were consistently greater than those from winter months, although estimates varied considerably among years. The same model was used to calculate an annual survival rate estimate of 0.951 (95% CI = 0.882–1.00) for marked individuals within the population. A high degree of transience, demonstrated by seasonal influxes of single-sighted individuals, made it difficult to differentiate between mortality and permanent emigration. The results support the occurrence of three distinct dolphin groups found in Charleston waters: year-round residents; seasonal residents; and transients. Reporting abundance and survivorship estimates together is useful in explaining and validating results for populations in which transient individuals occur. These results provide important information for stock and viability assessment of coastal bottlenose dolphins in the western North Atlantic.

KEYWORDS: BOTTLENOSE DOLPHIN; PHOTO-ID; SURVIVORSHIP; ABUNDANCE ESTIMATE; MARK-RECAPTURE; NORTH AMERICA; NORTHERN HEMISPHERE

INTRODUCTION

Limited published accounts exist on the abundance and survival of bottlenose dolphins (*Tursiops truncatus*) from the eastern coast of the United States. While previous studies (Barco *et al.*, 1999; Read *et al.*, 2003) have reported abundance estimates for bottlenose dolphins in localised areas, to date Read *et al.* (2003) have provided the only estimate for estuarine dolphins included in the most recent NMFS stock assessment (Waring *et al.*, 2009). Similarly, to our knowledge only one published report (Stolen and Barlow, 2003) provides estimates of annual mortality rates from strandings of US east coast bottlenose dolphins.

Bottlenose dolphins have been identified for decades using natural markings (Caldwell, 1955). Individual recognition through photographs, a process known as photo-id, has become the recognised tool for tracking small cetaceans over time (Würsig and Jefferson, 1990). These markings, primarily in the thin connective tissue of the trailing edge of the dorsal fin, may last throughout a dolphin's lifetime and can be used to identify and monitor individuals (i.e. 'capture' an individual dolphin) (Irvine *et al.*, 1982; Lockyer and Morris, 1990; Read *et al.*, 2003; Würsig and Jefferson, 1990). In general, fins are considered distinctive or 'marked' if they contain a readily identifiable feature (e.g. a mutilated fin) or intermediate features (e.g. fins with at least two distinguishing or one major feature) that are recognisable over time (Friday *et al.*, 2000). Given that mark-recapture requires accurate identification of individuals within a population, correct identification and cataloguing of fins is crucial to obtaining unbiased estimates (Friday *et al.*, 2000; Read *et al.*, 2003; Würsig and Jefferson, 1990).

Photo-id research on bottlenose dolphins near Charleston, SC began in October 1994, where Zolman (2002) documented year-round residents in the Stono River estuary (SRE). Effort was eventually expanded to adjacent areas (i.e. Charleston Harbor and coastal waters). Speakman *et al.* (2006) identified 839 distinctive individuals from 1994–2003. In addition to residents, dolphins that appeared to be infrequent, short-term visitors (i.e. transients) to the study area were identified. Herein, photo-id data collected from 2004–06 and mark-recapture techniques are used to model both survivorship and seasonal abundance of dolphins near Charleston.

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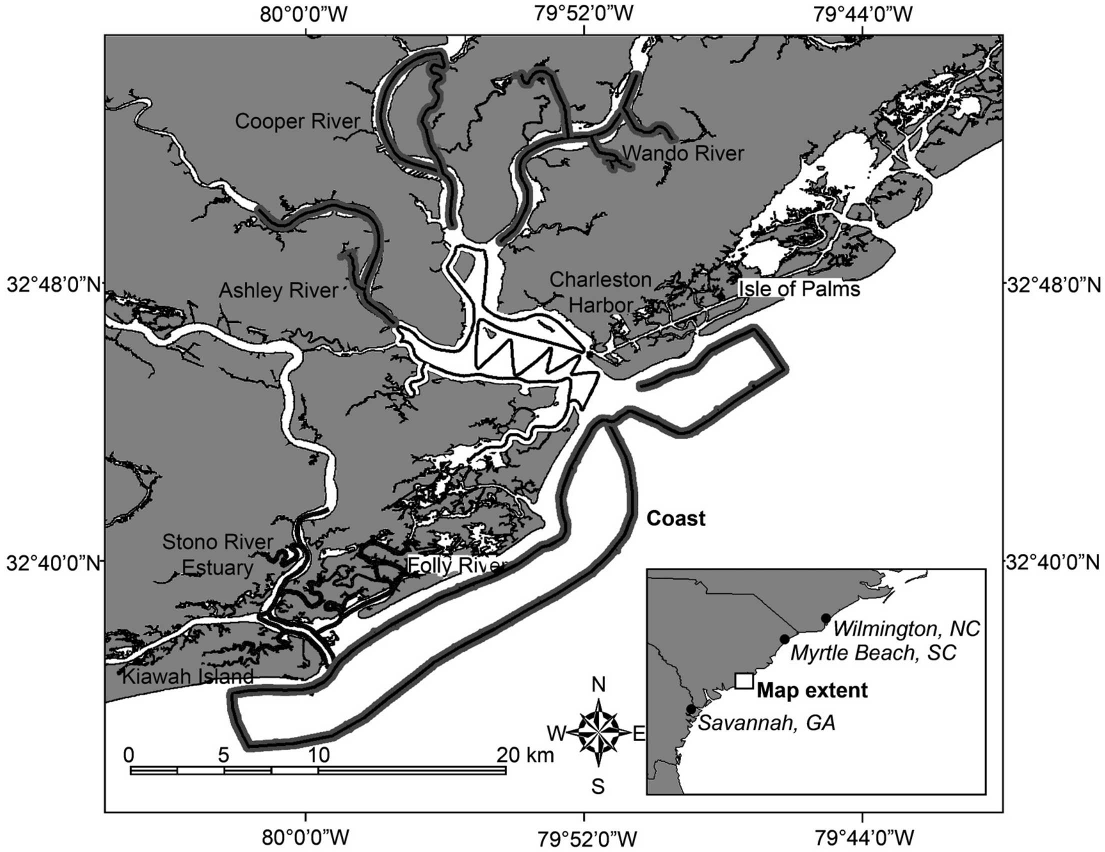

Fig. 1. Charleston, SC study area with survey routes.

METHODS

Study area and field effort

The study area is comprised of four regions in estuarine and coastal waters near Charleston, SC (32˚40'N, 79˚55'W; Fig. 1):

(1) SRE: the southernmost region is comprised of the main channel and creeks of the lower Stono River estuary, including portions of the Kiawah and Folly rivers;

(2) CHS: the upper and lower portions of Charleston Harbor which contains a deep ship channel as well as a large inlet to the Atlantic Ocean. A few small creeks and sounds are also part of this survey region;

(3) ACW: includes stretches of the Ashley, Cooper and Wando rivers and selected associated creeks, inland of CHS; and

(4) CST: the coastal region which includes two transects, an 'on-effort' transect approximately 1km from shore as well as an 'off-effort' route approximately 3km from shore, both stretching from the middle of the Isle of Palms in the east to the eastern end of Kiawah Island to the west.

From 2004–06, boat-based photo-id surveys of bottlenose dolphins were conducted as part of a long-term project to study their abundance and distribution. A complete survey consisted of finishing all transects in each of the four regions in the shortest time possible and under optimal sighting conditions (less than Beaufort Sea State 3). Sixteen systematic surveys were conducted each year; 12 monthly surveys and an additional seasonal survey in January (winter), April (spring), July (summer) and October (autumn). These seasonal, bi-monthly surveys were the basis for the mark-recapture abundance and survivorship estimates, carried out in close temporal proximity (three weeks) and separated by a minimum of one week to allow for population mixing.

Surveys were conducted from 5–6m centre-console outboard-powered vessels with 3–4 crew members. Surveys followed a designated route at 28–30km hr^{-1} until a dolphin or group of dolphins were sighted. An attempt was made to photograph each member of the group, regardless of degree of 'markedness', using a Canon EOS-IDs digital camera equipped with a 100–400mm telephoto lens. A sighting datasheet was completed for each group, defined as all dolphins in close proximity (<100m) to one another, engaged in similar behaviour and heading in the same direction (Wells *et al.*, 1987). Time, location (via GPS), depth, group size (min, max and best estimate), composition and cohesiveness, environmental conditions, dolphin heading and behaviour were recorded for each group. All dolphin groups encountered while on the designated survey route were regarded as 'on-effort' sightings; whereas, dolphin groups observed while returning along an already completed survey route were labelled as 'off-effort' sightings.

Photo and data analysis

Digital photographs were downloaded and organised by survey date and sighting number. Photographs were then sorted using *Photoshop* 7.0 to obtain the best left and/or right-side dorsal fin image of each individual from each sighting (Mazzoil *et al.*, 2004). Sorted images were graded for quality using a weighted scale that incorporated five characteristics: focus; contrast; angle; fin visibility/obscurity; and proportion of the frame filled by the fin (Urian *et al.*, 1999). Any photographs not meeting quality criteria were removed from the data set. Only those photographs rated average (Q-2) to excellent (Q-1) quality were included in subsequent analyses.

Q-1 and Q-2 photographs were then matched to the Charleston bottlenose dolphin dorsal fin catalogue via *Finbase*, a customised database constructed using Microsoft *Access* (Adams *et al.*, 2006). All matches were verified by two researchers and catalogued in *Finbase* under a unique numerical code, determined by the most distinctive dorsal fin characteristic. When a fin image was not matched, two researchers independently searched for the fin against the entire catalogue before assigning a new database code. Each sighting of an individual was entered with additional information such as age class and distinctiveness. The extent of dorsal fin markings, in the form of scratches and notches, were used to assign a level of distinctiveness to each individual. Distinctiveness was graded independently of photographic quality. Fins with little to no markings were considered 'unmarked'. Average fins (D-2; 2 minor or 1 major mark) and very distinctive fins (D-1; obvious major marks) were considered 'marked' (Urian *et al.*, 1999).

Capture histories, a record of whether individuals were photographed during each sampling event, were compiled for all 'marked' individuals sighted while on-effort during seasonal mark-recapture months (Jan, Apr, Jul and Oct) from 2004–06. In addition, marked individuals photographed during off-effort sightings that occurred within the daily survey region were also included in the capture histories. Capture histories were then exported into *MARK*, a program used to model various parameter estimates from marked animals based on recaptures (Cooch and White, 2006).

Mark-recapture model

Mark-recapture models are defined as either open or closed. Closed population models are conducted over short periods of time and operate under the assumption that the population is constant, that is 'closed' to births, deaths, emigration, or immigration. Open models can be conducted over longer periods by allowing for a non-constant population (Pollock *et al.*, 1990). Closed models traditionally used to estimate abundance (e.g. the Lincoln-Petersen method) are further based on the assumptions that: (1) all marks are permanent; (2) being captured does not affect recapture; and (3) all individuals have an equal chance of being captured (Pollock *et al.*, 1990). However, as closure is difficult to achieve in wildlife populations over prolonged periods, survival rates are routinely estimated with open models, (e.g. the Jolly-Seber model) with their own set of assumptions (Pollock *et al.*, 1990). While survival estimates are generally more robust to assumption failures than abundance estimates, assumption violations have the potential to bias either type of estimate (Lebreton *et al.*, 1992). In particular, a violation of 'equal catchability', an assumption of both models, can be problematic. Open models somewhat rectify violations of 'equal catchability' but are limited in that all emigration from the population is considered permanent (Pollock *et al.*, 1990).

Charleston-area dolphins display a variety of residence patterns (Speakman *et al.*, 2006; Zolman, 2002). Zolman (2002) defined dolphins that were seen year-round in the study area as residents, dolphins that were identified in the same season in multiple years but not during intervening seasons as seasonal residents and dolphins identified in the area in only one season or only two consecutive seasons as transients. Dolphins from all three resident classes have been observed throughout the study area, but seasonal residents and transients are observed more frequently in the coastal region (Speakman *et al.*, 2006). Seasonal residents are commonly observed feeding behind working shrimp boats along the Charleston coast during peak shrimp season from June to November. These dolphins are often sighted in Charleston Harbor following returning shrimp boats and likely represent individuals who reside beyond the study area making seasonal forays into Charleston waters. Such movements through the study area would obviously test the assumption of 'equal catchability' if the recapture period extended across seasons.

Due to these considerations, Pollock's robust design model (Pollock, 1982) was applied to three years of mark-recapture data to estimate abundance and survival rates. This model follows a set of assumptions derived from both open and closed population models to estimate parameters. These assumptions include: (1) all marks are unique and permanent; (2) survival is equal among all individuals between primary sampling periods; (3) each individual's probability of capture and survival is independent of all others; (4) the population is closed within primary sampling periods; and (5) all emigration between primary sampling periods is temporary (Kendall *et al.*, 1995). By incorporating both open and closed population models, the robust model allows for the effects of temporary emigration on the population, thus making it less sensitive to violations of 'equal catchability' (Pollock, 1982). Advantages of the robust model include better precision and less biased results due to its ability to account for temporary emigration. The surveys produced data for 12 primary sampling periods (Jan, Apr, Jul, Oct for 2004–06), each containing two, secondary sampling occasions. The robust model enabled abundance estimates for each primary session (with closed population models) and survival estimates for intervals between primary sessions (using an open population model) (Pollock *et al.*, 1990).

Calculating abundance and survival estimates

The master, or 'complete' data set used in this study includes marked individuals identified during all sightings within the survey area from 2004–2006. Data were analysed within *MARK* via the robust design model with closed captures. Parameters were adjusted within the Parameter Index Matrix (PIM) to represent various closed population models, such as M_o, M_t and M_b. M_o, the simplest model, assumes no variation in capture probabilities among animals or sampling occasions (Seber, 1992). M_t assumes each animal has a constant capture probability on any sampling occasion but probabilities of capture can vary from one occasion to the next (Seber, 1992). The behavioural response model, M_b, incorporates change in capture probability as a result of previous capture (i.e. trap-happy or trap-shy) (Seber, 1992). Furthermore, each model was constrained to test for variations in emigration patterns (e.g. random or Markovian emigration) (Kendall *et al.*, 1997). Random emigration assumes that an individual emigrates out of the study area for just one sampling occasion and then always comes back, but can emigrate again randomly (Kendall *et al.*, 1997). Markovian movement assumes individuals that have temporarily emigrated from the study area at time t are more likely to be out of the study area at time $t+1$ than those that remained in the study area at time t (i.e. animals 'remember' they are out of the area) (Kendall *et al.*, 1997). Finally, survival was held constant among all models as historical stranding records from the area failed to show an effect of season on the number of non-neonate stranded dolphins (McFee *et al.*, 2006). The best fitting model was selected based on the variance inflation factor ($\hat{c}$), model deviance and Akaike's information criterion corrected for small sample size (AICc), which is an information criteria designed to maximise model fit without compromising precision (Burnham and Anderson, 2002).

Seasonal abundance estimates derived from *MARK* were compared to seasonal estimates calculated using a simple Lincoln-Petersen model following closed population assumptions (Pollock *et al.*, 1990). Additionally, for comparison, monthly counts of marked individuals were calculated. All on-effort sightings of distinctively marked individuals were used and monthly counts for single-sighted marked individuals were calculated to examine when permanent immigration/emigration might be occurring. Select data sets, such as those excluding sightings of all shrimp boat-associated individuals ('shrimp boat delimited') and of all individuals encountered during CST surveys ('CST delimited'), were also constructed and analysed. The 'shrimp boat delimited' data set was constructed to examine the effect that seasonal resident and transient dolphins, which are frequently associated with shrimp boats, might have on abundance estimates. Removing dolphins sighted along the CST, in combination with those associated with shrimp boats, allowed for estuarine abundance estimates.

MARK-derived estimates represent only the distinctively 'marked' portion of the Charleston dolphin population. To adjust this estimate of 'marked' abundance to estimate total abundance ('unmarked' plus 'marked' dolphins), the 'marked' estimates were divided by the 'marked' proportion of the population for each primary session. To calculate this proportion, all on-effort sightings were compiled for each primary session from 2004–06 in which all dolphins in the group, regardless of distinctiveness level, were photographed. Variance and confidence intervals for each seasonal total abundance estimate were calculated using the delta method (Wilson *et al.*, 1999).

Annual survival rates (ASR) for the 'marked' portion of the population were estimated from the product of the seasonal survival rates (i.e. $S_{Jan} \times S_{Apr} \times S_{Jul} \times S_{Oct} = S^4$). The delta method (Wilson *et al.*, 1999) was again used to calculate the variance and confidence intervals for the ASR. Dorsal fin markings in small cetaceans are cumulative (Würsig and Jefferson, 1990) and consequently, very young dolphins have a lower likelihood of having distinctive fins. Therefore, young-of-the-year (YOY) survivorship rates were estimated separately from the rest of the population. This was accomplished by tracking the sighting records of calves born to distinctive females from 2004 to 2006. Calves were classified as deceased if the mother was encountered either with the carcass of the calf or without the calf on three or more consecutive sightings. Age was approximated in months for each calf using the month of initial and final sighting as endpoints for the age interval. Birth was assumed to have occurred in the same month as each calf's initial sighting; therefore any individual thought to be an older calf (i.e. those lacking fetal folds) (Urian and Wells, 1996) was excluded from YOY survivorship estimation. For those individuals not classified as dead prior to the conclusion of the study, final sightings were treated as right censored observations; thereby allowing for the incorporation of all available lifetime data into the survival analysis although only a fraction of exact lifetimes were known. Due to the censoring of these data, the YOY survivorship rate was derived utilising a Kaplan-Meier product-limit estimator,

$$\hat{S}(t) = \prod_{ti \leq t}[1 - d_i / Y_i], \quad (1)$$

where t_i is time, d_i is the number of deaths at time t and Y_i is the number of individuals in the sample at time t (Klein and Moeschberger, 1997).

RESULTS

Forty seven surveys from January 2004 through December 2006 were completed. Only one survey (CST June 2004) was incomplete. During the three year project a total of 1,423hrs were spent on the water (n = 562hrs in contact with dolphins), 9,217km were surveyed on-effort, 96,153 photographs were taken and 2,272 (1,961 on-effort) dolphin groups were encountered. Within on-effort groups, 856 distinctively marked individuals were identified. The calculated marked proportion of individuals sighted varied across seasons and ranged from 60% to 73%. A total of 556 (65%) marked individuals were sighted more than once (Fig. 2).

An influx of transient dolphins was observed in the autumn months of both 2005 and 2006 as indicated by an increase in the number of individuals not previously sighted

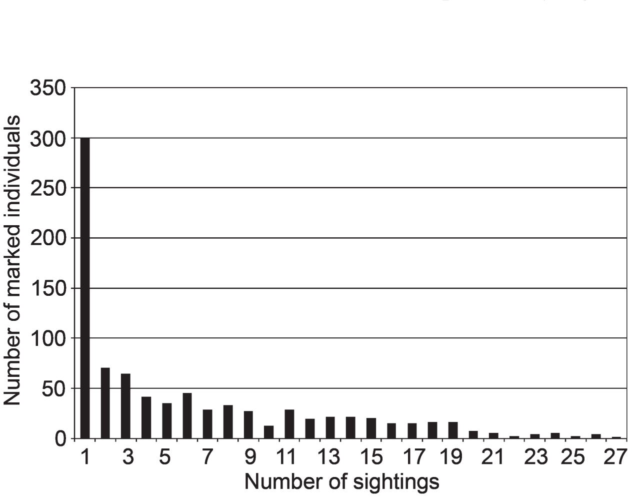

Fig. 2. Sighting frequency of marked individual dolphins within the Charleston study area from 2004–06.

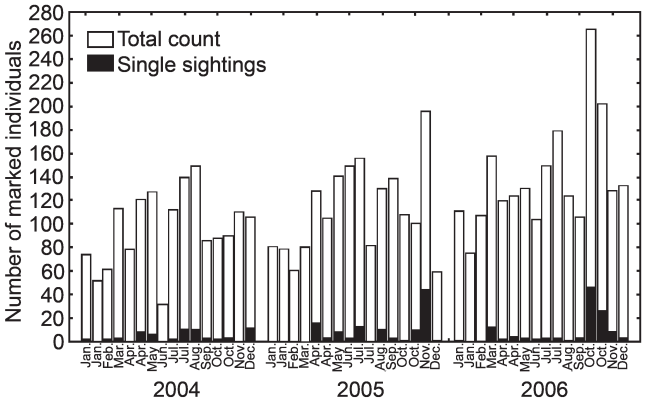

Fig. 3. Total counts and number of single-sighted marked dolphins per month within the Charleston study area from 2004–06.

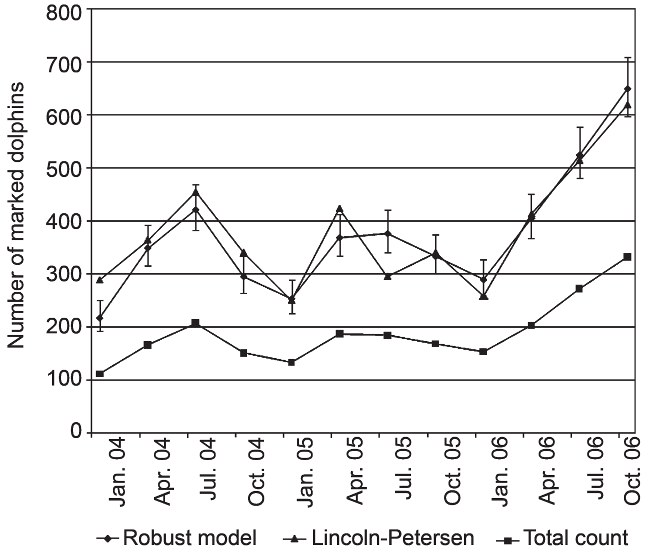

Fig. 4. Seasonal abundance of marked dolphins in the Charleston study area estimates from Pollock's robust design model, Lincoln-Petersen model and total counts from 2004–06.

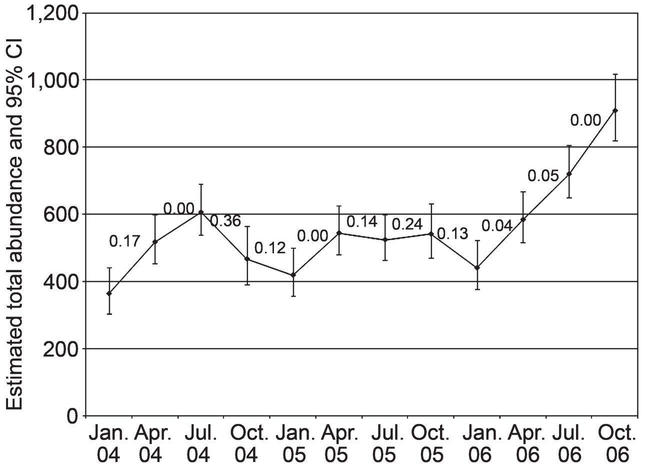

Fig. 5. Seasonal total (marked and unmarked) abundance estimates with 95% confidence intervals and emigration parameters for the Charleston study area from 2004–06.

(Fig. 3). Additionally, a near doubling of previous total marked dolphin counts was observed in the summer and autumn of 2006 (Fig. 4).

The M_o model with Markovian movement demonstrated the lowest AICc and variance inflation factor ($\hat{c}$), but still suggested a poor model fit and over dispersion (Table 1). The variance inflation factor, the degree to which an individual variable is correlated with other individual variables in the model (O'Brien, 2007), equal to one generally represents a good fitting model. The observed $\hat{c}$ value of 7.86 reflects over dispersion likely resulting from a violation of one or more model assumptions (Anderson *et al.*, 1994).

Abundance estimates

Estimates derived from both the Lincoln-Petersen and robust design (M_o, Markovian) models followed the same general seasonal trend with the greatest abundance estimates seen in the summer and the lowest abundance estimates in the winter (Fig. 4). The highest abundance estimates of marked individuals resulting from the robust design model occurred in autumn 2006 (N = 649, 95% CI = 598–709) while the lowest were found in winter 2004 (N = 217, 95% CI = 192–250). These corresponded to overall abundance estimates (after adjustment for seasonal unmarked proportion) of 910 (95% CI = 819–1018) and 364 (95% CI = 305–442) in autumn 2006 and winter 2004, respectively (Fig. 5).

Excluding 2006, estimated emigration parameters (Fig. 5) were also suggestive of an efflux of dolphins from the study area between summer and autumn. The highest probabilities of emigration were for the periods between July and October 2004 (γ'' = 0.36) and July and October 2005 (γ'' = 0.24).

The 'shrimp boat delimited' data set resulted in lower summer 2004 estimates ('complete' data set' N = 421; 'shrimp boat delimited' data set N = 363) while there was very little difference observed in either 2005 ('complete' data set' N = 376; 'shrimp boat delimited' data set N = 378) or 2006 summer ('complete' data set' N = 524; 'shrimp boat delimited' data set N = 513) estimates. The 'CST and shrimp boat delimited' data set, representing the estuarine portion of

Table 1

MARK program results summarising AICc, number of parameters, deviance and variance inflation factor ($\hat{c}$) from closed population models utilising Pollock's robust design.

Model	AICc	Delta AICc	No. of parameters	Deviance	$\hat{c}$
M_o (Markovian)	–9,715.41	0	35	3,214.81	7.86
M_b (Markovian)	–9,713.97	1.44	36	3,214.19	7.88
M_t (Markovian)	–9,706.76	8.64	46	3,200.79	8.04
M_b (Random)	–9,669.71	45.70	26	3,278.90	7.84
M_o (Random)	–9,659.75	55.66	25	3,290.90	7.85
M_t (Random)	–9,645.85	69.56	36	3,282.31	8.04

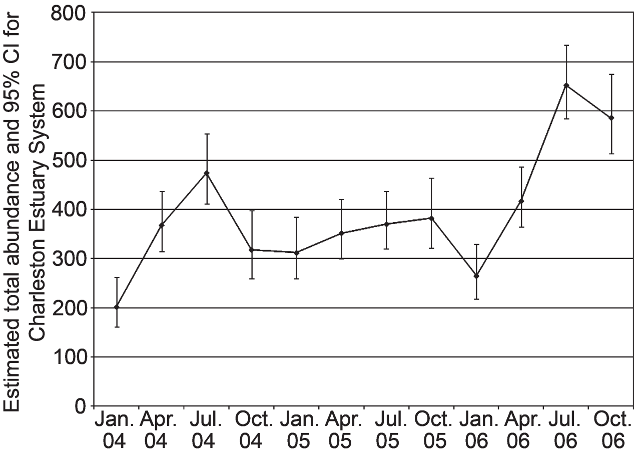

Fig. 6. Seasonal total (marked and unmarked) abundance estimates with 95% confidence intervals for the Charleston Estuarine System (excludes CST) from 2004–06.

the study area, resulted in total abundance estimates ranging from 202 (95% CI = 162–262) to 652 (95% CI = 585–734) (Fig. 6).

Survival estimates

The M_o model with Markovian movement provided a seasonal survival rate of 0.987 (SE = 0.009, 95% CI = 0.949–0.997) resulting in an ASR of 0.951 (SE = 0.035, 95% CI = 0.882–1.00). For YOY survival, a total of 62 calves were sighted with distinctive mothers during monthly photo-ID surveys from 2004–06 and were included in a survival analysis. By December 2006, 17 individuals were considered dead, 13 (76%) of which were estimated to have died within three months of birth. Using the Kaplan-Meier product-limit estimator, a YOY survival rate of 0.754 was estimated (SE = 0.059, 95% CI = 0.647–0.878).

DISCUSSION

Assessment of mark-recapture assumptions

The present analysis of abundance and survivorship is contingent upon a set of assumptions derived from both open and closed population models (see the 'Mark-recapture model' section of 'Methods'). Violations of these assumptions have the potential to bias parameter estimates and should be considered.

A violation of assumption 1 (all marks are unique and permanent) is unlikely. The major distinguishing characteristics used to identify bottlenose dolphins (marks from conspecifics, shark bites, dorsal fin mutilations and tears, collision injuries, etc.) are generally persistent and can last throughout an individual's lifetime (Lockyer and Morris, 1990; Würsig and Jefferson, 1990). Implementation of the fin and photo grading processes helped mitigate the possibility of fin misidentification. Misidentification due to the appearance of new markings altering or obstructing previous marks is more likely. However, with the exception of total fin mutilation/amputation, itself an infrequent phenomenon, the classification criteria requiring that 'marked' fins exhibit at least two distinguishing fin characteristics reduces the chance of this occurring. Additionally, the monthly frequency in which surveys were conducted further decreases the likelihood of altered fin misidentifications.

The second assumption (equal survival among all individuals between primary sampling periods) may potentially be violated with the inclusion of all age classes in the analysis. While long-lived species generally exhibit strong age-specific survivorship (Pearl and Miner, 1935), the period between primary sampling occasions is relatively short (three months) compared to a dolphin's overall lifetime; therefore, it is reasonable to assume survival rates for all individuals are equal over this time period. Furthermore, the individuals with the highest likely mortality rates, young-of-the-year (Stolen and Barlow, 2003), were generally excluded in the mark-recapture analysis due to their inherent lack of distinctive markings (Würsig and Jefferson, 1990).

Given that most young-of-the-year were excluded from the survivorship analysis, a violation of assumption 3 (independence of capture and survival probabilities between individuals) is also unlikely. Bottlenose dolphins live in a social society in which mother/calf associations are normally maintained throughout the first few years of a calf's lifetime (Wells *et al.*, 1987). While unmarked calves are generally only identified by association with their mother, sample independence can be upheld with the removal of these individuals from the analysis. Although other associations also form within dolphin groups (e.g. subadult and nursery groups), the fluid nature of these associations reduces the likelihood of violating this assumption (Wells *et al.*, 1987).

As for previous photo-id efforts in this area (Speakman *et al.*, 2006; Zolman, 2002), this study found evidence of transient individuals which could violate assumption 4 (population closure within primary sampling periods). Specifically, a significant influx of dolphins during summer and autumn 2006 was suggested by the unusually large total counts during this period, combined with a high number of single-sighted individuals (Fig. 3). The presence of transient individuals which move out of the study within a single primary session could result in an upward bias of abundance estimates and for this reason, the abundance estimates for the latter part of 2006 should be viewed with caution.

Similarly, the presence of transient individuals may violate assumption 5 (all emigration between primary sampling periods is temporary). Approximately 300 marked individuals were sighted only once representing individuals that either died or permanently emigrated (Fig. 2). Given that the robust model only accounts for temporary emigration, it is unable to differentiate between permanent emigration and death, resulting in a downward bias of the survival estimate.

Abundance estimates

Total abundance estimates, including both marked and unmarked dolphins, varied considerably among primary survey sessions, ranging from 364 (95% CI = 305–442) in January 2004 to 910 (95% CI = 819–1018) in October 2006 (Fig. 5). A consistent trend of low winter estimates, increasing in the spring, is evident for all three years. Excluding 2005, estimates continue to increase through summer. All three autumn estimates varied greatly, dropping off from summer 2004, holding steady with spring and summer 2005 and continuing to increase in 2006.

Although estimates exhibited a great deal of seasonal and annual variability, differences were detected between summer and winter in all three years (evidenced by a lack of overlap between 95% CIs; Fig. 5). The three winter estimates represented the lowest seasonal estimates across all three years. The data suggest that certain dolphins move into the Charleston area throughout spring and summer before emigrating beyond the study area for the winter, supporting earlier findings of short-term or seasonal resident dolphins around Charleston (Speakman *et al.*, 2006). High sighting frequencies (Fig. 2) and year-round presence suggest that other dolphins remain in the Charleston study area throughout the year, a finding first reported by Zolman (2002). Similar patterns of seasonal variability in abundance have been noted for bottlenose dolphin populations in Florida (Weigle, 1990) and Texas (Bräger, 1993; Fertl, 1994).

The observed low abundance in winter could be due to a shift in prey distribution during colder months. Both Irvine *et al.* (1981) and Fazioli *et al.* (2006) noted a shift in distribution of 'inshore' dolphins toward passes leading to the Gulf of Mexico near Sarasota, Florida, during the winter months perhaps in association with the migration of spawning mullet. Young and Phillips (2002) found a decline in prey availability in a South Carolina estuary during the winter months, resulting in a shift in creek utilisation patterns of the dolphins. It is hypothesised that dolphins move outside the study area during winter months, either into the upper reaches of the rivers and creeks or offshore, where greater densities of prey may be located (Pate, 2008).

Conversely, the observed differences could be due to increases in dolphin numbers during summer. Summer abundance estimates of marked individuals were highest in both 2004 and 2005 and were even higher in 2006 (only to be surpassed by the following autumn estimate; Fig. 4). Additional dolphins might utilise the Charleston study area during the summer for increased reproductive activity (Thayer *et al.*, 2003). This could cause an increase in receptive females and also males seeking mating opportunities. Increased shrimp trawling during summer could also lead to more dolphins. In Galveston, Texas, where dolphins have also been documented interacting with shrimp boats, Fertl (1994) reported an increase in recognisable dolphins in late summer. Dolphins were often observed within the CHS region following shrimp boats in from the coast, actively feeding on discarded bycatch. To assess the impact of trawling-related changes in dolphin abundance, abundance estimates were re-calculated using the 'shrimp boat delimited' data set. Although this resulted in a decline in the summer 2004 estimate ('complete' data set' N = 421; 'shrimp boat delimited' data set N = 363), there was very little difference observed in either 2005 or 2006 summer estimates.

The largest variability in abundance occurred in 2006, where estimates were highest for each season and steadily increased from winter through to autumn. This influx, which is inconsistent with the patterns seen in the two previous years, suggests that stock movements and/or migration may occur sporadically and not necessarily predictably across years. No unusual circumstances (e.g. extreme weather patterns or water temperatures) could be found that might have prompted the additional movement of dolphins into the study area in 2006. The pattern of single-sighted individuals, along with estimated emigration parameters, provides insight into the inconsistent trend of abundance. In 2004 and 2005, the highest probabilities of emigration occurred between July and October (Fig. 5), consistent with a decrease in abundance. This suggests an efflux of seasonal residents from the study area between summer and autumn. In these same years, the autumn influx of single-sighted individuals (transients) occurred later in the autumn (November 2005) or winter (December 2005) (see Fig. 3), after the October abundance estimate. On the other hand, the peak in single-sighted individuals occurred earlier (October) in 2006 while emigration was low (0.00), suggesting that transients immigrated into the study area earlier in 2006. At the same time, seasonal residents had yet to emigrate as in the previous two years, hence the extremely high summer and autumn estimates in 2006.

There is some evidence for extralimital movements by a number of Charleston transient dolphins. Seven individuals have been matched to sites ranging from Jacksonville, FL to Wilmington, NC (K. Urian, pers. comm.) through the Mid-Atlantic Bottlenose Dolphin Catalog (MABDC) (Urian *et al.*, 1999). The MABDC was established by NMFS in 1997 as a cooperative program that includes images and data from multiple photo-id researchers along the mid-Atlantic in order to clarify stock structure of coastal bottlenose dolphins along the western North Atlantic (Urian *et al.*, 1999). These seven matches, all sighted during coastal surveys, were made as part of the curator's selection process of the Charleston catalogue; at present, a more rigorous matching effort has not been undertaken. Of the seven matches, three were sighted between 2004 and 2006; two of these were off-effort coastal sightings and thus, not included in the survivorship or abundance analyses, with the lone on-effort dolphin sighted off Jacksonville, FL in 1997. Future work should involve additional matching effort to the MABDC in order to determine if more Charleston dolphins have been sighted in other areas along the Atlantic coast and if there is a seasonal migratory trend.

Additionally, these findings suggest a need for extending our survey efforts over the next several years to assess whether the observed influx was temporary or indicative of a permanent movement or pattern of movement. They also suggest that caution should be used in employing abundance estimates or observed patterns of movement obtained from studies that have been conducted over relatively short time periods. Such studies may be influenced by unusual events, such as we observed in 2006, without obvious cause.

The accuracy of abundance estimates can be determined by examining capture probabilities (Otis *et al.*, 1978, e.g. for this study, capture probability is the likelihood that a dolphin is photographed). For example, Otis *et al.* (1978) found that capture probabilities less than 0.10 resulted in significant bias of abundance estimates whereas when capture probabilities were greater than 0.30, abundance estimates were reliable and useful, with good confidence interval coverage. Using these criteria, the average capture probability for our three year study was 0.31, within the range of reliable values.

Survival estimates

By reporting the survival estimates in conjunction with abundance estimates it is possible to better evaluate potential biases associated with the survival estimate. Although Speakman *et al.* (2006) previously identified the presence of seasonal residents and transients within the study area, the extent to which these individuals occur is unknown. The abundance estimates presented in this study exhibit seasonal differences with significantly higher estimates in the summer than in the winter every year (Fig. 4). This pattern, in conjunction with the relatively high temporary emigration rates, γ”, observed between the summer and autumn of 2004 and 2005 (γ” = 0.36 and γ” = 0.24 respectively; Fig. 5), suggests an influx of seasonal residents throughout the summer months. The temporary, seasonal movement patterns exhibited by these individuals are accounted for within the model by the temporary emigration parameter, γ”; however, permanent movements by individuals captured once within the study area (i.e. transients) may alter the temporary emigration parameter, thus affecting survival estimates. Accordingly, the lack of precision and high variability in the temporary emigration estimates (Table 2) likely reflects the repeated autumnal influx of single-sighted individuals observed over all three years (Fig. 3), a movement pattern indicative of transient individuals. Because the robust model is unable to differentiate between permanent emigration and death, such imprecision and variability in the temporary emigration estimates suggests the survival estimate may also be biased.

Temporary emigration was modelled by incorporating Markovian and random movement patterns into each model. For each model (M_o, M_t and M_b), the data provided greater support for Markovian movement (Table 1). Markovian movements, where individuals that temporarily emigrate from the study area ‘remember’ they are out of the area (Kendall *et al.*, 1997), are biologically reasonable for seasonal migration.

Transient individuals, i.e. permanent emigrants, may have influenced the estimation of survival rates, resulting in downward bias (ASR = 0.951, SE = 0.030, 95% CI = 0.891–1.00). However, this rate is comparable to survival rates reported for other *Tursiops* populations within the southeastern US (Fig. 7, and see Stolen and Barlow, 2003; Wells and Scott, 1990). Potential biases associated with the YOY survival estimate must also be considered. Until the time of weaning (~2–3 years) calves entirely depend on their mothers (Wells *et al.*, 1987). Consequently, if a mother dies within her calf’s first year of life there is little chance the dependent calf will survive. Calves included in the analysis were identified by their associations with distinctive mothers; if a mother disappeared it was not possible to determine the fate of her calf. This has the potential to bias survival estimates if a calf dies subsequent to its mother’s final sighting. Furthermore, the estimate does not reflect the mortality of neonates that died before initial capture (i.e. before being observed). Therefore, the YOY survival rate of 0.754 (SE = 0.059, 95% CI = 0.647–0.878) should be regarded as a minimum level of mortality for this population. The estimate obtained in this study is lower than that reported for YOY in other *Tursiops* populations (Fig. 7, and see Stolen and Barlow, 2003; Wells and Scott, 1990). This difference may be due to environmental variations between the study sites including geography (Stolen and Barlow, 2003; Wells and Scott, 1990) and contaminant levels (Fair *et al.*, 2007; Hansen *et al.*, 2004; Schwacke *et al.*, 2002; Wells *et al.*, 2005); however, due to the high degree of variance associated with our estimate, a statistically significant difference between sites could not be detected.

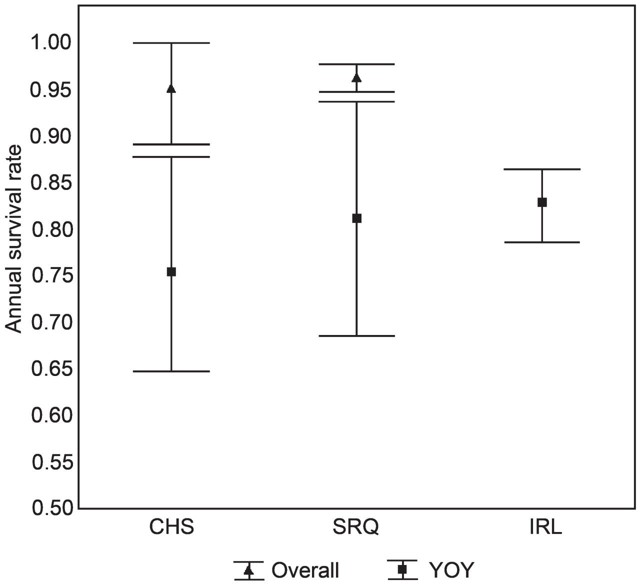

Fig. 7. Survival estimates for marked individuals and the young-of-the-year age class derived for various bottlenose dolphin communities in the southeastern US: Sarasota Bay, FL[a] (SRQ), the Indian River Lagoon, FL[b] (IRL) and Charleston, SC (CHS). Error bars represent 95% CI of the estimated mean.

Table 2

Temporary emigration parameter estimates for periods between each consecutive primary sampling occasison derived from the robust design (M_o, Markovian) model in *MARK*.

Parameter	Estimate	Standard error	95% CI
γ” Jan. 04–Apr. 04	0.168	0.090	0.054–0.417
γ” Apr. 04–Jul. 04	0.000	0.000	N/A
γ” Jul. 04–Oct. 04	0.359	0.055	0.260–0.472
γ” Oct. 04–Jan. 05	0.121	0.061	0.043–0.297
γ” Jan. 05–Apr. 05	0.000	0.000	N/A
γ” Apr. 05–Jul. 05	0.141	0.050	0.068–0.269
γ” Jul. 05–Oct. 05	0.235	0.045	0.157–0.334
γ” Oct. 05–Jan. 06	0.132	0.055	0.056–0.281
γ” Jan. 06–Apr. 06	0.039	0.059	0.002–0.471
γ” Apr. 06–Jul. 06	0.047	0.040	0.008–0.224
γ” Jul. 06–Oct. 06	0.00	0.00	N/A

Management implications

An important goal of this study was to establish baseline abundance estimates for bottlenose dolphins inhabiting the Charleston study area and understand seasonal movements through the area. Ideally, these estimates would be used to resolve some of the complexities of bottlenose dolphin stock structure along the coast of the WNA by providing a more comprehensive definition for the local stock. Recently,

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[a] Wells and Scott (1990).

[b] Data reported by Stolen and Barlow (2003).

scientists from the NMFS Southeast Fisheries Science Center began drafting Stock Assessment Reviews for previously unaddressed estuarine areas along the USA Atlantic Coast (Waring *et al.*, 2009; L. Hansen pers. comm.). Based on research conducted over the past 14 years on bottlenose dolphins around Charleston, a new 'Charleston Estuarine System Stock' was defined and boundaries for this new stock include the study area reported here. The boundaries have been defined as the inshore, estuarine subareas to the north and south of Charleston Harbor, excluding the coast. Thus, the analysis herein provides an abundance estimate for this newly proposed estuarine stock of dolphins. Estimates were calculated from the 'CST and shrimp boat delimited' data set using the robust design model (M_o, Markovian) in *MARK* and adjusted for seasonal unmarked proportions (ranging from 0.28 to 0.44). The Delta method was used to calculate variance and confidence intervals (Wilson *et al.*, 1999, and see Fig. 6). By excluding coastal and shrimp boat sightings, the number of single-sighted dolphins was reduced by more than half (300 to 112), thus better representing the more resident, estuarine segment of the population. Total abundance estimates ranged from 202 (95% CI = 162–262) in January 2004 to 652 (95% CI = 585–734) in July 2006. Estuarine abundance exhibited trends similar to the 'complete' data set with significantly higher estimates in summer than in winter as well as the highest estimates for each season in 2006. The autumn 2006 estimate was noticeably smaller (from 910 to 586) after removing the single-sighted dolphins associated with the CST region.

Read *et al.* (2003) conducted a similar mark-recapture study of bottlenose dolphins in the bays, sounds and estuaries of North Carolina during July 2000. Their study resulted in a summer abundance estimate of 1,033 dolphins which, to date, is the only estimate for estuarine dolphins in the most recent NMFS stock assessment for the WNA population (Waring *et al.*, 2009). The July estimates from 2004 and 2005 (474 and 370, respectively), presented herein, appear to best represent summer abundance, while January estimates from 2005 and 2006 (312 and 265, respectively) provide the most accurate winter abundance estimate for the Charleston estuarine population.

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Cetacean strandings in San Diego County, California, USA: 1851–2008

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ABSTRACT

There were 717 cetacean strandings recorded in San Diego County, California, USA between 1851 and 2008. These strandings comprised 18 odontocete and 6 mysticete species. Common dolphins (both the short-beaked (*Delphinus delphis*) and long-beaked common dolphin (*D. capensis*)) were the most commonly stranded cetacean species (43.2%), followed by bottlenose dolphins (*Tursiops truncatus*) (16.5%), gray whales (*Eschrictius robustus*) (11.0%), and Pacific white-sided dolphins (*Lagenorhyncus obliquidens*) (7.0%). A higher number of strandings was observed in the La Jolla and Coronado/Imperial Beach areas, which likely reflects the influence of coastal protrusions in those regions. Strandings of bottlenose dolphin neonates suggests their calving season extends from May to September. Strandings of common dolphin species peaked in the early- to mid-1970s and in the late-1990s to 2008, coincident with cool oceanographic regimes. In addition, extralimital strandings of harbour porpoises and temporal changes in stranding rates of Dall's porpoises (*Phocoenoides dalli*) and short-finned pilot whales (*Globicephala macrorhynchus*) may have been associated with changes in oceanographic conditions. Evidence of human interaction in strandings included entanglements, boat strikes, shootings and harpooning. Overall, the stranding record largely reflected the species composition of the Southern California Bight and provided confirmation for presence of cryptic species not previously recorded by aerial and ship surveys.

KEY WORDS: STRANDINGS; NORTHERN HEMISPHERE; PACIFIC OCEAN; CLIMATE CHANGE; DISTRIBUTION; SEASONALITY; COMMON DOLPHIN; LONG-BEAKED COMMON DOLPHIN; BOTTLENOSE DOLPHIN; DALL'S PORPOISE; SHORT-FINNED PILOT WHALE; GRAY WHALE; PACIFIC WHITE-SIDED DOLPHIN

INTRODUCTION

Stranded marine mammals allow researchers to gather valuable data which is otherwise unobtainable. They offer a unique opportunity to learn about a species' life history (Greig *et al.*, 2005; Murphy, 2004; Toperoff, 2002; Westgate and Read, 2007), population structure (McFee *et al.*, 2006; McLellan *et al.*, 2002), occurrence (Woodhouse, 1991), disease prevalence (Greig *et al.*, 2005), anthropogenic causes of mortality (Balcomb and Claridge, 2001; Cox *et al.*, 1998) and to understand fossil assemblages (Pyenson, 2010). Additionally, stranding patterns may reflect changes in environmental conditions, health status or species distribution.

The Marine Mammal Protection Act (MMPA) of 1972 specified that a national stranding network should be established. This became part of the broader Marine Mammal Health and Stranding Response Program (MMHSRP) established under the 1992 amendment to the MMPA. This program is overseen by the National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service (NMFS). The MMHSRP coordinates the national stranding network, responses and investigations of mortality events, biomonitoring, tissue and serum banking, and analytical quality assurance.

The California Marine Mammal Stranding Network (CMMSN) is part of the national stranding program. San Diego County is one of six sub regions in the CMMSN and the most southern region in California. Most of the approximately 80 miles (125km) of beaches in San Diego County are public beaches that are routinely patrolled by lifeguards or beach clean-up crews throughout the year. Public use is limited along 17 miles (27.4km) of coastline at Camp Pendleton Marine Corp Base (27.4km), 1 mile (1.6km) at Naval Air Station North Island and 2 miles (3.2km) at Naval Amphibious Base. However, these sections of coastline are routinely monitored by game wardens and biologists on base. Consequently, in San Diego County, it is thought that few strandings go unnoticed.

In this paper both live and dead cetacean strandings documented in San Diego County between 1851 and 2008 are summarised. When possible, spatial, temporal, and sex-specific trends in strandings were analysed.

METHODS

Stranding events were primarily recorded by local scientists actively seeking information about stranded marine mammals. However, strandings were also documented in newspapers (n = 17), museum records (n = 4), historical photos (n = 2) and in the files of William E. Ritter (n = 1) of Scripps Institution of Oceanography (SIO). Newspaper documentation was obtained from the *San Diego Herald* (1851–60) and the *San Diego Union Tribune* (1868–2008). In addition, all records were compared to those collected by NOAA's Southwest Region to ensure the dataset was complete.

Prior to 1945 there was no systematic effort to record marine mammal strandings. After 1944, strandings were more routinely recorded, primarily by Carl L. Hubbs of SIO and Raymond M. Gilmore of the US Fish and Wildlife Service and later of the San Diego Natural History Museum.

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By 1946, local scientists started to publish on cetacean strandings from San Diego County (Hubbs, 1946; Hubbs, 1951; 1953; Kenyon, 1952; Moore, 1963; Moore and Gilmore, 1965; Mitchell, 1968; Brownell, 1971). Sea World began cetacean rehabilitation efforts in 1963, although the park did not open until 1964. The US Navy Marine Mammal Program (MMP) responded to live stranded cetaceans in San Diego County from 1972–79. In 1966, the Southwest Fisheries Science Center (SWFSC) began responding to and documenting dead stranded cetaceans. However, the number of strandings investigated was limited because no formal effort was made to notify beach personnel of the SWFSC's interest in cetacean strandings.

In 1972, following the passage of the MMPA, the National Marine Fisheries Service (NMFS) and the California Department of Fish and Game (CDFG) began to collect state wide information on strandings and the first marine mammal report form was drafted. During this time there was a general increase in knowledge on the part of beach personnel as to SWFSC's desire to collect stranded cetaceans. In 1979, the Cooperative Marine Mammal Salvage Program was formed in San Diego County. Under this agreement, the SWFSC and Hubbs-Sea World Research Institute responded to dead marine mammals while Sea World and the MMP responded to live animals (Henderson and Hansen, 1983). Currently, Sea World and SWFSC are the only organisations that respond to marine mammal strandings in San Diego County.

For each stranding event that occurred after 1971, at minimum the following information (Geraci and Lounsbury, 2005) was recorded: species; number of animals; location and date of stranding; total body length (Norris, 1961); decomposition state; and sex. Skulls, skeletons, life history and health assessment data were collected when possible. However, results from these collections are not discussed here. San Diego County was divided into 11 regions in order to track the geographic occurrence of strandings (Fig. 1). San Diego County lies within the Southern California Bight (SCB), which is the body of water from Point Conception to a point just south of the United States/Mexico border, with a

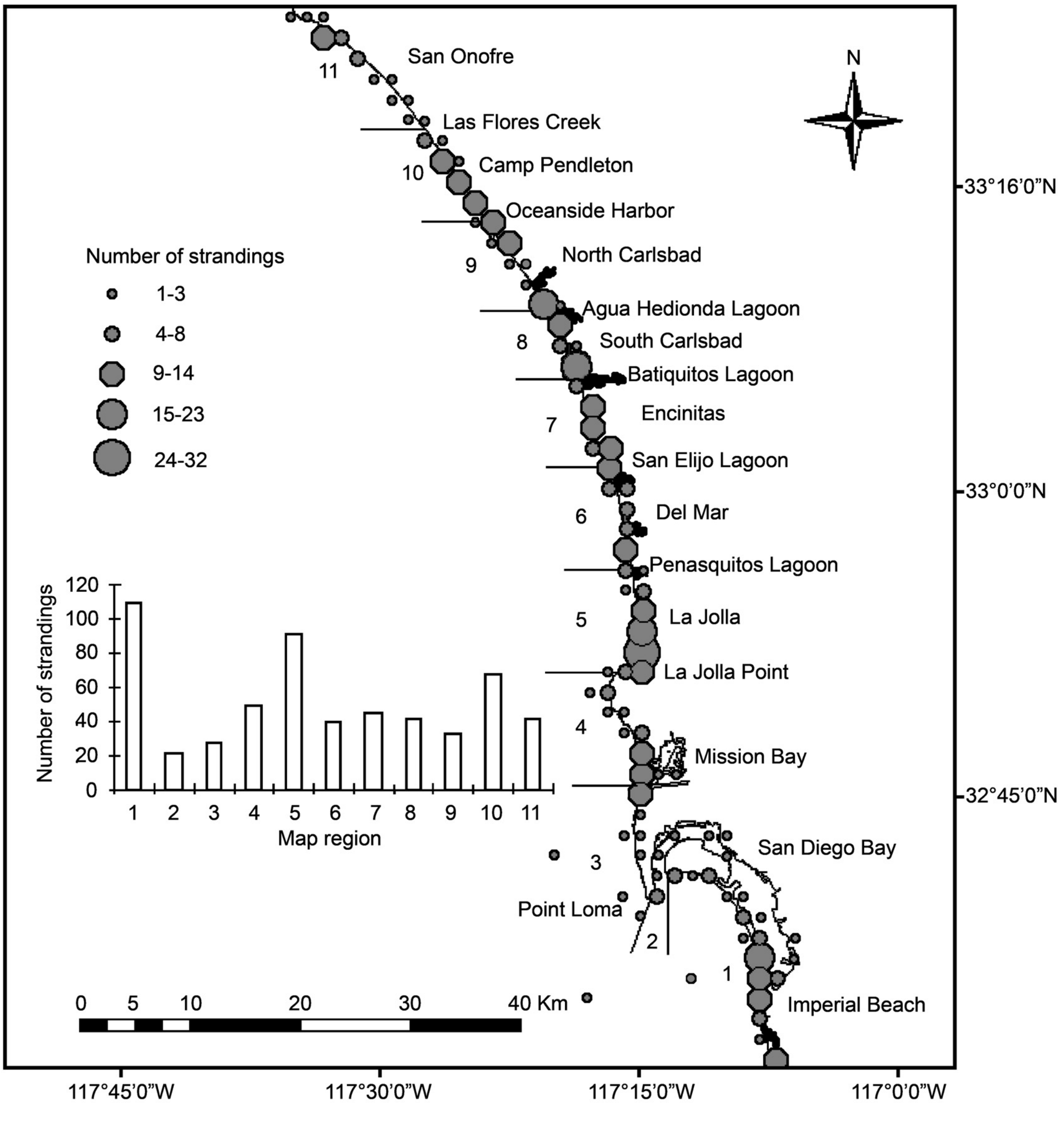

Fig. 1. Cetacean strandings recorded along the San Diego County coastline from 1972 to 2008. Map region two includes San Diego Bay coastline. Regions bordering San Diego County (Orange County to the north and Mexico to the south) are not depicted on map. Cetacean strandings were most common in regions 1, 5 and 10.

maximum width of 300km from shore at the Patton Escarpment (Dailey *et al.*, 1993). Statistical analyses were restricted to data that were collected after 1971, when formal reporting of marine mammal strandings began.

All data collected were verified whenever possible, paying particular attention to the accuracy of species identifications. Whenever photographs, morphological data, or tissue for genetic analysis were available, species identifications were confirmed. This was especially important in the case of short-beaked common dolphins (*Delphinus delphi*s) and long-beaked common dolphins (*Delphinus capensis*). Heyning and Perrin (1994) revised the taxonomy of *Delphinus* to include two species, the short-beaked common dolphin and long-beaked common dolphin, based on cranial characteristics, genetic data and colour pattern variation. For specimens collected prior to the revision, common dolphin records have been updated to accord with the current taxonomy whenever possible. Since a number of unidentified common dolphin remain in the data set prior to the 1994 revision, only specimens collected after 1993 were used in statistical analyses of the two species.

Both coastal and offshore stocks of bottlenose dolphin (*Tursiops truncatus*) occur off California (Carretta *et al.*, 2009) and they are genetically distinct (Lowther, 2006). When tissue or bone was available, coastal and offshore stock designations were determined using genetic analyses of mitochondrial (mt) DNA, as outlined by Lowther (2006).

Stillbirths were defined as specimens without inflated lungs. Inflation of the lungs was determined either by histopathology or flotation of lungs (from freshly dead specimens) in water. Neonates were defined as specimens with both fetal folds and inflated lungs. Although neonates by definition are four weeks or less in age, this definition has been extended to approximately 6–8 weeks, since fetal folds are visible for this length of time in bottlenose dolphins (Cockcroft and Ross, 1990; Kastelein *et al.*, 1990). The above information was not available for all bottlenose dolphins and none of the gray whale (*Eschrictius robustus*) specimens. In lieu of the above criteria, bottlenose dolphin neonates were defined as specimens with a total standard body length between 111cm (smallest animal in data set with fetal folds and inflated lungs) and 137cm (largest animal with fetal folds). Using Sanchez Pacheco (1998) and Rice and Wolman (1971) as guidelines, gray whale length classes were defined as follows: calf (340–639cm); yearling (640–950cm); juvenile (female: 951–1,169cm; males: 951–1,109cm); and adult (females: 1,170+cm; males: 1,110+cm).

For common dolphins, sex ratios and standard total body length were compared between stranded specimens and those incidentally killed in the California drift and small-mesh gillnet (California gillnet – CAGN) fisheries between 1994 and 2008. Observers placed onboard CAGN fishing vessels recorded at a minimum the location and date of each net set and the species and sex of incidentally killed cetaceans. When possible biological data and samples such as standard total body length, gonads, skin and teeth were collected (Carretta *et al.*, 2005a)

Stranding records were examined for evidence of human interaction. However, the human interaction data should be interpreted cautiously as its collection has varied over time, which is why statistical analyses were not performed on the available data. The occurrence of human interaction does not necessarily equate with cause of death and the absence of human interaction does not mean it did not occur. An animal was considered to be shot if a bullet was recovered from the carcass. Entangled animals were considered to be those with net impressions, appendages removed or had gear attached to their bodies. Ship strikes were either reported by mariners or determined by the presence of propeller marks across an animal's body.

Kuiper's test (Batschelet, 1981) was used to determine whether the distribution of strandings was uniform. This is a nonparametric goodness-of-fit test for cumulative distributions that is used for comparisons of circular distributions. Pearson's chi-square test was used to determine whether stranding frequencies varied by season, geographic location, sex or size class. The non-parametric Mann-Whitney test was used to compare standard total length between stranded and CAGN short-beaked common dolphin specimens because the data were not normally distributed.

RESULTS

For the period 1851 to 2008 a total of 717 cetacean strandings (150 live and 567 dead), representing 18 odontocete and 6 mysticete species were recorded in San Diego County (Appendix I). Between 1972 and 2008, strandings of the two common dolphin species occurred the most frequently (43.2%), followed by bottlenose dolphins (16.5%), gray whales (11.1%), and Pacific white-sided dolphins (*Lagenorhyncus obliquidens*) (7.0%). The remaining 22.2% of strandings comprised nineteen other cetacean species (Table 1). All strandings were of individuals, with the exception of three group events: (1) a juvenile and pregnant female pygmy sperm whale (*Kogia breviceps*) stranded together alive in 1955; (2) two adult female bottlenose dolphin stranded together alive in 1963; and (3) two live adult Cuvier's beaked whales (*Ziphius cavirostris*) became entangled in a fishing net in 1963. It is possible that there have been other group events because other cetaceans have been found dead on the same day and location but it is not known whether they washed in on the same day or were simply found on the same day. Of particular note was the observation of five dead adult long-beaked common dolphin on Silver Strand State Beach between 9–10 July 2007. All specimens tested positive for the biotoxin domoic acid.

In general, a bimodal trend in strandings is apparent, with additional peaks scattered throughout the record (Fig. 2). From 1972 to 2008, the average stranding rate was 15.5 (SE = 1.01) individuals per year (2.9 live, 12.6 dead). In general, strandings were most common from March through August ($p<0.01$, $K = 3.7311$). A significantly higher number of strandings were recorded in map regions one (Coronado/Imperial Beach), five (La Jolla), and ten (Camp Pendleton) ($\chi^2 = 146.668$, df = 10, $p<0.0001$) (Fig. 1).

Common dolphins

Two modes in common dolphin strandings occurred, one in the early- to mid-1970s and the other beginning in the late-1990s to 2008 (Fig. 3). Significant seasonality in strandings was found for both short-beaked common dolphin ($K = 2.2481$, $p<0.01$) and long-beaked common dolphin

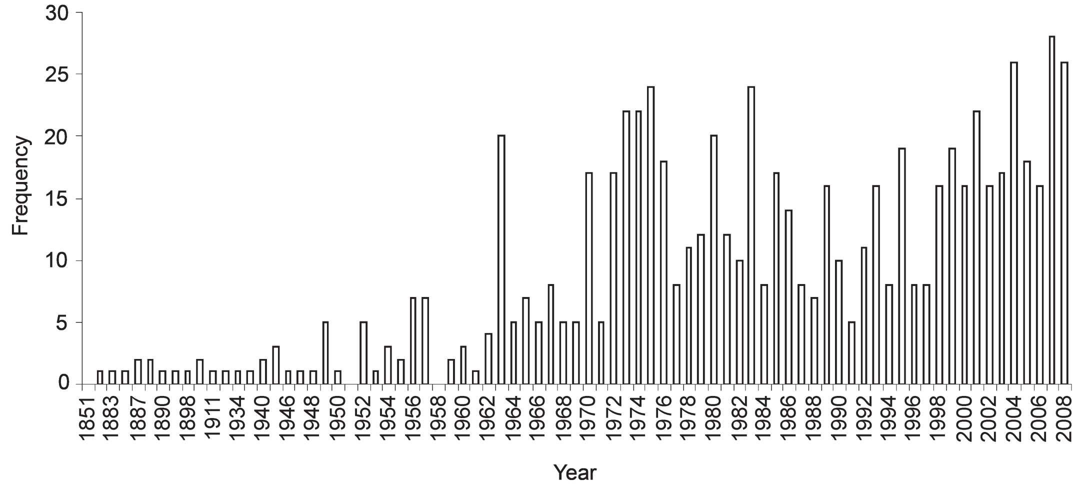

Fig. 2. Frequency distribution of recorded cetacean strandings in San Diego County, California.

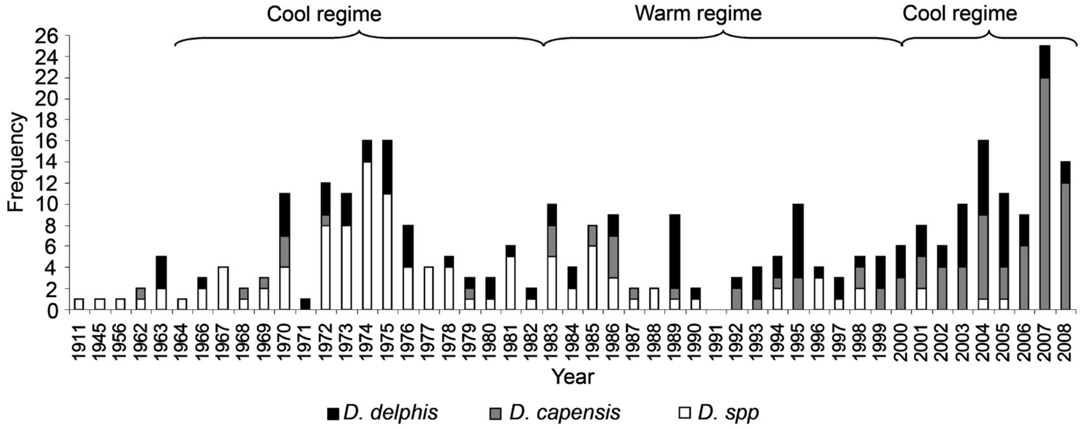

Fig. 3. Frequency distribution of recorded San Diego County common dolphin strandings. Cool and warm water oceanographic regime designations are approximate.

($K = 3.0166$, $p<0.01$). Both short-beaked and long-beaked common dolphin strandings peaked from March through to July (Fig. 4). One neonate stranding was recorded for each common dolphin species: (1) an approximately 100cm long-beaked common dolphin stranded freshly dead in July 2004; and (2) an 85.8cm freshly dead short-beaked common dolphin stranded in June 2007.

An average of 3.5 (SE = 0.60) and 4.9 (SE = 1.46) short-beaked common dolphins and long-beaked common dolphins stranded per year, respectively. Peaks in short-beaked common dolphin strandings occurred in 1989, 1995 and 2003–05. Long-beaked common dolphin strandings peaked in 2007 and 2008 (Fig. 3). A notable increase in the proportion of long-beaked common dolphins compared to short-beaked common dolphins began in 2006. The stranded short-beaked common dolphin male-to-female ratio of 1.04:1 ($n = 47$) was not significantly different ($\chi^2 = 0.021$, df = 1, $p = 0.884$), whereas the 1.68:1 ratio ($n = 252$) observed in the CAGN fishery was significantly male biased ($\chi^2 = 16.254$, df = 1, $p = 0.0001$). The male-to-female ratios of stranded (1.2:1, $n = 70$) and CAGN (1.5:1, $n = 20$) long-beaked common dolphin were not significantly different from parity ($\chi^2 = 0.514$, df = 1, $p = 0.473$ and $\chi^2 = 0.800$, df = 1, $p = 0.371$, respectively)

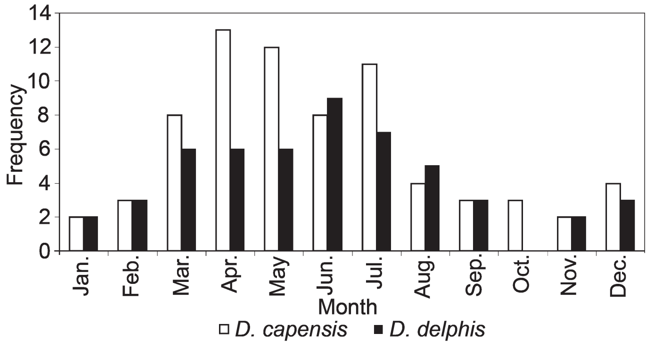

Fig. 4. Frequency distribution of common dolphin strandings by month.

For short-beaked common dolphins there are sufficient data to compare the standard total body lengths of strandings to those observed in the CAGN fisheries (Fig. 5). The average standard total body length for stranded and CAGN male short-beaked common dolphins was not significantly different (Mann-Whitney: $p = 0.464$) at 166.2cm ($n = 21$) and 166.6 cm ($n = 136$), respectively. However, standard total body length of stranded females (168.1cm, $n = 22$) was significantly different (Mann-Whitney: $p = 0.016$) from those in the gillnet fisheries (158.5cm, $n = 74$).

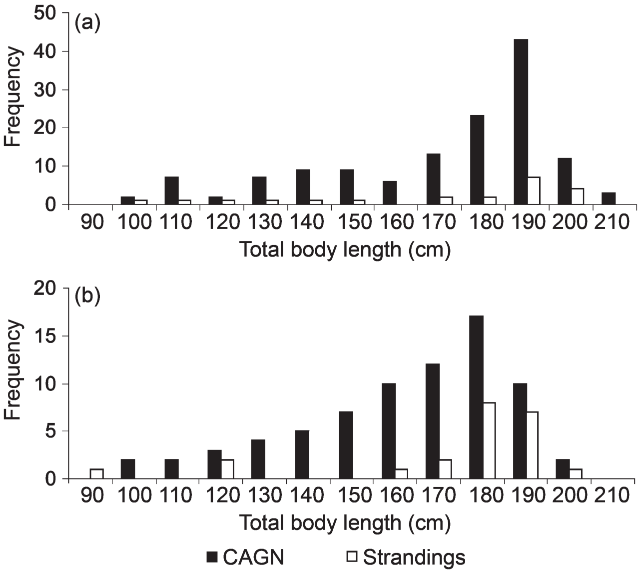

Fig. 5. Total body length frequency distributions of (a) male and (b) female stranded and CAGN short-beaked common dolphins. The *x*-axis labels represent the upper bound of the length interval.

Bottlenose dolphin

Preliminary stock designation analyses were run on 83 of the 118 bottlenose dolphin specimens that have stranded in San Diego County (Appendix II). None of these were assigned by genetic analysis to the offshore stock, while 61 were assigned to the coastal stock, and 22 of these are currently considered to be undetermined because they share a mitochondrial haplotype with the offshore stock ($n = 18$) or are a new haplotype ($n = 4$) that has not yet been matched with a known coastal or offshore animal. Further research is needed to resolve stock designations for these individuals.

An average of 2.9 (SE = 0.32) bottlenose dolphins stranded per year in San Diego County. Bottlenose dolphin strandings peaked in 1980, with a notably low stranding rate from 1996–99 (Fig. 6). Bottlenose dolphin strandings varied seasonally ($K = 3.3227$, $p<0.01$), with peaks from May through August (Fig. 7). Neonates only occurred from May to September. If neonates and stillbirths are removed from the dataset, seasonality in bottlenose dolphin strandings is no longer significant ($K = 1.7467$, $0.05<p<0.10$). The 0.85:1 ratio of stranded males to females ($n = 98$) was not significantly different ($\chi^2 = 0.653$, df = 1, $p = 0.419$).

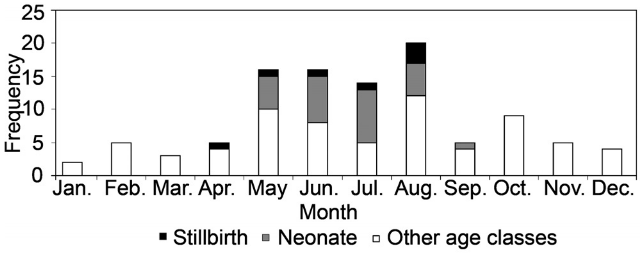

Fig. 7. Frequency distribution of bottlenose dolphin strandings by month.

Gray whale

The gray whale is the only large whale to regularly strand in San Diego County (Table 1). On average, 1.81 (SE = 0.279) gray whales stranded in San Diego County per year, with a high of five individuals in 1999 (Fig. 8). Although this species has stranded in every month, these strandings were not uniformly distributed throughout the year ($K = 2.7906$, $p<0.01$). Two peaks, corresponding with the migratory period, occurred in January and April (Fig. 9). Neonates and yearlings were most common ($\chi^2 = 18.279$, df = 3, $p<0.0001$). The significantly different ($\chi^2 = 4.091$, df = 1, $p = 0.043$) male-to-female ratio for stranded individuals was 1.8:1 ($n = 55$).

Pacific white-sided dolphin

Pacific white-sided dolphins stranded sporadically throughout the study period, with a notable peak in 1980 (Fig. 10). The number of Pacific white-sided dolphin strandings did not vary significantly by season ($K = 0.9532$, $p>0.15$; Fig. 9). The ratio of stranded males to females was 0.77:1 ($n = 20$), which was not significantly different ($\chi^2 = 0.533$, df = 1, $p = 0.465$).

Other species

Dall's porpoise (*Phocoenoides dalli*) occurred regularly in the stranding record from 1960 to 1979 at a rate of 0.7 per year, was absent 1980–1997 and stranded at a rate of 0.2 per year from 1998–2008 (Fig. 11). There has been a

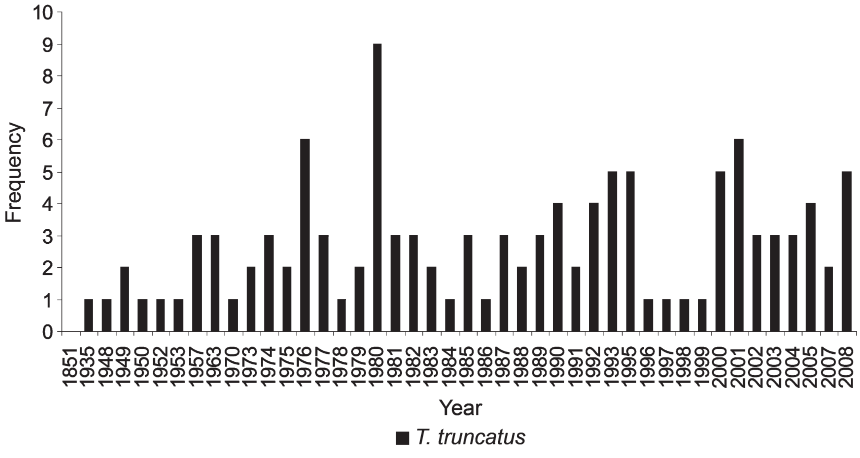

Fig. 6. Frequency distribution of recorded San Diego County bottlenose dolphin strandings.

Table 1

Number of cetaceans stranded along San Diego County coastline between 1851 and 2008.

	Alive	Dead	Total
Balaenoptera spp.	0	4	4
Balaenoptera acutorostrata	0	3	3
Balaenoptera musculus	0	4	4
Balaenoptera physalus	0	6	6
Delphinus capensis	7	88	95
Delphinus delphis	21	81	102
Delphinus sp.	52	61	113
Eschrictius robustus	3	77	80
Eubalaena japonica	0	1	1
Globicephala macrorhynchus	3	17	20
Grampus griseus	3	5	8
Kogia breviceps	10	5	15
Lagenorhyncus obliquidens	9	41	50
Lissodelphis borealis	4	9	13
Megaptera novaeangliae	1	3	4
Mesoplodon carlhubbsi	2	1	3
Mesoplodon ginkodens	0	1	1
Mesoplodon perrini	0	4	4
Mesoplodon stejnegeri	1	0	1
Phocoena phocoena	0	2	2
Phocoenoides dalli	6	13	19
Physeter macrocephalus	0	2	2
Stenella coeruleoalba	1	4	5
Tursiops truncatus	12	106	118
Unidentified cetacean	0	2	2
Unidentified dolphin or porpoise	6	15	21
Unidentified large whale	1	3	4
Unidentified whale	3	0	3
Ziphius cavirostris	5	9	14
Total	150	567	717

steady decline in short-finned pilot whale (*Globicephala macrorhynchus*) strandings since the 1960s (Fig. 11). Pygmy sperm whale strandings have fluctuated over time, peaking in the 1990s and absent 2000–2008 (Fig. 11). Extralimital strandings of harbour porpoises (*Phocoena phocoena*) occurred in 2005 and 2006. A North Pacific right whale (*Eubalaena japonica*) stranded in Oceanside (map region 9, Fig. 1) in February 1856.

Beaked whales rarely stranded with only 23 strandings observed between 1946 and 2008. However, these records represent five species (Table 1). Fourteen Cuvier's beaked whales were recorded between 1945 and 2007, five of which were alive at the time of stranding. On 12 June 1963, two Cuvier's beaked whales were caught in fishing net off La Jolla Cove (region 5, Fig. 1). One was freed alive, the other died after disentangling itself. On this same day, another Cuvier's beaked whale stranded alive in Del Mar (region 6, Fig. 1) and died on the beach. Nine individuals of the genus *Mesoplodon,* representing four species, stranded between 1946 and 1986. All of these stranded as single individuals and three stranded alive. Four of the beaked whale specimens were first identified as Hector's beaked whale (*M. hectori*) (Mead, 1981) but they were later described as a new species, Perrin's beaked whale (*M. perrini*) (Dalebout *et al.*, 2002).

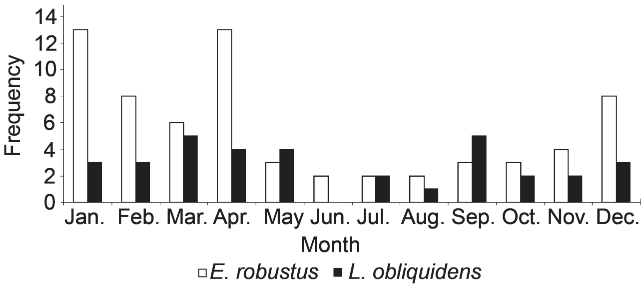

Fig. 9. Frequency distribution of gray whale and Pacific white-sided dolphin strandings by month.

Human interaction

The most common forms (in descending order) of human interaction observed in San Diego County cetaceans were entanglement, boat strikes, and gunshots (Table 2). Entanglement was noted in eight different cetacean species and was most commonly observed for long-beaked common dolphins and gray whales. Ship strikes were observed for five different cetacean species and were most commonly observed in gray whales. Three cetacean species were impacted by gunshots. The long-beaked common dolphin shootings ($n = 4$) occurred during one event in 2007. One dead gray whale was observed with a harpoon tip embedded in its back on 12 December 1999. The harpoon is believed to have originated from an aboriginal Russian hunt (R. Brownell, pers. comm.).

DISCUSSION

Stranding records do not reflect all cetaceans that have stranded. The general increase in strandings after 1972,

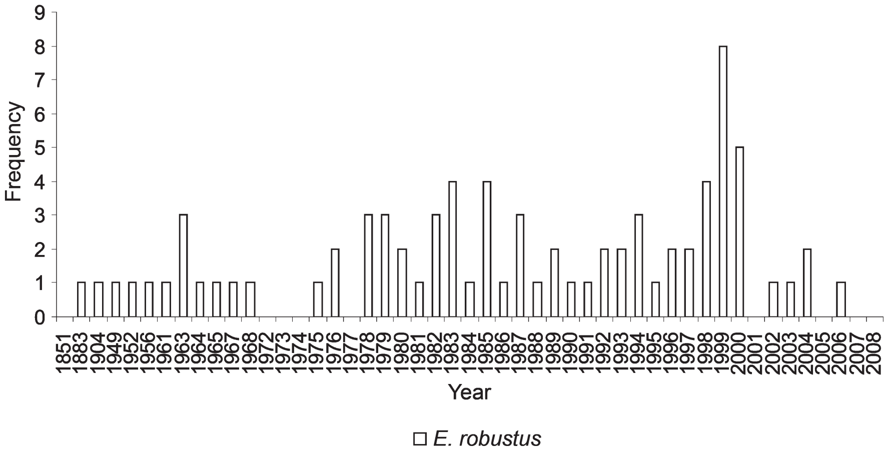

Fig. 8. Frequency distribution of recorded San Diego County gray whale strandings.

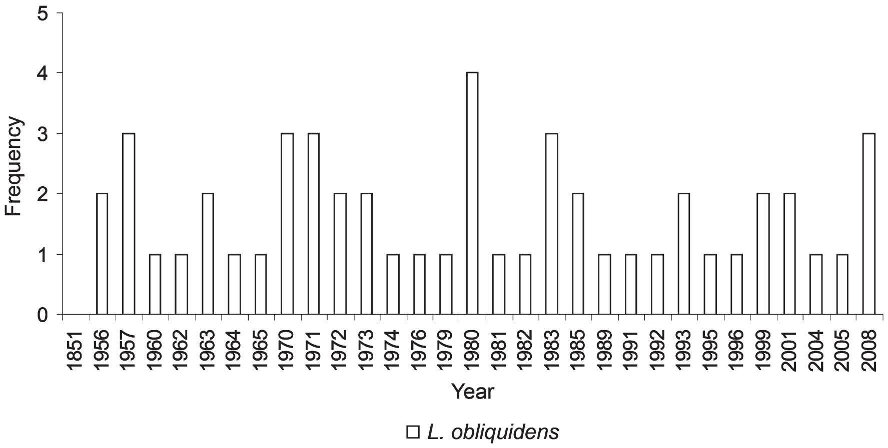

Fig. 10. Frequency distribution of recorded San Diego County Pacific white-sided dolphin strandings.

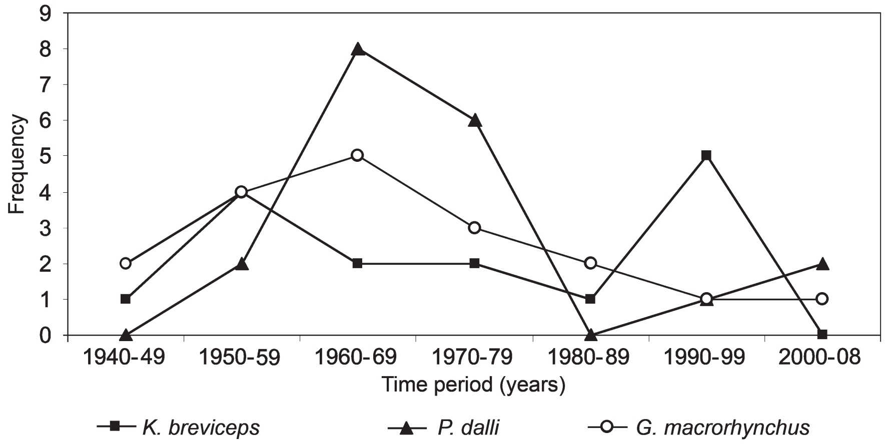

Fig. 11. Temporal changes in stranding frequency for pygmy sperm whales, Dall's porpoise, and short-finned pilot whales in San Diego County.

shown in Fig. 2, probably does not reflect an increase in actual strandings but an increase in reporting of strandings. Prior to 1972, beach personnel may not have known of SWFSC's interest in strandings, and animals may have been disposed of without being reported. There is also inherent variability in strandings reported due to beach personnel turnover and differences in their interest and knowledge of stranded marine mammals and the CMMSN.

Although there may be variability in reporting of strandings, the stranding record largely reflected the species composition of live animals observed in the Southern California Bight (SCB) during boat and aerial surveys (Barlow and Forney, 2007; Forney and Barlow, 1998; Forney *et al.*, 1995; Shane, 1994), with a few exceptions. Killer whales (*Orcinus orca*) were observed in the SCB during one survey (Forney and Barlow, 1998) but not in the stranding record. Killer whales may not appear in the stranding record because they are not very common in the SCB, as indicated by only one survey sighting on the outer edge of the SCB (Forney and Barlow, 1998) and their abundance off the west coast ($n = 810$) is relatively low (Barlow and Forney, 2007). Conversely, harbour porpoise and pygmy sperm whales were recorded in the stranding record and not observed during live animal surveys in the SCB. Pygmy sperm whales could have been missed in the SCB during live surveys because it is a cryptic species with a relatively low abundance off the west coast ($n = 1{,}237$) (Barlow and Forney, 2007). Harbour porpoise is also a cryptic species and was only observed stranded in 2006 and 2007, during which period there were no surveys. Overall the stranding record reflected a greater species richness than live animal surveys, which is what Pyenson (2010) also found in his survey of California cetacean strandings. This highlights the importance of stranding records because they are essentially an uninterrupted record, whereas surveys generally

Table 2

Number of documented San Diego County cetaceans with signs of human interaction.

Species	Entanglement	Boat strike	Gunshot	Harpoon
Balaenoptera acutorostrata	1	1	–	–
Balaenoptera physalus	–	1	–	–
Delphinus capensis	9	–	4	–
Delphinus delphis	1	–	–	–
Delphinus sp.	–	1	–	–
Eschrictius robustus	8	5	–	1
Grampus griseus	2	–	1	–
Lagenoryhncus obliquidens	1	–	–	–
Tursiops truncatus	3	1	1	–
Ziphius cavirostris	2	–	–	–
Unidentified whale	1	1	–	–
Total	28	10	6	1

document species distributions during relatively brief time periods.

Coastal geography is likely the main factor influencing the deposition rates of carcasses in map regions one and five. Brabyn and McLean (1992) observed a similar trend in New Zealand, where mass strandings were associated with protrusions from the coastline. La Jolla Point and Point Loma likely 'capture' drifting carcasses into map regions five and one (Fig. 1). In addition, the presence of small coastal eddies just North of map regions one and five (DiGiacomo and Holt, 2001) may contribute to the 'capture' of carcasses offshore of these regions. It is also possible that increased effort, either by those reporting or responding to strandings, could have been a factor in map regions one, five, and ten at some point in time.

Common dolphins

The general bimodal trend of cetacean strandings over time (Fig. 2) was mostly driven by the large number of common dolphins in the stranding record, which has a distinct bimodal trend in strandings over time (Fig. 3). Peaks in common dolphin strandings occurred during cool oceanographic regimes in the Northeast Pacific (Chavez *et al.*, 2003; Peterson and Schwing, 2003) (Fig. 3). This suggests that either common dolphin distribution shifted or their population health declined in response to the regime shifts. Off California, the distribution of common dolphins has been shown to vary seasonally in response to changing oceanographic conditions (Forney and Barlow, 1998). Therefore, it is possible that temporal trends in common dolphin strandings may reflect a shift of this species closer to the San Diego County shoreline, allowing more carcasses to drift to shore. The increased proportion of long-beaked common dolphin strandings beginning in 2006 (Fig. 3) may reflect increased numbers of this species off California. This is supported by increased abundance estimates for this species from 11,714 in 2005 to 62,447 in 2008 (Barlow, 2010; Forney, 2007). Alternatively, the health of common dolphin populations could have been affected by a change in biotoxin presence or prey type associated with changing oceanographic conditions.

The biotoxin, domoic acid, which is produced by the diatom *Pseudonitzchia spp*., was first implicated in marine mammal deaths off California in 1998 (Scholin *et al.*, 2000) and was first detected in common dolphins in 2002 (Berman and Fahy, 2003). Half of all stranded San Diego County common dolphin samples that tested positive for domoic acid were as high as those reported in California sea lions (*Zalophus californianus*) exhibiting acute effects of domoic acid toxicosis (Goldstein *et al.*, 2008). Anchovies have been implicated as the primary vector for domoic acid toxicity in long-beaked common dolphins (Berman and Fahy, 2003) and they are known to be more prevalent in cool water regimes (Chavez *et al.*, 2003). The peak in long-beaked common dolphins in 2007 (Fig. 3) was likely due to a combination of human interaction (four were shot) and domoic acid toxicosis (9 out of 14 tested positive for domoic acid).

The seasonality in both species of common dolphin strandings (Fig. 4) suggests that these species shift their distribution offshore of San Diego County or experience increased mortality from March to July. As mentioned above, a change in biotoxin or prey could play a role in mortality. Domoic acid concentrations typically increase during the spring and summer off California (Langlois, 2007; Schnetzer *et al.*, 2007). Previous stranding events of long-beaked common dolphins due to domoic acid toxicosis have occurred during these seasons (Berman and Fahy, 2003).

The observation that the sex ratio for both common dolphin species was not significantly different in the stranded sample likely reflects a 1:1 ratio that would be expected in the population as a whole and suggests that both sexes have similar mortality rates. The significantly male dominated short-beaked common dolphin sex ratio observed in the CAGN sample suggests that the fishery incidentally captured more males due to behavioural differences between the sexes, such as schooling in different areas or interacting with fishing gear differently. A male-dominated sex ratio has also been reported for central North Pacific and North Atlantic short-beaked common dolphins (Ferrero and Walker, 1995; Murphy, 2004; Westgate and Read, 2007) that were incidentally killed in fisheries.

The greater female average standard total body length for stranded specimens compared to CAGN specimens can be explained by examining the length frequency distributions for each group. Smaller (younger) females are lacking in the stranded sample (Fig. 5). This may indicate that young females have a lower mortality rate than young males or that they school farther offshore, making it less likely that their carcasses would drift to shore.

Bottlenose dolphin

The high percentage (73.5%) of bottlenose dolphin specimens definitively assigned to the coastal stock suggests that the majority of stranded bottlenose dolphins in San Diego County belong to the coastal stock, a population of approximately 450 individuals (Carretta *et al.*, 2009). This population estimate was a modification of the mark recapture population estimate by Dudzik *et al*. (2006) and accounts for animals that lacked distinguishing marks in their study. It is plausible that almost all coastal bottlenose dolphins that die strand along the coastline given that their range is within one nautical mile of shore. Based on this assumption, between 0.47% and 0.64% of the coastal population dies and strands along the San Diego County coastline every year. This range was calculated by assigning the 26.5% of bottlenose dolphins whose stock designation is currently undetermined to either offshore or coastal for the minimum and maximum estimates, respectively.

The reason for the bottlenose dolphin stranding peaks in 1980 is unknown. However, possibilities include disease outbreak, a southerly distributional shift of the coastal stock or the movement of the offshore stock closer to shore. Since seven of the nine dolphins that stranded in 1980 were determined to be from the coastal stock, movement of the offshore stock is an unlikely reason for the peak in strandings. The decrease in bottlenose dolphin strandings from 1996–99 cannot be attributed to a distribution shift out of the area as there were no significant changes in sighting rates or abundance for bottlenose dolphins off San Diego County during that time period (D. Weller, pers. comm.).

The seasonality in bottlenose dolphin strandings that was detected actually reflects a calving season from May to

September, rather than seasonality of occurrence (Fig. 7). When neonates were removed from the dataset, this seasonality was no longer significant. Defran and Weller (1999) also found that there was no seasonality in bottlenose dolphin occurrence off San Diego County during their boat-based surveys of this population, which were conducted year-round from 1982–89.

The bottlenose dolphin sex ratio (0.84:1) found in this study was not significantly different from a 1:1 ratio. However, Lowther (2006) found a significantly male-biased ratio (1.9:1) of biopsied bottlenose dolphins off San Diego County. The difference between data sets supports the possibility presented by Lowther (2006) that a sampling bias existed in biopsied bottlenose dolphins, rather than representing a skewed sex ratio for the population.

Gray whale

The peak in gray whale strandings occurred during the 1999/2000 die-off, which may have been related to overall food availability (LeBoeuf *et al.*, 2000; Moore *et al.*, 2001; Perryman *et al.*, 2002). The low number and sometimes absence of gray whale strandings following the 1999/2000 die-off is curious (Fig. 8). It is possible that the die-off reduced the population to the extent that there were simply fewer whales to strand. Or, alternatively, the die-off could have reduced the number of compromised individuals such that the population is now comprised of healthier individuals that are less likely to strand. The January and April peaks in strandings likely correspond with southbound and northbound migrating whales, respectively. The higher proportion of males and yearlings in the San Diego County stranding record may indicate that young males are more likely to migrate than females.

Pacific white-sided dolphin

The lack of seasonality in strandings for Pacific white-sided dolphins was surprising considering that their distribution shifts seasonally from California waters in the winter to Oregon and Washington waters in the summer (Forney and Barlow, 1998). Thus, a winter peak in strandings was expected. Pacific white-sided dolphin strandings peaked in 1980, which is the same year bottlenose dolphin strandings peaked. This may suggest that an environmental change occurred that significantly affected their health or shifted their distribution such that they were more likely to strand along the San Diego County coastline. These species are not known to interact, thus disease transmission between the two populations is not likely.

Other species

Dall's porpoise is endemic to the cool temperate North Pacific and San Diego is at approximately the southern limit of its range (Reeves *et al.*, 2002; Rice, 1998). Thus, a shift in its distribution may be more easily detected here. The cool to warm oceanographic regime shift of the late 1970s in the North Pacific may have prompted a northward movement of Dall's porpoise which resulted in its absence off San Diego County from 1980–1997. Its appearance in the San Diego County stranding record again from 1998 to 2006 may be due to the shift into a cooler oceanographic regime, allowing it to expand its range south again.

The decrease in short-finned pilot whale strandings reflects a decline in density of this species in the SCB. Pilot whales moved from the area following the strong El Niño event of 1982–83 (Shane, 1995). Sighting surveys (Barlow, 1995; 1997; Carretta *et al.*, 1995; 2009; Forney *et al.*, 1995; Von Saunder and Barlow, 1999) and incidental takes in the CAGN fishery (Carretta *et al.*, 2005b) indicate short-finned pilot whales returned to California waters nine years after the El Niño event, but not to the SCB.

Risso's dolphins are thought to have replaced short-finned pilot whales in the SCB in the mid to late 1980s (Shane, 1995). The temporal trend of Risso's dolphins in the San Diego County stranding record supports this hypothesis. Although there were only eight recorded Risso's dolphins, 75% of these occurred between 1990 and 2008.

Little is known about pygmy sperm whales off California and thus it is difficult to make any comparisons. Four sightings of *Kogia spp*. have been recorded off central and northern California during ship surveys (Barlow and Forney, 2007). The stranding records presented here represent the only published information available for this species in southern California.

The appearance of harbour porpoises in 2005 and 2006 was surprising since it is a cool-temperate species that normally only ranges as far south as Point Conception (Carretta *et al.*, 2009), although Norris and McFarland (1958) reported bycatch of this species within Los Angeles County. Harbour porpoises are thought to shift their distribution in response to changing oceanographic conditions (Forney, 1999) and thus their appearance in San Diego County may either reflect anomalous oceanographic conditions during 2005 and 2006 or an expansion of their range to the south, perhaps in response to the current cool oceanographic regime. However, harbour porpoises were not reported during the previous cool oceanographic regime (the harbour porpoise reported by Norris and McFarland (1958) in the SCB was captured in 1934 when oceanographic temperatures in this region were reported as being highly variable (Rebstock, 2003)). Interestingly, an extralimital stranding of a southern sea otter in San Diego County occurred on the same day as the stranding of a harbour porpoise in 2006.

The North Pacific right whale observation is the only stranding record for this species in the literature for the mainland United States (one was reported in 1916 on Santa Cruz Island, CA (Woodhouse and Strickley, 1982)). There have been 14 sightings of this species off California in the 20th century, all of which occurred between February and May (Brownell *et al.*, 2001). This stranding occurred in February, which follows the apparent migratory season for this species off the coast of California.

Based on the cetaceans recorded and collected during the study period, two new species were discovered and described from specimens collected in San Diego County: Hubb's beaked whale (*Mesoplodon carlhubbsi*) and Perrin's beaked whale (Dalebout *et al.*, 2002; Moore and Gilmore, 1965).

Human interaction

The most common type of human interaction observed in San Diego County cetaceans was entanglement and this was most frequently observed in long-beaked common dolphins and gray whales. The origin of gray whale entanglements observed off San Diego could have occurred anywhere along their migratory path whereas long-beaked common dolphin entanglements likely occurred within the SCB or northern Mexico. There are two Category I fisheries (i.e. those with frequent mortality or serious injury of marine mammals) that operate off southern California: (1) the shark/swordfish drift gillnet fishery, of which short-beaked common dolphins are the most commonly entangled cetacean (Carretta *et al.*, 2005b); and (2) the halibut set gillnet fishery of which harbour porpoise are the most commonly entangled cetacean (Julian and Beeson, 1998). Thus, it seems likely that an unobserved or minimally observed fishery is responsible for long-beaked common dolphin entanglements off San Diego County; either a Category II (occasional marine mammal mortality/injury) or Category III US fishery (unknown marine mammal mortality/injury), or a fishery off northern Mexico.

Conclusion

In summary, San Diego County cetacean stranding records reflected the species composition of the SCB and over the long-term were better at detecting the presence of cryptic species likely missed during aerial and ship surveys. The results of this study demonstrate the value of stranding networks in monitoring cetacean species and highlight the importance of stranding records for documenting extralimital sightings, cryptic species and revealing changes in mortality or distribution due to oceanographic conditions.

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Appendix I

List of San Diego County cetacean strandings recorded between 1851 and 2008

If geographic coordinates were not available but general area was known, map regions consistent with Fig. 1 were listed instead.

Specimen	Year	Month	Day	Species	Sex	Latitude	Longitude
XXX0075	1856	2	13	*Eubalaena japonica*	U	33º12’N	117º23’W
XXX0076	1883	1	29	*Eschrichtius robustus*	U	-	-
XXX0077	1884	7	12	Unidentified whale	U	-	-
XXX0078	1887	4	1	Unidentified whale	U	32º41’N	117º11’W
XXX0079	1887	8	16	*Megaptera novaeangliae*	U	32º45’N	117º15’W
XXX0081	1888	1	6	Unidentified dolphin or porpoise	U	-	-
XXX0080	1888	10	6	*Balaenoptera*	U	32º32’N	117º07’W
XXX0082	1890	6	14	Unidentified large whale	U	33º04’N	117º18’W
XXX0083	1897	2	14	*Balaenoptera physalus*	U	33º13’N	117º27’W
XXX0084	1898	4	24	Unidentified large whale	U	32º59’N	117º16’W
CLH0055	1904	1	-	*Eschrichtius robustus*	U	32º51’N	117º16’W
CLH0037	1904	1	-	*Globicephala macrorhynchus*	U	32º46’N	117º15’W
CLH0002	1911	11	9	*Delphinus* sp.	U	32º51’N	117º15’W
XXX0008	1927	7	2	*Balaenoptera musculus*	U	32º51’N	117º16’W
XXX0085	1934	10	18	*Balaenoptera*	U	32º41’N	117º11’W
XXX0007	1935	1	7	*Tursiops truncatus*	M	32º48’N	117º15’W
XXX0005	1940	2	14	*Stenella coeruleoalba*	M	32º46’N	117º15’W
XXX0006	1940	10	16	*Globicephala macrorhynchus*	F	32º48’N	117º15’W
CLH0001	1945	-	0	*Delphinus* sp.	F	32º51’N	117º15’W
CLH0077	1945	7	25	*Mesoplodon carlhubbsi*	M	32º51’N	117º16’W
CLH0066	1945	9	24	*Ziphius cavirostris*	F	32º58’N	117º16’W
CLH0021	1946	1	7	*Physeter macrocephalus*	U	32º52’N	117º15’W
CLH0084	1947	6	30	Unidentified dolphin or porpoise	U	32º56’N	117º15’W
CLH0046	1948	5	10	*Tursiops truncatus*	M	32º43’N	117º13’W
CLH0056	1949	4	8	*Eschrichtius robustus*	U	32º42’N	117º14’W
CLH0047	1949	11	27	*Tursiops truncatus*	F	32º43’N	117º13’W
CLH0078	1949	12	10	*Kogia breviceps*	M	32º33’N	117º08’W
CLH0048	1949	12	11	*Tursiops truncatus*	U	32º52’N	117º15’W
CLH0045	1949	-	-	*Globicephala macrorhynchus*	U	32º51’N	117º16’W
CLH0049	1950	12	24	*Tursiops truncatus*	M	32º56’N	117º16’W
WFP0241	1952	3	22	*Phocoenoides dalli*	F	32º52’N	117º15’W
CLH0057	1952	3	30	*Eschrichtius robustus*	F	32º45’N	117º15’W
CLH0082	1952	7	12	*Tursiops truncatus*	U	32º35’N	117º08’W
WFP0237	1952	7	26	*Globicephala macrorhynchus*	M	32º35’N	117º08’W
WFP0238	1952	8	20	*Globicephala macrorhynchus*	F	33º02’N	117º18’W
RMG4551	1953	10	9	*Tursiops truncatus*	F	32º48’N	117º15’W
RMG4556	1954	1	23	*Globicephala macrorhynchus*	F	32º58’N	117º16’W
RMG4558	1954	5	21	*Phocoenoides dalli*	M	32º46’N	117º15’W
RMG4559	1954	6	10	*Mesoplodon ginkgodens*	F	32º58’N	117º16’W
CLH0071	1955	2	6	*Kogia breviceps*	F	33º02’N	117º17’W
CLH0072	1955	2	6	*Kogia breviceps*	F	33º02’N	117º18’W
RMG4605	1956	1	8	*Lagenorhynchus obliquidens*	M	32º51’N	117º15’W
CLH0081	1956	2	9	*Globicephala macrorhynchus*	F	32º36’N	117º17’W
CLH0058	1956	3	15	*Eschrichtius robustus*	M	32º36’N	117º08’W
RMG4636	1956	6	23	*Delphinus* sp.	M	32º51’N	117º15’W
WFP0291	1956	7	3	*Lissodelphis borealis*	U	32º53’N	117º15’W
CLH0022	1956	10	3	*Lagenorhynchus obliquidens*	M	32º48’N	117º15’W
CLH0079	1956	11	30	*Kogia breviceps*	U	32º58’N	117º16’W
RMG4659	1957	1	7	*Lagenorhynchus obliquidens*	M	32º58’N	117º16’W
WFP0240	1957	1	25	*Lagenorhynchus obliquidens*	F	32º59’N	117º16’W
RMG4660	1957	1	27	*Ziphius cavirostris*	F	32º41’N	117º12’W
CLH0083	1957	6	29	*Tursiops truncatus*	U	32º40’N	117º07’W
RMG4700	1957	8	20	*Lagenorhynchus obliquidens*	M	32º54’N	117º15’W
RMG4701	1957	10	15	*Tursiops truncatus*	M	32º51’N	117º15’W
SDNHM21213	1957	12	2	*Tursiops truncatus*	F	Region 2	-
CLH0067	1959	6	13	*Ziphius cavirostris*	M	32º51’N	117º16’W
CLH0073	1959	10	11	*Kogia breviceps*	M	32º46’N	117º15’W
CLH0044	1960	1	28	*Globicephala macrorhynchus*	F	32º33’N	117º08’W
CLH0075	1960	2	16	*Kogia breviceps*	F	32º57’N	117º16’W
WFP0239	1960	4	25	*Lagenorhynchus obliquidens*	M	32º52’N	117º15’W
CLH0059	1961	3	31	*Eschrichtius robustus*	U	32º38’N	117º09’W
CLH0003	1962	2	13	*Delphinus capensis*	M	32º50’N	117º17’W
CLH0031	1962	2	27	*Phocoenoides dalli*	M	32º53’N	117º15’W
CLH0004	1962	2	28	*Delphinus* sp.	M	32º54’N	117º15’W
CLH0025	1962	7	12	*Lagenorhynchus obliquidens*	F	32º51’N	117º15’W
CLH0060	1963	1	28	*Eschrichtius robustus*	U	32º35’N	117º08’W
CLH0062	1963	3	14	*Eschrichtius robustus*	M	32º41’N	117º15’W
CLH0027	1963	3	15	*Lagenorhynchus obliquidens*	U	33º09’N	117º21’W
CLH0042	1963	3	15	*Globicephala macrorhynchus*	M	32º56’N	117º16’W
CLH0085	1963	3	17	Unidentified dolphin or porpoise	U	32º56’N	117º16’W

Cont.

Specimen	Year	Month	Day	Species	Sex	Latitude	Longitude
CLH0026	1963	3	27	*Lagenorhynchus obliquidens*	M	32º57’N	117º16’W
CLH0005	1963	4	15	Unidentified dolphin or porpoise	U	33º00’N	117º16’W
CLH0006	1963	4	16	*Delphinus delphis*	M	32º51’N	117º16’W
CLH0007	1963	4	17	*Delphinus delphis*	F	33º03’N	117º18’W
CLH0008	1963	4	18	*Delphinus delphis*	F	33º04’N	117º18’W
CLH0069	1963	6	12	*Ziphius cavirostris*	M	32º58’N	117º16’W
XXX0090	1963	6	12	*Ziphius cavirostris*	U	32º51’N	117º16’W
CLH0070	1963	6	13	*Ziphius cavirostris*	F	32º51’N	117º16’W
CLH0063	1963	6	14	*Eschrichtius robustus*	M	32º49’N	117º17’W
CLH0050	1963	8	7	*Tursiops truncatus*	F	32º53’N	117º15’W
CLH0051	1963	8	7	*Tursiops truncatus*	F	32º53’N	117º15’W
CLH0009	1963	9	1	*Delphinus* sp.	M	32º53’N	117º15’W
CLH0052	1963	9	23	*Tursiops truncatus*	F	32º44’N	117º15’W
CLH0074	1963	10	2	*Kogia breviceps*	F	32º35’N	117º08’W
CLH0010	1963	11	18	*Delphinus* sp.	M	33º00’N	117º16’W
XXX0086	1964	2	25	*Eschrichtius robustus*	U	Region 3	-
CLH0011	1964	4	4	*Delphinus* sp.	M	32º56’N	117º16’W
CLH0032	1964	4	23	*Phocoenoides dalli*	U	32º35’N	117º08’W
CLH0033	1964	5	17	*Phocoenoides dalli*	F	32º51’N	117º16’W
CLH0028	1964	6	21	*Lagenorhynchus obliquidens*	M	32º53’N	117º15’W
CLH0043	1965	3	15	*Globicephala macrorhynchus*	F	33º06’N	117º19’W
CLH0034	1965	3	28	*Phocoenoides dalli*	F	32º51’N	117º16’W
RMG4752	1965	7	2	*Balaenoptera musculus*	M	32º48’N	117º15’W
RMG4751	1965	7	10	*Phocoenoides dalli*	M	32º37’N	117º08’W
XXX0009	1965	9	14	*Eschrichtius robustus*	U	33º21’N	117º31’W
CLH0029	1965	9	28	*Lagenorhynchus obliquidens*	U	32º52’N	117º15’W
CLH0068	1965	11	23	*Ziphius cavirostris*	F	32º48’N	117º15’W
SWC0060	1966	5	7	*Delphinus* sp.	M	33º12’N	117º23’W
CLH0012	1966	8	6	*Delphinus* sp.	M	32º51’N	117º16’W
CLH0035	1966	8	13	*Phocoenoides dalli*	M	32º51’N	117º16’W
WFP0236	1966	9	8	*Delphinus delphis*	M	32º52’N	117º15’W
RMG4753	1966	9	12	*Ziphius cavirostris*	U	32º35’N	117º08’W
CLH0064	1967	1	23	*Eschrichtius robustus*	F	32º54’N	117º15’W
CLH0014	1967	4	5	*Delphinus* sp.	U	32º56’N	117º16’W
CLH0036	1967	6	1	*Phocoenoides dalli*	U	32º58’N	117º16’W
CLH0080	1967	7	21	*Delphinus* sp.	U	32º53’N	117º15’W
CLH0015	1967	8	21	*Delphinus* sp.	U	33º01’N	117º17’W
CLH0041	1967	8	23	*Globicephala macrorhynchus*	U	33º00’N	117º16’W
SWC0001	1967	8	27	*Delphinus* sp.	M	32º35’N	117º08’W
CLH0019	1967	11	7	*Lissodelphis borealis*	M	32º34’N	117º08’W
SWC0002	1968	2	3	*Delphinus* sp.	F	32º45’N	117º15’W
CLH0016	1968	4	20	*Delphinus capensis*	M	32º56’N	117º16’W
CLH0065	1968	6	18	*Eschrichtius robustus*	U	32º51’N	117º15’W
SWC0067	1968	8	10	*Mesoplodon stejnegeri*	F	33º01’N	117º17’W
SWC0051	1968	10	19	*Phocoenoides dalli*	M	32º51’N	117º16’W
RMG4755	1969	1	22	*Grampus griseus*	M	32º34’N	117º08’W
SWC0061	1969	3	10	*Delphinus* sp.	F	32º51’N	117º15’W
WFP0616	1969	4	7	*Delphinus* sp.	M	33º05’N	117º19’W
WFP0612	1969	11	29	*Delphinus capensis*	F	32º51’N	117º15’W
CLH0040	1969	12	26	*Globicephala macrorhynchus*	U	32º46’N	117º15’W
SWC0003	1970	3	23	*Delphinus* sp.	U	32º47’N	117º15’W
WFP0033	1970	4	6	*Delphinus delphis*	M	32º56’N	117º16’W
WFP0036	1970	4	27	*Tursiops truncatus*	M	32º56’N	117º16’W
WFP0038	1970	5	8	*Delphinus delphis*	F	32º54’N	117º15’W
WFP0037	1970	5	8	*Lagenorhynchus obliquidens*	F	32º50’N	117º17’W
WFP0039	1970	5	9	*Delphinus* sp.	M	32º58’N	117º16’W
WFP0040	1970	5	19	*Delphinus delphis*	M	32º54’N	117º15’W
XXX0013	1970	5	28	*Delphinus* sp.	U	32º53’N	117º15’W
SWC0043	1970	6	3	*Lagenorhynchus obliquidens*	U	32º35’N	117º08’W
XXX0015	1970	6	8	Unidentified dolphin or porpoise	M	32º48’N	117º15’W
XXX0014	1970	6	8	Unidentified dolphin or porpoise	U	32º44’N	117º15’W
WFP0043	1970	6	17	*Lagenorhynchus obliquidens*	F	32º53’N	117º15’W
WFP0044	1970	8	17	*Delphinus capensis*	M	32º56’N	117º16’W
WFP0045	1970	8	17	*Delphinus capensis*	M	32º52’N	117º15’W
WFP0046	1970	8	28	*Delphinus capensis*	M	32º56’N	117º16’W
WFP0060	1970	10	22	*Delphinus delphis*	M	32º52’N	117º15’W
WFP0061	1970	11	8	*Delphinus* sp.	M	33º04’N	117º18’W
CLH0076	1971	3	25	*Kogia breviceps*	M	32º56’N	117º16’W
SWC0044	1971	4	15	*Lagenorhynchus obliquidens*	U	32º48’N	117º15’W
WFP0082	1971	5	16	*Lagenorhynchus obliquidens*	M	32º52’N	117º15’W
NUC8020	1971	7	20	*Delphinus delphis*	U	32º35’N	117º08’W
WFP0185	1971	12	3	*Lagenorhynchus obliquidens*	F	32º58’N	117º16’W
XXX0057	1972	1	22	*Delphinus capensis*	M	Region 3	-
NUC0204	1972	3	30	*Delphinus* sp.	M	32º58’N	117º16’W
NUC0215	1972	4	10	*Delphinus* sp.	F	33º09’N	117º21’W
WFP0217	1972	4	11	*Delphinus delphis*	M	32º51’N	117º16’W

Cont.

Specimen	Year	Month	Day	Species	Sex	Latitude	Longitude
WFP0218	1972	6	3	*Delphinus* sp.	M	32º53’N	117º15’W
WFP0221	1972	6	27	*Delphinus delphis*	M	32º53’N	117º15’W
WFP0220	1972	6	27	*Delphinus* sp.	U	32º53’N	117º15’W
WFP0225	1972	7	5	*Delphinus delphis*	M	33º19’N	117º30’W
XXX0003	1972	7	5	*Delphinus* sp.	U	33º16’N	117º27’W
WFP0227	1972	7	5	*Delphinus* sp.	M	33º15’N	117º26’W
WFP0226	1972	7	5	*Phocoenoides dalli*	U	33º15’N	117º26’W
WFP0224	1972	7	5	*Delphinus* sp.	M	33º14’N	117º25’W
WFP0223	1972	7	5	*Delphinus* sp.	M	33º14’N	117º25’W
WFP0222	1972	7	5	*Lagenorhynchus obliquidens*	M	33º14’N	117º25’W
WFP0230	1972	11	7	*Phocoenoides dalli*	F	33º16’N	117º27’W
WFP0231	1972	11	14	*Lagenorhynchus obliquidens*	F	33º02’N	117º17’W
WFP0232	1972	12	20	*Physeter macrocephalus*	M	33º16’N	117º27’W
WFP0233	1973	1	2	*Delphinus* sp.	F	32º45’N	117º15’W
WFP0234	1973	1	15	*Delphinus delphis*	U	33º01’N	117º17’W
XXX0058	1973	2	12	*Lagenorhynchus obliquidens*	F	32º51’N	117º17’W
WFP0246	1973	3	9	*Delphinus delphis*	M	33º13’N	117º24’W
WFP0247	1973	3	12	*Globicephala macrorhynchus*	F	33º00’N	117º17’W
WFP0248	1973	3	14	*Phocoenoides dalli*	F	32º52’N	117º15’W
XXX0067	1973	3	15	*Globicephala macrorhynchus*	U	Region 10	-
WFP0249	1973	3	15	*Globicephala macrorhynchus*	F	32º53’N	117º15’W
NUC0253	1973	3	28	*Delphinus* sp.	M	32º37’N	117º08’W
WFP0264	1973	3	29	*Delphinus delphis*	M	33º03’N	117º18’W
XXX0066	1973	3	-	*Lagenorhynchus obliquidens*	U	-	-
WFP0265	1973	4	2	*Globicephala macrorhynchus*	F	33º17’N	117º28’W
XXX0059	1973	4	15	*Delphinus* sp.	U	Region 1	-
WFP0266	1973	4	25	*Delphinus* sp.	F	32º53’N	117º15’W
XXX0068	1973	4	-	*Delphinus* sp.	U	Region 1	-
WFP0272	1973	6	8	*Lissodelphis borealis*	M	32º48’N	117º15’W
SWC0055	1973	7	13	*Tursiops truncatus*	U	32º35’N	117º08’W
XXX0069	1973	8	5	*Delphinus* sp.	U	-	-
NUC0381	1973	8	6	*Delphinus* sp.	M	33º22’N	117º34’W
WFP0278	1973	8	22	*Tursiops truncatus*	M	32º32’N	117º07’W
WFP0279	1973	9	11	*Lissodelphis borealis*	F	32º52’N	117º15’W
SWC0007	1973	10	12	*Delphinus* sp.	U	32º42’N	117º14’W
SWC0008	1974	3	3	*Delphinus* sp.	M	32º46’N	117º15’W
WFP0309	1974	3	4	*Delphinus* sp.	F	32º51’N	117º16’W
SWC0009	1974	3	11	*Delphinus* sp.	F	32º51’N	117º15’W
SWC0010	1974	4	2	*Delphinus* sp.	M	32º51’N	117º15’W
WFP0465	1974	4	16	*Delphinus* sp.	M	32º53’N	117º15’W
NUC0385	1974	4	27	*Delphinus* sp.	F	32º41’N	117º13’W
SWC0012	1974	5	5	*Delphinus* sp.	M	32º32’N	117º07’W
SWC0013	1974	6	29	*Delphinus* sp.	U	32º35’N	117º08’W
RMG4795	1974	7	6	*Delphinus* sp.	M	32º53’N	117º15’W
RMG4794	1974	7	10	*Delphinus* sp.	M	32º46’N	117º15’W
WFP0472	1974	7	15	*Lagenorhynchus obliquidens*	F	32º51’N	117º15’W
SWC0016	1974	7	22	*Delphinus* sp.	M	32º45’N	117º15’W
WFP0473	1974	7	27	*Delphinus delphis*	F	33º04’N	117º18’W
WFP0474	1974	8	2	*Tursiops truncatus*	F	33º09’N	117º21’W
RMG4797	1974	10	3	*Tursiops truncatus*	M	32º51’N	117º16’W
WFP0482	1974	10	3	*Mesoplodon carlhubbsi*	F	32º45’N	117º15’W
NUC0390	1974	10	18	*Delphinus* sp.	M	32º52’N	117º15’W
WFP0475	1974	10	31	*Tursiops truncatus*	F	32º51’N	117º15’W
WFP0477	1974	11	3	*Lissodelphis borealis*	F	32º41’N	117º11’W
WFP0479	1974	12	2	*Delphinus* sp.	M	32º56’N	117º16’W
WFP0480	1974	12	7	*Delphinus* sp.	M	32º52’N	117º15’W
WFP0481	1974	12	27	*Delphinus delphis*	F	32º51’N	117º15’W
CLH0086	1975	1	21	Unidentified whale	U	32º36’N	117º12’W
WFP0485	1975	3	11	*Delphinus delphis*	M	33º04’N	117º18’W
WFP0487	1975	3	15	*Delphinus* sp.	M	33º02’N	117º17’W
WFP0490	1975	3	31	*Delphinus delphis*	F	33º06’N	117º19’W
WFP0488	1975	3	31	*Delphinus delphis*	M	32º47’N	117º15’W
WFP0492	1975	4	23	*Eschrichtius robustus*	F	33º19’N	117º29’W
WFP0493	1975	4	25	*Phocoenoides dalli*	F	33º04’N	117º18’W
WFP0495	1975	5	21	*Delphinus* sp.	F	32º49’N	117º17’W
WFP0496	1975	5	22	*Mesoplodon perrini*	M	33º15’N	117º26’W
WFP0497	1975	5	28	*Mesoplodon perrini*	F	33º15’N	117º26’W
WFP0498	1975	6	10	*Delphinus* sp.	M	33º05’N	117º19’W
WFP0505	1975	7	6	*Delphinus delphis*	F	33º07’N	117º20’W
SWC0017	1975	7	13	*Delphinus* sp.	M	32º41’N	117º13’W
NUC0397	1975	8	5	*Delphinus* sp.	F	32º46’N	117º15’W
WFP0514	1975	8	14	*Phocoenoides dalli*	M	32º32’N	117º07’W
WFP0515	1975	9	-	*Tursiops truncatus*	F	32º42’N	117º15’W
NUC0417	1975	9	13	*Delphinus* sp.	M	33º06’N	117º19’W
WFP0508	1975	9	17	*Delphinus delphis*	M	32º53’N	117º15’W
XXX0070	1975	9	-	*Delphinus* sp.	F	-	-

Cont.

Specimen	Year	Month	Day	Species	Sex	Latitude	Longitude
XXX0060	1975	9	-	*Delphinus* sp.	F	-	-
SWC0018	1975	10	12	*Delphinus* sp.	F	32º51’N	117º15’W
WFP0509	1975	10	22	*Tursiops truncatus*	F	-	-
SWC0020	1975	11	29	*Delphinus* sp.	M	33º00’N	117º16’W
WFP0510	1975	12	15	*Delphinus* sp.	M	32º56’N	117º16’W
WFP0511	1976	1	8	*Tursiops truncatus*	M	33º09’N	117º21’W
WFP0512	1976	1	15	*Delphinus delphis*	M	32º54’N	117º15’W
SWC0021	1976	3	3	*Delphinus* sp.	F	32º41’N	117º13’W
SWC0022	1976	3	28	*Delphinus* sp.	F	32º57’N	117º16’W
WFP0517	1976	4	19	*Delphinus delphis*	M	32º41’N	117º13’W
WFP0518	1976	5	20	*Lagenorhynchus obliquidens*	M	33º13’N	117º24’W
WFP0519	1976	6	21	*Delphinus delphis*	M	33º09’N	117º21’W
WFP0520	1976	6	28	*Tursiops truncatus*	M	33º02’N	117º17’W
SWC0023	1976	6	30	*Delphinus* sp.	F	32º46’N	117º15’W
NUC0409	1976	7	11	*Delphinus* sp.	M	33º22’N	117º34’W
WFP0522	1976	7	27	*Tursiops truncatus*	F	32º56’N	117º16’W
WFP0523	1976	8	2	*Tursiops truncatus*	F	32º33’N	117º08’W
WFP0535	1976	8	8	*Tursiops truncatus*	M	32º54’N	117º15’W
WFP0537	1976	8	31	*Tursiops truncatus*	F	33º03’N	117º18’W
WFP0552	1976	10	3	*Delphinus delphis*	M	33º02’N	117º17’W
WFP0553	1976	10	14	*Eschrichtius robustus*	M	32º47’N	117º15’W
SWC0040	1976	10	18	*Kogia breviceps*	F	32º35’N	117º08’W
RMG5000	1976	12	17	*Eschrichtius robustus*	M	32º40’N	117º16’W
WFP0559	1977	2	5	*Tursiops truncatus*	M	32º53’N	117º15’W
SWC0025	1977	3	24	*Delphinus* sp.	M	32º46’N	117º15’W
WFP0560	1977	3	27	*Delphinus* sp.	M	33º06’N	117º19’W
WFP0561	1977	5	4	*Delphinus* sp.	M	32º59’N	117º16’W
WFP0562	1977	5	7	*Delphinus* sp.	M	33º05’N	117º19’W
WFP0563	1977	5	16	*Tursiops truncatus*	F	32º52’N	117º15’W
WFP0564	1977	6	14	*Ziphius cavirostris*	F	32º53’N	117º15’W
WFP0565	1977	6	27	*Tursiops truncatus*	M	32º57’N	117º16’W
WFP0570	1978	1	25	*Eschrichtius robustus*	F	33º15’N	117º26’W
NUC0420	1978	2	13	*Delphinus* sp.	M	33º02’N	117º17’W
WFP0573	1978	3	2	*Eschrichtius robustus*	M	32º57’N	117º16’W
WFP0575	1978	3	14	*Grampus griseus*	F	32º43’N	117º15’W
SWC0026	1978	4	23	*Delphinus* sp.	F	32º37’N	117º08’W
WFP0577	1978	5	5	*Eschrichtius robustus*	F	33º04’N	117º18’W
SWC0027	1978	5	6	*Delphinus* sp.	F	32º51’N	117º15’W
SWC0056	1978	7	16	*Tursiops truncatus*	F	33º16’N	117º27’W
WFP0583	1978	9	8	*Delphinus delphis*	M	33º05’N	117º19’W
JGM0391	1978	9	9	*Mesoplodon perrini*	M	33º08’N	117º20’W
SWC0028	1978	9	15	*Delphinus* sp.	M	32º46’N	117º15’W
WFP0585	1979	2	1	*Eschrichtius robustus*	U	32º36’N	117º08’W
WFP0586	1979	3	3	*Phocoenoides dalli*	F	32º45’N	117º15’W
WFP0591	1979	4	16	*Lagenorhynchus obliquidens*	F	32º52’N	117º15’W
WFP0593	1979	5	1	*Tursiops truncatus*	F	32º54’N	117º15’W
WFP0595	1979	5	11	*Delphinus delphis*	F	33º03’N	117º18’W
JRH0046	1979	5	21	*Eschrichtius robustus*	M	32º45’N	117º15’W
JRH0047	1979	6	26	*Stenella coeruleoalba*	M	32º35’N	117º08’W
XXX0063	1979	7	15	*Delphinus* sp.	F	32º40’N	117º10’W
JRH0049	1979	7	26	*Delphinus capensis*	M	32º57’N	117º16’W
JRH0050	1979	8	21	*Tursiops truncatus*	F	33º05’N	117º19’W
RMG5001	1979	12	12	*Eschrichtius robustus*	F	32º43’N	117º16’W
JRH0052	1979	12	26	*Mesoplodon perrini*	M	32º54’N	117º15’W
JRH0053	1980	1	11	*Eschrichtius robustus*	F	33º02’N	117º18’W
JRH0054	1980	3	6	*Lagenorhynchus obliquidens*	F	33º05’N	117º19’W
JRH0055	1980	3	30	*Eschrichtius robustus*	M	32º46’N	117º15’W
SWC0047	1980	4	2	*Lagenorhynchus obliquidens*	M	32º58’N	117º16’W
JRH0057	1980	5	13	*Tursiops truncatus*	F	32º52’N	117º15’W
JRH0058	1980	5	31	*Tursiops truncatus*	M	32º55’N	117º15’W
JRH0065	1980	6	16	*Delphinus* sp.	F	33º02’N	117º18’W
JRH0067	1980	7	7	*Tursiops truncatus*	M	32º37’N	117º08’W
JRH0070	1980	7	24	*Tursiops truncatus*	F	32º48’N	117º16’W
JRH0071	1980	7	28	*Delphinus delphis*	M	33º08’N	117º20’W
JRH0073	1980	8	3	*Tursiops truncatus*	F	33º22’N	117º34’W
JRH0074	1980	8	13	*Delphinus delphis*	M	32º42’N	117º14’W
JRH0077	1980	9	10	*Tursiops truncatus*	M	32º53’N	117º15’W
JRH0078	1980	9	16	*Lagenorhynchus obliquidens*	U	33º15’N	117º26’W
JRH0084	1980	10	21	*Tursiops truncatus*	F	32º59’N	117º16’W
JRH0086	1980	11	2	*Globicephala macrorhynchus*	M	33º22’N	117º34’W
JRH0087	1980	11	20	*Ziphius cavirostris*	M	32º53’N	117º15’W
JRH0094	1980	12	21	*Lagenorhynchus obliquidens*	F	32º47’N	117º15’W
JRH0095	1980	12	31	*Tursiops truncatus*	M	33º15’N	117º26’W
JRH0098	1980	12	31	*Tursiops truncatus*	M	32º54’N	117º15’W
JRH0096	1981	1	2	*Eschrichtius robustus*	M	32º39’N	117º09’W
SWC0029	1981	3	23	*Delphinus* sp.	F	32º50’N	117º17’W

Cont.

Specimen	Year	Month	Day	Species	Sex	Latitude	Longitude
SWC0030	1981	4	7	*Delphinus* sp.	M	33º03’N	117º18’W
JRH0120	1981	4	18	*Lagenorhynchus obliquidens*	M	32º47’N	117º15’W
JRH0128	1981	5	5	*Tursiops truncatus*	M	32º55’N	117º15’W
JRH0141	1981	5	25	*Delphinus delphis*	F	32º48’N	117º16’W
SWC0069	1981	5	28	*Delphinus* sp.	M	32º53’N	117º15’W
JRH0160	1981	6	13	*Lissodelphis borealis*	F	33º14’N	117º25’W
SWC0031	1981	6	29	*Delphinus* sp.	F	33º09’N	117º21’W
JRH0192	1981	9	3	*Tursiops truncatus*	U	33º22’N	117º33’W
SWC0032	1981	10	2	*Delphinus* sp.	M	32º32’N	117º07’W
LJH0006	1981	11	14	*Tursiops truncatus*	F	32º52’N	117º15’W
LJH0012	1982	2	3	*Lagenorhynchus obliquidens*	M	33º07’N	117º20’W
LJH0015	1982	4	3	*Delphinus* sp.	U	32º48’N	117º15’W
LJH0053	1982	5	30	*Balaenoptera acutorostrata*	M	32º43’N	117º11’W
LJH0054	1982	6	2	*Delphinus delphis*	F	33º23’N	117º36’W
LJH0066	1982	7	29	*Tursiops truncatus*	F	32º53’N	117º15’W
LJH0124	1982	8	10	*Eschrichtius robustus*	F	32º50’N	117º17’W
LJH0123	1982	8	24	*Eschrichtius robustus*	M	32º42’N	117º14’W
MSL0267	1982	10	5	*Tursiops truncatus*	M	33º06’N	117º19’W
MSL0269	1982	10	15	*Tursiops truncatus*	M	33º06’N	117º19’W
MSL0279	1982	12	13	*Eschrichtius robustus*	F	32º36’N	117º07’W
LJH0077	1983	1	12	*Lagenorhynchus obliquidens*	F	32º55’N	117º15’W
LJH0078	1983	1	19	*Delphinus delphis*	F	33º17’N	117º28’W
LJH0079	1983	1	24	Unidentified large whale	U	32º52’N	117º15’W
LJH0080	1983	1	31	*Eschrichtius robustus*	M	32º43’N	117º13’W
XXX0087	1983	3	14	*Eschrichtius robustus*	U	Region 9	-
LJH0082	1983	3	15	*Stenella coeruleoalba*	M	33º16’N	117º26’W
LJH0085	1983	4	11	*Eschrichtius robustus*	F	32º36’N	117º08’W
MSL0290	1983	4	15	*Delphinus* sp.	U	33º04’N	117º18’W
MSL0292	1983	4	19	*Megaptera novaeangliae*	F	32º41’N	117º11’W
LJH0086	1983	5	3	*Stenella coeruleoalba*	F	33º03’N	117º18’W
LJH0094	1983	5	19	*Delphinus capensis*	M	33º02’N	117º17’W
SWC0033	1983	5	22	*Delphinus* sp.	M	32º52’N	117º15’W
LJH0096	1983	5	25	*Tursiops truncatus*	F	33º13’N	117º25’W
LJH0099	1983	6	27	*Delphinus capensis*	M	32º38’N	117º08’W
LJH0105	1983	8	10	*Tursiops truncatus*	F	33º22’N	117º33’W
SWC0048	1983	8	11	*Lagenorhynchus obliquidens*	F	33º12’N	117º23’W
MSL0295	1983	8	17	*Balaenoptera physalus*	F	32º36’N	117º08’W
LJH0106	1983	8	22	*Delphinus delphis*	M	33º09’N	117º21’W
LJH0107	1983	8	24	*Delphinus* sp.	U	32º49’N	117º16’W
LJH0125	1983	9	3	*Delphinus* sp.	M	32º51’N	117º16’W
LJH0119	1983	9	23	*Lagenorhynchus obliquidens*	F	32º58’N	117º16’W
LJH0121	1983	10	16	*Delphinus capensis*	F	32º39’N	117º09’W
LJH0127	1983	11	22	*Delphinus* sp.	M	33º13’N	117º24’W
LJH0128	1983	12	26	*Eschrichtius robustus*	M	32º46’N	117º15’W
LJH0129	1984	4	4	*Eschrichtius robustus*	U	32º40’N	117º14’W
SWC0034	1984	4	19	*Delphinus* sp.	M	32º41’N	117º13’W
LJH0130	1984	5	5	*Tursiops truncatus*	F	32º35’N	117º08’W
HJB0001	1984	7	19	*Delphinus* sp.	M	33º06’N	117º19’W
HJB0002	1984	8	20	*Balaenoptera musculus*	F	33º02’N	117º17’W
HJB0003	1984	11	6	*Delphinus delphis*	M	33º22’N	117º33’W
HJB0004	1984	11	15	*Delphinus delphis*	M	32º43’N	117º10’W
HJB0005	1984	12	17	*Kogia breviceps*	F	32º34’N	117º08’W
HJB0009	1985	1	28	*Eschrichtius robustus*	M	33º13’N	117º24’W
HJB0011	1985	3	6	*Delphinus capensis*	M	33º22’N	117º33’W
HJB0010	1985	3	20	*Delphinus* sp.	F	33º22’N	117º34’W
HJB0013	1985	3	25	*Delphinus capensis*	M	32º57’N	117º16’W
HJB0012	1985	4	4	*Eschrichtius robustus*	M	32º44’N	117º15’W
HJB0014	1985	4	9	*Eschrichtius robustus*	F	32º35’N	117º08’W
AAH0001	1985	4	13	*Tursiops truncatus*	F	32º38’N	117º08’W
HJB0017	1985	5	3	*Delphinus* sp.	U	32º32’N	117º07’W
HJB0018	1985	6	11	*Tursiops truncatus*	M	32º37’N	117º08’W
HJB0019	1985	6	14	*Tursiops truncatus*	F	32º55’N	117º15’W
WFP0699	1985	7	0	*Globicephala macrorhynchus*	U	33º12’N	117º23’W
HJB0021	1985	7	17	*Delphinus* sp.	F	33º09’N	117º21’W
DK-85-18	1985	9	16	*Delphinus* sp.	M	33º09’N	117º21’W
HJB0022	1985	9	25	*Lagenorhynchus obliquidens*	F	32º32’N	117º07’W
HJB0023	1985	9	27	*Eschrichtius robustus*	M	32º38’N	117º06’W
HJB0025	1985	10	22	*Lagenorhynchus obliquidens*	M	32º47’N	117º15’W
SWC0038	1985	10	24	*Delphinus* sp.	M	32º51’N	117º16’W
DK-86-01	1986	1	4	*Delphinus capensis*	M	33º21’N	117º32’W
HJB0026	1986	2	11	*Delphinus* sp.	F	33º01’N	117º17’W
HJB0027	1986	3	31	*Delphinus delphis*	M	32º37’N	117º08’W
HJB0030	1986	4	14	*Delphinus* sp.	M	33º07’N	117º20’W
HJB0029	1986	4	14	*Delphinus capensis*	F	33º03’N	117º18’W
HJB0031	1986	4	24	*Delphinus capensis*	M	33º00’N	117º17’W
HJB0032	1986	5	2	*Delphinus delphis*	M	33º08’N	117º20’W

Cont.

Specimen	Year	Month	Day	Species	Sex	Latitude	Longitude
HJB0033	1986	5	30	*Balaenoptera*	U	33º04’N	117º18’W
JEH0335	1986	6	3	*Mesoplodon carlhubbsi*	F	33º23’N	117º34’W
DK-86-10	1986	6	3	*Delphinus capensis*	F	33º21’N	117º32’W
HJB0035	1986	7	7	*Eschrichtius robustus*	M	33º06’N	117º19’W
HJB0036	1986	8	29	*Tursiops truncatus*	M	33º00’N	117º16’W
HJB0037	1986	10	16	*Delphinus* sp.	M	32º43’N	117º13’W
HJB0038	1986	11	21	Unidentified dolphin or porpoise	U	32º53’N	117º15’W
HJB0040	1987	2	24	*Tursiops truncatus*	F	33º22’N	117º33’W
HJB0044	1987	3	30	*Delphinus* sp.	F	32º56’N	117º15’W
HJB0045	1987	4	17	*Eschrichtius robustus*	M	33º08’N	117º20’W
HJB0046	1987	5	14	*Tursiops truncatus*	F	32º43’N	117º15’W
HJB0048	1987	6	24	*Tursiops truncatus*	M	33º06’N	117º19’W
HJB0049	1987	8	21	*Delphinus capensis*	F	33º01’N	117º17’W
HJB0050	1987	9	14	*Eschrichtius robustus*	F	33º01’N	117º17’W
XXX0073	1987	11	19	*Eschrichtius robustus*	U	-	-
JEH0381	1988	5	31	*Tursiops truncatus*	M	33º16’N	117º27’W
JEH0382	1988	5	31	*Tursiops truncatus*	F	33º16’N	117º27’W
SWC0068	1988	6	17	*Delphinus* sp.	F	32º44’N	117º15’W
XXX0089	1988	7	2	Unidentified dolphin or porpoise	U	Region 7	-
JWG0105	1988	8	1	*Balaenoptera acutorostrata*	M	33º02’N	117º18’W
SWC0062	1988	8	15	*Delphinus* sp.	M	32º46’N	117º15’W
JWG0106	1988	12	19	*Eschrichtius robustus*	M	32º50’N	117º17’W
JEH0412	1989	0	0	*Delphinus delphis*	U	33º12’N	117º23’W
KZP0001	1989	1	8	*Delphinus delphis*	M	33º13’N	117º24’W
SWC0063	1989	1	11	*Delphinus delphis*	M	32º52’N	117º15’W
KZP0002	1989	2	9	*Delphinus delphis*	M	33º12’N	117º23’W
KZP0003	1989	4	15	*Eschrichtius robustus*	F	33º16’N	117º27’W
KZP0004	1989	5	7	*Delphinus* sp.	F	32º45’N	117º15’W
KZP0005	1989	5	10	*Lagenorhynchus obliquidens*	F	33º00’N	117º16’W
KZP0007	1989	5	27	*Delphinus capensis*	F	32º51’N	117º17’W
KZP0008	1989	6	22	*Tursiops truncatus*	M	33º22’N	117º34’W
KZP0009	1989	8	1	*Balaenoptera acutorostrata*	M	32º50’N	117º18’W
KZP0010	1989	9	11	*Tursiops truncatus*	M	33º22’N	117º33’W
KZP0011	1989	9	18	*Delphinus delphis*	M	32º51’N	117º15’W
KZP0012	1989	10	30	*Tursiops truncatus*	F	32º57’N	117º16’W
SWC0064	1989	11	26	*Delphinus delphis*	M	32º46’N	117º15’W
KZP0013	1989	11	27	*Eschrichtius robustus*	M	32º50’N	117º18’W
SWC0065	1989	12	28	*Delphinus delphis*	F	32º58’N	117º16’W
SWC0066	1990	2	18	*Delphinus* sp.	F	32º47’N	117º15’W
KZP0014	1990	2	21	*Delphinus delphis*	F	32º52’N	117º15’W
KZP0016	1990	4	16	*Grampus griseus*	F	32º56’N	117º16’W
KZP0015	1990	4	16	*Eschrichtius robustus*	F	32º42’N	117º10’W
KZP0017	1990	5	10	*Tursiops truncatus*	F	33º12’N	117º23’W
TDL0128	1990	5	21	Unidentified dolphin or porpoise	U	33º16’N	117º27’W
KZP0018	1990	8	3	*Tursiops truncatus*	F	32º54’N	117º15’W
KZP0019	1990	8	4	*Tursiops truncatus*	M	32º39’N	117º09’W
KZP0020	1990	8	13	*Tursiops truncatus*	F	32º50’N	117º17’W
JVK0044	1990	9	16	*Globicephala macrorhynchus*	F	32º37’N	117º08’W
JVK0045	1991	1	5	*Lagenorhynchus obliquidens*	F	33º03’N	117º18’W
JEH0429	1991	1	8	*Grampus griseus*	M	32º51’N	117º17’W
JEH0431	1991	3	10	*Eschrichtius robustus*	M	33º16’N	117º27’W
JVK0046	1991	5	17	*Tursiops truncatus*	F	33º08’N	117º20’W
JVK0047	1991	6	5	*Tursiops truncatus*	F	32º50’N	117º17’W
JVK0049	1992	1	6	*Delphinus delphis*	F	32º52’N	117º15’W
TDL0149	1992	1	28	*Eschrichtius robustus*	M	33º16’N	117º27’W
JVK0050	1992	2	25	*Tursiops truncatus*	M	32º49’N	117º16’W
JVK0051	1992	4	29	*Eschrichtius robustus*	M	32º43’N	117º13’W
JVK0052	1992	5	31	*Lagenorhynchus obliquidens*	M	33º02’N	117º17’W
XXX0011	1992	6	26	Unidentified dolphin or porpoise	U	32º59’N	117º16’W
JVK0053	1992	7	16	*Tursiops truncatus*	F	33º22’N	117º34’W
WTN0003	1992	8	13	*Tursiops truncatus*	F	32º34’N	117º08’W
WTN0004	1992	10	9	*Tursiops truncatus*	M	32º35’N	117º08’W
WTN0005	1992	10	15	*Delphinus capensis*	M	32º52’N	117º15’W
WTN0006	1992	11	4	*Delphinus capensis*	F	32º46’N	117º15’W
WTN0009	1993	1	9	*Delphinus capensis*	F	32º54’N	117º15’W
WTN0011	1993	1	16	*Eschrichtius robustus*	M	32º57’N	117º16’W
KZP0032	1993	1	26	*Eschrichtius robustus*	M	32º38’N	117º08’W
WTN0013	1993	3	28	*Delphinus delphis*	F	33º13’N	117º24’W
XXX0027	1993	4	2	Unidentified dolphin or porpoise	U	33º17’N	117º26’W
JEH0445	1993	5	21	*Kogia breviceps*	M	Region 6	-
WTN0019	1993	5	28	*Delphinus delphis*	M	33º09’N	117º21’W
WTN0020	1993	6	25	*Tursiops truncatus*	M	32º37’N	117º08’W
KZP0023	1993	8	8	*Tursiops truncatus*	F	32º37’N	117º08’W
KZP0024	1993	8	9	*Tursiops truncatus*	M	32º36’N	117º08’W
KZP0025	1993	8	11	*Tursiops truncatus*	M	32º35’N	117º08’W
KZP0026	1993	8	31	*Tursiops truncatus*	M	32º37’N	117º08’W

Cont.

Specimen	Year	Month	Day	Species	Sex	Latitude	Longitude
KZP0027	1993	9	5	*Lagenorhynchus obliquidens*	U	32º37’N	117º08’W
KZP0028	1993	9	21	*Delphinus delphis*	M	32º35’N	117º08’W
KZP0029	1993	9	28	*Lagenorhynchus obliquidens*	F	32º52’N	117º15’W
KZP0030	1993	11	15	*Balaenoptera physalus*	M	32º50’N	117º17’W
KZP0031	1994	1	25	*Eschrichtius robustus*	F	32º58’N	117º16’W
JEH0449	1994	1	26	*Eschrichtius robustus*	M	Region 1	-
XXX0017	1994	3	7	*Eschrichtius robustus*	U	Region 4	-
SWC-Dc-9426B	1994	4	7	*Delphinus capensis*	M	33º06’N	117º19’W
KZP0034	1994	7	7	*Delphinus delphis*	F	33º06’N	117º19’W
SW94076	1994	7	31	*Delphinus* sp.	M	32º51’N	117º15’W
SWC-Dd-9493B	1994	8	22	*Delphinus* sp.	F	32º41’N	117º11’W
MZH0007	1994	9	5	*Delphinus delphis*	F	33º22’N	117º34’W
MZH0011	1995	2	16	*Delphinus delphis*	M	32º33’N	117º08’W
MZH0012	1995	3	3	*Delphinus delphis*	F	33º08’N	117º20’W
MZH0013	1995	3	6	*Eschrichtius robustus*	U	32º43’N	117º15’W
KZP0035	1995	3	9	*Tursiops truncatus*	F	32º53’N	117º15’W
TDL0190	1995	3	13	*Delphinus capensis*	F	Region 11	-
MZH0014	1995	3	20	*Stenella coeruleoalba*	M	32º35’N	117º08’W
MZH0016	1995	4	10	*Delphinus delphis*	U	33º07’N	117º19’W
MZH0017	1995	4	20	*Lagenorhynchus obliquidens*	F	32º33’N	117º08’W
MZH0018	1995	5	4	*Delphinus delphis*	F	32º53’N	117º15’W
MZH0019	1995	5	15	*Delphinus delphis*	F	32º35’N	117º08’W
MZH0022	1995	5	16	*Delphinus capensis*	F	32º45’N	117º15’W
SW9543	1995	6	5	*Tursiops truncatus*	F	32º51’N	117º15’W
SW95034	1995	7	11	*Delphinus capensis*	M	33º09’N	117º21’W
MZH0024	1995	7	27	*Tursiops truncatus*	F	33º00’N	117º17’W
MZH0023	1995	7	28	*Delphinus delphis*	U	32º47’N	117º15’W
KZP0036	1995	8	10	*Delphinus delphis*	U	32º55’N	117º15’W
MZH0026	1995	8	16	*Tursiops truncatus*	M	32º52’N	117º15’W
MZH0027	1995	9	5	*Tursiops truncatus*	M	33º00’N	117º16’W
KZP0039	1995	10	9	*Kogia breviceps*	F	32º54’N	117º15’W
KZP0042	1996	2	1	*Eschrichtius robustus*	F	33º01’N	117º17’W
MZH0033	1996	2	2	*Delphinus* sp.	M	32º46’N	117º14’W
MZH0035	1996	3	15	*Lagenorhynchus obliquidens*	M	32º32’N	117º07’W
MZH0034	1996	5	7	*Delphinus delphis*	F	33º08’N	117º20’W
MZH0037	1996	5	14	*Delphinus* sp.	M	32º57’N	117º16’W
KZP0043	1996	6	4	*Delphinus* sp.	F	33º09’N	117º21’W
MZH0036	1996	6	12	*Eschrichtius robustus*	M	32º36’N	117º08’W
KZP0044	1996	7	2	*Tursiops truncatus*	M	32º58’N	117º16’W
KZP0050	1997	1	20	*Eschrichtius robustus*	M	32º43’N	117º16’W
KZP0046	1997	1	27	*Delphinus delphis*	M	32º48’N	117º15’W
KZP0047	1997	4	17	*Eschrichtius robustus*	F	32º39’N	117º08’W
XXX0029	1997	5	6	Unidentified dolphin or porpoise	U	32º41’N	117º11’W
SW97042	1997	6	22	*Delphinus* sp.	M	32º39’N	117º09’W
MZH0041	1997	7	7	*Tursiops truncatus*	F	32º38’N	117º08’W
MZH0042	1997	7	15	*Delphinus delphis*	M	32º38’N	117º08’W
KZP0049	1997	10	2	*Ziphius cavirostris*	M	32º37’N	117º08’W
MZH0045	1998	2	3	*Eschrichtius robustus*	F	32º45’N	117º15’W
SW98033	1998	3	20	*Delphinus* sp.	M	32º47’N	117º15’W
KZP0051	1998	3	27	*Kogia breviceps*	F	32º40’N	117º14’W
SW98083	1998	4	19	*Phocoenoides dalli*	M	32º41’N	117º11’W
KZP0052	1998	5	7	*Delphinus capensis*	M	33º14’N	117º25’W
MZH0047	1998	5	12	*Tursiops truncatus*	M	32º39’N	117º08’W
XXX0032	1998	5	17	*Delphinus* sp.	F	Region 1	-
MZH0050	1998	8	3	*Kogia breviceps*	M	33º22’N	117º34’W
MZH0051	1998	9	8	*Balaenoptera physalus*	F	32º36’N	117º07’W
MZH0053	1998	9	18	*Delphinus delphis*	M	32º51’N	117º16’W
MZH0046	1998	9	29	*Lissodelphis borealis*	M	33º14’N	117º25’W
KZP0055	1998	11	9	*Eschrichtius robustus*	M	33º01’N	117º17’W
KZP0056	1998	12	2	*Eschrichtius robustus*	M	33º12’N	117º23’W
KZP0057	1998	12	6	*Delphinus capensis*	M	32º51’N	117º15’W
XXX0033	1998	12	22	Unidentified cetacean	U	Region 10	-
XXX0034	1998	12	27	*Eschrichtius robustus*	U	33º23’N	117º35’W
KZP0058	1999	1	13	*Eschrichtius robustus*	F	32º49’N	117º17’W
XXX0036	1999	1	14	*Eschrichtius robustus*	U	32º41’N	117º15’W
KZP0059	1999	1	28	*Lagenorhynchus obliquidens*	F	32º50’N	117º17’W
KZP0060	1999	2	10	*Eschrichtius robustus*	F	32º55’N	117º15’W
XXX0037	1999	2	19	*Eschrichtius robustus*	U	Region 3	-
KZP0061	1999	2	25	*Delphinus delphis*	F	32º57’N	117º16’W
XXX0038	1999	4	8	Unidentified dolphin or porpoise	U	32º59’N	117º16’W
KZP0062	1999	4	9	*Delphinus delphis*	F	33º09’N	117º20’W
KZP0063	1999	4	28	*Delphinus capensis*	M	32º35’N	117º08’W
XXX0039	1999	5	3	Unidentified dolphin or porpoise	U	Region 10	-
XXX0040	1999	6	1	*Eschrichtius robustus*	U	33º23’N	117º35’W
SW99031	1999	6	2	*Kogia breviceps*	F	32º48’N	117º15’W
XXX0041	1999	6	13	Unidentified dolphin or porpoise	U	Region 8	-

Cont.

Specimen	Year	Month	Day	Species	Sex	Latitude	Longitude
KZP0064	1999	6	21	*Delphinus capensis*	F	33º04’N	117º18’W
KZP0065	1999	7	25	*Tursiops truncatus*	M	33º22’N	117º33’W
SJC0001	1999	7	31	*Eschrichtius robustus*	M	33º15’N	117º26’W
SJC0002	1999	8	3	*Delphinus delphis*	M	33º01’N	117º17’W
KZP0067	1999	9	13	*Eschrichtius robustus*	M	33º09’N	117º21’W
KZP0068	1999	12	12	*Eschrichtius robustus*	F	32º40’N	117º14’W
XXX0064	2000	1	-	*Tursiops truncatus*	U	Region 1	-
XXX0072	2000	2	1	*Eschrichtius robustus*	U	-	-
KZP0069	2000	2	3	*Tursiops truncatus*	F	33º03’N	117º18’W
KXD0001	2000	2	11	*Eschrichtius robustus*	M	32º40’N	117º09’W
KXD0002	2000	2	16	*Delphinus capensis*	F	33º22’N	117º33’W
KXD0003	2000	3	24	*Tursiops truncatus*	M	32º35’N	117º08’W
KZP0070	2000	4	2	*Eschrichtius robustus*	M	33º17’N	117º28’W
KXD0004	2000	4	12	*Delphinus delphis*	M	33º22’N	117º34’W
KZP0072	2000	4	12	*Delphinus delphis*	F	33º12’N	117º23’W
KZP0073	2000	4	17	*Tursiops truncatus*	M	32º44’N	117º15’W
KZP0074	2000	4	26	*Eschrichtius robustus*	F	32º40’N	117º14’W
DSJ1877	2000	6	9	*Delphinus capensis*	F	33º21’N	117º32’W
KZP0075	2000	8	16	*Tursiops truncatus*	F	32º56’N	117º15’W
KZP0076	2000	10	6	*Eschrichtius robustus*	M	33º1’N	117º17’W
SW00162	2000	12	12	*Delphinus delphis*	M	33º01’N	117º17’W
KZP0077	2000	12	31	*Delphinus capensis*	M	33º1’N	117º17’W
KZP0078	2001	2	8	*Tursiops truncatus*	F	33º18’N	117º28’W
KXD0007	2001	2	26	*Lagenorhynchus obliquidens*	M	32º53’N	117º15’W
SWC-Dd-0116B	2001	3	7	*Delphinus delphis*	F	32º53’N	117º15’W
SW01072	2001	3	10	*Delphinus delphis*	F	33º02’N	117º18’W
KXD0010	2001	3	20	*Lagenorhynchus obliquidens*	M	32º36’N	117º08’W
KXD0012	2001	3	27	*Phocoenoides dalli*	M	33º07’N	117º20’W
KXD0014	2001	5	17	*Tursiops truncatus*	F	33º04’N	117º18’W
KZP0080	2001	5	23	*Lissodelphis borealis*	F	32º47’N	117º15’W
KZP0081	2001	6	14	*Grampus griseus*	F	33º05’N	117º19’W
KZP0082	2001	6	25	*Delphinus capensis*	M	32º53’N	117º15’W
KZP0083	2001	6	27	*Delphinus delphis*	U	33º04’N	117º18’W
KZP0084	2001	7	16	*Tursiops truncatus*	F	33º02’N	117º17’W
KZP0086	2001	7	25	*Tursiops truncatus*	M	32º34’N	117º08’W
XXX0044	2001	8	5	*Delphinus* sp.	M	32º33’N	117º08’W
KZP0087	2001	8	18	*Delphinus capensis*	M	32º51’N	117º15’W
KZP0088	2001	8	29	*Balaenoptera physalus*	F	33º22’N	117º34’W
SW01245	2001	9	4	*Delphinus* sp.	M	32º52’N	117º15’W
KXD0015	2001	11	26	*Delphinus capensis*	F	33º21’N	117º32’W
XXX0065	2001	11	-	*Tursiops truncatus*	U	Region 3	-
KXD0016	2001	12	4	*Tursiops truncatus*	F	32º41’N	117º11’W
KXD0017	2001	12	7	*Lissodelphis borealis*	F	32º37’N	117º08’W
KZP0089	2001	12	11	*Megaptera novaeangliae*	F	32º50’N	117º17’W
KXD0019	2002	1	17	*Ziphius cavirostris*	F	33º15’N	117º26’W
KXD0020	2002	2	7	*Grampus griseus*	M	33º22’N	117º34’W
KXD0025	2002	4	23	*Tursiops truncatus*	F	32º37’N	117º08’W
KXD0029	2002	5	22	*Delphinus capensis*	F	33º13’N	117º24’W
KXD0028	2002	5	22	*Delphinus capensis*	F	33º13’N	117º24’W
SWC-Dsp-DOA-5-26-02	2002	5	26	*Delphinus delphis*	M	32º54’N	117º15’W
XXX0045	2002	5	27	Unidentified dolphin or porpoise	U	32º59’N	117º16’W
KZP0090	2002	6	2	*Delphinus capensis*	F	33º04’N	117º18’W
DSJ1990	2002	6	19	*Ziphius cavirostris*	F	33º20’N	117º31’W
KXD0037	2002	7	-	*Delphinus delphis*	F	33º14’N	117º25’W
KXD0032	2002	8	23	*Tursiops truncatus*	F	32º53’N	117º15’W
KXD0033	2002	10	10	*Balaenoptera musculus*	M	33º15’N	117º26’W
KXD0034	2002	10	22	*Delphinus capensis*	M	32º34’N	117º08’W
KXD0035	2002	10	23	*Eschrichtius robustus*	M	33º02’N	117º18’W
KXD0036	2002	11	2	*Lissodelphis borealis*	F	32º52’N	117º15’W
SWC-Tt-02221B	2002	11	6	*Tursiops truncatus*	M	32º46’N	117º13’W
KXD0039	2003	2	19	*Eschrichtius robustus*	M	32º52’N	117º15’W
KXD0040	2003	2	24	*Delphinus capensis*	F	33º11’N	117º23’W
KXD0041	2003	3	7	*Delphinus delphis*	M	32º37’N	117º08’W
KXD0042	2003	3	13	*Tursiops truncatus*	M	33º18’N	117º29’W
KXD0044	2003	4	23	*Delphinus capensis*	M	33º18’N	117º28’W
KXD0045	2003	5	29	*Delphinus capensis*	F	32º45’N	117º15’W
XXX0046	2003	5	31	Unidentified dolphin or porpoise	U	33º23’N	117º35’W
XXX0047	2003	6	6	Unidentified dolphin or porpoise	U	33º09’N	117º21’W
KXD0046	2003	6	11	*Delphinus delphis*	F	33º14’N	117º25’W
KXD0047	2003	6	22	*Tursiops truncatus*	F	32º41’N	117º11’W
SW03585	2003	6	23	*Delphinus delphis*	M	32º46’N	117º15’W
KXD0048	2003	6	23	*Tursiops truncatus*	F	32º41’N	117º12’W
KXD0051	2003	10	1	*Balaenoptera physalus*	M	32º39’N	117º15’W
KXD0052	2003	10	15	*Delphinus capensis*	F	32º40’N	117º10’W
SW03921	2003	11	1	*Delphinus delphis*	M	33º23’N	117º35’W
KXD0053	2003	11	3	*Delphinus delphis*	M	32º45’N	117º15’W

Cont.

Specimen	Year	Month	Day	Species	Sex	Latitude	Longitude
KXD0054	2003	11	4	*Delphinus delphis*	F	32º59’N	117º16’W
SW04002	2004	1	5	*Delphinus delphis*	F	33º23’N	117º35’W
KXD0055	2004	1	6	*Delphinus capensis*	M	33º07’N	117º20’W
KXD0057	2004	3	5	*Lagenorhynchus obliquidens*	F	33º07’N	117º20’W
KXD0058	2004	3	5	*Delphinus capensis*	M	32º41’N	117º14’W
KXD0059	2004	3	13	*Delphinus delphis*	M	33º00’N	117º16’W
SW04240	2004	3	26	*Delphinus capensis*	F	32º52’N	117º15’W
KXD0061	2004	4	7	*Tursiops truncatus*	M	33º23’N	117º36’W
KXD0060	2004	4	7	*Eschrichtius robustus*	M	33º02’N	117º17’W
KXD0062	2004	4	13	*Delphinus capensis*	U	33º01’N	117º17’W
SW04392	2004	4	29	*Delphinus delphis*	M	32º41’N	117º11’W
KXD0066	2004	5	19	*Delphinus capensis*	M	33º13’N	117º24’W
KXD0067	2004	6	18	*Delphinus delphis*	F	33º01’N	117º17’W
KXD0068	2004	6	23	*Delphinus delphis*	M	33º13’N	117º24’W
KXD0069	2004	7	9	*Delphinus capensis*	F	32º52’N	117º15’W
KXD0073	2004	8	5	*Delphinus delphis*	F	33º15’N	117º26’W
XXX0074	2004	8	13	Unidentified large whale	U	-	-
KXD0074	2004	8	19	*Phocoenoides dalli*	F	32º52’N	117º15’W
KXD0075	2004	8	26	*Delphinus capensis*	F	32º52’N	117º15’W
XXX0049	2004	8	28	*Balaenoptera*	U	Region 4	-
XXX0048	2004	8	28	Unidentified dolphin or porpoise	U	-	-
KXD0077	2004	8	30	*Delphinus capensis*	F	33º14’N	117º25’W
SW041118	2004	9	29	*Delphinus delphis*	M	33º09’N	117º21’W
SW041182	2004	10	27	*Delphinus* sp.	M	32º32’N	117º07’W
KXD0080	2004	11	17	*Tursiops truncatus*	M	32º41’N	117º13’W
KXD0081	2004	11	26	*Eschrichtius robustus*	M	32º47’N	117º15’W
KXD0082	2004	12	26	*Tursiops truncatus*	U	32º36’N	117º08’W
XXX0050	2005	1	1	*Delphinus* sp.	U	Region 5	-
XXX0051	2005	1	7	Unidentified cetacean	U	32º32’N	117º07’W
KXD0083	2005	2	13	*Delphinus capensis*	M	33º05’N	117º19’W
KXD0084	2005	3	1	*Delphinus capensis*	F	33º10’N	117º22’W
KXD0086	2005	3	23	*Delphinus delphis*	M	33º09’N	117º21’W
SJC0012	2005	4	7	*Delphinus capensis*	M	32º53’N	117º15’W
KXD0087	2005	4	22	*Delphinus delphis*	F	32º56’N	117º15’W
KXD0088	2005	4	24	*Phocoena phocoena*	F	32º41’N	117º11’W
KXD0090	2005	5	6	*Delphinus delphis*	M	33º04’N	117º18’W
KXD0091	2005	5	9	*Delphinus delphis*	M	32º53’N	117º15’W
KXD0093	2005	5	30	*Tursiops truncatus*	M	33º19’N	117º30’W
KXD0094	2005	6	15	*Tursiops truncatus*	M	32º32’N	117º07’W
KXD0095	2005	7	4	*Delphinus delphis*	M	33º06’N	117º19’W
SW050587	2005	7	10	*Delphinus delphis*	F	33º14’N	117º25’W
KXD0096	2005	7	14	*Delphinus delphis*	M	33º00’N	117º17’W
KXD0098	2005	10	16	*Tursiops truncatus*	F	33º06’N	117º19’W
KXD0099	2005	11	22	*Lagenorhynchus obliquidens*	M	32º37’N	117º08’W
KXD0100	2005	11	30	*Tursiops truncatus*	F	32º34’N	117º08’W
SW060088	2006	2	15	*Lissodelphis borealis*	F	33º13’N	117º24’W
PMMC-L-06-02-18-001	2006	2	18	*Lissodelphis borealis*	M	33º24’N	117º36’W
KXD0101	2006	2	22	*Delphinus delphis*	F	33º20’N	117º30’W
KXD0102	2006	4	1	*Delphinus capensis*	M	33º14’N	117º25’W
KXD0103	2006	4	16	*Delphinus capensis*	M	33º18’N	117º28’W
SW060261	2006	4	16	*Delphinus capensis*	M	32º47’N	117º15’W
KXD0110	2006	4	21	*Delphinus capensis*	U	32º39’N	117º09’W
KXD0106	2006	5	13	*Eschrichtius robustus*	U	33º00’N	117º17’W
KXD0109	2006	6	1	*Phocoena phocoena*	F	32º36’N	117º08’W
XXX0054	2006	6	23	Unidentified dolphin or porpoise	U	Region 1	-
XXX0055	2006	7	24	Unidentified dolphin or porpoise	U	Region 10	-
NXH0001	2006	8	14	*Delphinus delphis*	U	32º56’N	117º16’W
SJC0015	2006	9	5	*Delphinus capensis*	F	32º55’N	117º15’W
KXD0112	2006	11	15	*Megaptera novaeangliae*	M	33º07’N	117º20’W
SW070013	2006	12	27	*Delphinus delphis*	F	32º46’N	117º15’W
KXD0113	2006	12	28	*Delphinus capensis*	F	33º14’N	117º25’W
NXH0003	2007	1	3	*Ziphius cavirostris*	M	32º38’N	117º08’W
KXD0117	2007	4	25	*Delphinus capensis*	M	32º51’N	117º16’W
KXD0118	2007	4	26	*Delphinus capensis*	M	33º03’N	117º18’W
KXD0119	2007	4	29	*Delphinus capensis*	F	33º13’N	117º25’W
KXD0120	2007	5	28	*Delphinus capensis*	M	33º12’N	117º24’W
KXD0122	2007	5	30	*Delphinus capensis*	M	33º06’N	117º19’W
SJC0016	2007	5	31	*Delphinus capensis*	M	33º12’N	117º24’W
KXD0123	2007	6	2	*Delphinus capensis*	M	33º11’N	117º22’W
KXD0124	2007	6	5	*Delphinus capensis*	M	33º12’N	117º23’W
SJC0017	2007	6	5	*Delphinus delphis*	M	32º38’N	117º09’W
KXD0125	2007	6	9	*Tursiops truncatus*	F	33º12’N	117º23’W
KXD0126	2007	6	14	*Tursiops truncatus*	F	33º17’N	117º28’W
SWC-Dd-07151B	2007	6	19	*Delphinus delphis*	M	32º55’N	117º16’W
KXD0129	2007	6	28	*Delphinus delphis*	F	33º06’N	117º19’W
KXD0128	2007	6	30	*Delphinus capensis*	M	32º37’N	117º08’W

Cont.

Specimen	Year	Month	Day	Species	Sex	Latitude	Longitude
KXD0130	2007	7	5	*Delphinus capensis*	F	33º09’N	117º21’W
KXD0136	2007	7	5	*Delphinus capensis*	U	32º37’N	117º06’W
KXD0131	2007	7	5	*Delphinus capensis*	F	32º36’N	117º07’W
KXD0132	2007	7	5	*Delphinus capensis*	F	32º36’N	117º07’W
KXD0133	2007	7	9	*Delphinus capensis*	F	32º38’N	117º09’W
KXD0135	2007	7	9	*Delphinus capensis*	M	32º38’N	117º08’W
KXD0134	2007	7	9	*Delphinus capensis*	M	32º37’N	117º08’W
KXD0137	2007	7	10	*Delphinus capensis*	M	32º36’N	117º08’W
KXD0138	2007	7	10	*Delphinus capensis*	M	32º36’N	117º08’W
KXD0139	2007	9	4	*Delphinus capensis*	M	32º35’N	117º08’W
KXD0140	2007	9	30	*Delphinus capensis*	F	32º14’N	117º25’W
SJC0019	2007	11	24	*Delphinus capensis*	M	33º09’N	117º21’W
KXD0141	2007	12	21	*Delphinus capensis*	F	33º08’N	117º20’W
KXD0143	2008	1	28	*Delphinus capensis*	M	33º05’N	117º19’W
KXD0144	2008	3	2	*Delphinus capensis*	M	32º34’N	117º08’W
KXD0145	2008	3	9	*Delphinus capensis*	F	33º10’N	117º22’W
KXD0146	2008	3	19	*Delphinus capensis*	F	32º37’N	117º08’W
KXD0147	2008	3	31	*Delphinus capensis*	M	33º08’N	117º20’W
NXH0004	2008	4	5	*Delphinus capensis*	M	33º10’N	117º22’W
KXD0148	2008	4	7	*Tursiops truncatus*	M	32º56’N	117º16’W
JLL0002	2008	5	13	*Lissodelphis borealis*	M	33º17’N	117º27’W
SJC0020	2008	5	14	*Delphinus capensis*	M	33º17’N	117º28’W
JLL0004	2008	5	20	*Tursiops truncatus*	M	32º37’N	117º08’W
JLL0005	2008	5	21	*Delphinus capensis*	F	32º52’N	117º15’W
JLL0007	2008	5	25	*Globicephala macrorhynchus*	M	32º35’N	117º18’W
JLL0006	2008	5	26	*Delphinus capensis*	F	32º38’N	117º08’W
KXD0150	2008	5	28	*Lagenorhynchus obliquidens*	M	33º06’N	117º19’W
JLL0009	2008	6	7	*Delphinus capensis*	M	32º54’N	117º15’W
KXD0152	2008	6	28	*Delphinus delphis*	F	33º13’N	117º24’W
KXD0153	2008	6	29	*Tursiops truncatus*	F	33º17’N	117º28’W
JLL0010	2008	6	30	*Tursiops truncatus*	M	32º34’N	117º08’W
KXD0156	2008	7	26	*Tursiops truncatus*	U	32º47’N	117º15’W
KXD0154	2008	8	1	*Delphinus delphis*	M	32º59’N	117º16’W
KXD0157	2008	8	7	*Grampus griseus*	F	33º04’N	117º18’W
KXD0158	2008	8	22	*Delphinus capensis*	F	33º11’N	117º23’W
SWC-Gg-08122B	2008	10	18	*Grampus griseus*	M	32º50’N	117º18’W
JHY0001	2008	10	21	*Lagenorhynchus obliquidens*	M	32º48’N	117º16’W
GSV0001	2008	10	26	*Delphinus capensis*	F	32º41’N	117º12’W
SW080913	2008	12	30	*Lagenorhynchus obliquidens*	F	32º51’N	117º16’W

Appendix II

List of stranded San Diego bottlenose dolphin specimens with preliminary stock designations

Specimen	SWFSC Lab ID	Stock
AAH0001	67829	Undetermined
CLH0050	67548	Coastal
CLH0051	67551	Coastal
CLH0052	67546	Coastal
HJB0019	67968	Coastal
HJB0036	61558	Coastal
HJB0040	17434	Undetermined
JEH0381	4371	Coastal
JLL0004	74330	Undetermined
JLL0010	74634	Undetermined
JRH0057	67963	Coastal
JRH0058	23310	Coastal
JRH0067	67833	Coastal
JRH0070	67834	Coastal
JRH0073	67962	Coastal
JRH0077	67835	Coastal
JRH0095	67837	Undetermined
JRH0098	67964	Coastal
JRH0192	67965	Coastal
JVK0046	60359	Coastal
JVK0047	221	Coastal
JVK0050	402	Coastal
JVK0053	743	Undetermined
KXD0014	23623	Undetermined
KXD0016	26136	Coastal
KXD0025	26708	Coastal
KXD0032	28448	Coastal
KXD0042	32003	Undetermined
KXD0047	34075	Coastal
KXD0048	34076	Undetermined
KXD0061	39626	Undetermined
KXD0080	43380	Coastal
KXD0082	44518	Coastal
KXD0093	47193	Coastal
KXD0094	47816	Undetermined
KXD0100	51613	Coastal
KXD0148	74224	Coastal
KXD0153	74636	Coastal
KXD0156	74702	Undetermined
KZP0008	4367	Coastal
KZP0010	60355	Coastal
KZP0012	60354	Coastal
KZP0017	300	Coastal
KZP0018	298	Coastal
KZP0019	60358	Undetermined
KZP0020	60357	Coastal
KZP0023	60363	Coastal
KZP0024	1693	Coastal
KZP0025	1694	Coastal
KZP0026	62360	Coastal
KZP0035	3886	Coastal
KZP0044	62361	Coastal
KZP0065	13354	Undetermined
KZP0069	17363	Coastal

Cont.

Specimen	SWFSC Lab ID	Stock
KZP0073	15493	Coastal
KZP0075	17108	Coastal
KZP0078	18934	Undetermined
KZP0084	24217	Coastal
KZP0086	24218	Coastal
LJH0006	67840	Coastal
MSL0267	67842	Undetermined
MSL0269	67843	Undetermined
MZH0024	4507	Undetermined
MZH0026	11198	Coastal
MZH0027	4533	Coastal
MZH0041	62363	Coastal
MZH0047	9804	Undetermined
RMG4551	67955	Coastal
RMG4797	67549	Coastal
SDNHM21213	67547	Coastal
SW9543	4199	Undetermined
SWC-Tt-02221B	29881	Coastal
WFP0036	67956	Coastal
WFP0278	67957	Coastal
WFP0474	60352	Coastal
WFP0475	60351	Coastal
WFP0509	67958	Coastal
WFP0559	61559	Coastal
WFP0563	62462	Coastal
WFP0565	62463	Undetermined
WTN0001	632	Coastal
WTN0003	633	Coastal
WTN0004	4368	Undetermined

Commercial and subsistence harvests of bowhead whales (*Balaena mysticetus*) in eastern Canada and West Greenland

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ABSTRACT

Commercial harvesting of bowhead whales (*Balaena mysticetus*) from the eastern Canada-West Greenland population started with Basque whalers in the Strait of Belle Isle *ca* 1530 AD. Subsistence harvests have an even longer history, and the first culture to be active bowhead whalers was the Thule, which replaced the Dorset culture in the central and eastern Arctic *ca* 1200 AD. Previous harvest compilations have been incomplete, and back-calculated population models have thus been negatively biased. In recent decades this population has shown significant recovery and is the subject of Inuit subsistence harvests in both Canada and West Greenland. A revised historic abundance estimate is needed to examine the level of recovery; this requires *inter alia* a revised and updated catch series. Available information from multiple anthropological, archaeological, historic and recent sources, and estimate commercial and subsistence harvests in eastern Canada and West Greenland is summarised. From 1530–1915, commercial whalers took an estimated 55,916–67,537 (median 61,537) bowhead whales (varying assumptions on the intensity of the Basque harvest), which is known to be incomplete. Inuit harvests before commercial whaling began (1200–1529 AD) were estimated at 11,435 whales, based on the abundance of whale bone at winter houses excavated by archaeologists. After 1500 AD, Inuit whaling declined, and the total estimated harvest between 1530 AD and the end of commercial whaling was 8,406 whales. Inuit whaling declined again after commercial whalers overharvested the population and only 65 whales are known to have been harvested (or struck and lost) from 1918–2009. The Inuit harvest statistics are based on scattered data and a number of assumptions, with some evidence that at least parts of the series are underestimated. Even if harvests were higher, they would have probably not been large enough to cause population declines. The long tradition of Inuit bowhead whaling was negatively impacted by commercial harvests. Combining all harvests from 1530–2009 AD results in a total estimated kill of some 70,000 whales (not including struck and lost whales and known gaps for some nations and eras), with most (88%) taken by commercial whalers. Data quality varies considerably by nation and era, and was assigned to a 3-point scale for reliability, with over half the harvest considered to be the least reliable. This is the most comprehensive summary and estimate of bowhead harvests for this region, but is still known to be incomplete and is based on a number of assumptions and disparate data sources.

KEYWORDS: STATISTICS; WHALING – ABORIGINAL; WHALING – HISTORICAL; WHALING – REVISED CATCHES; ARCTIC OCEAN; ATLANTIC OCEAN; MODELLING

INTRODUCTION

The bowhead or Greenland right whale (*Balaena mysticetus*), found in circumpolar waters, is the most northerly distributed baleen whale. Both it and the closely-related North Atlantic right whale (*Eubalaena glacialis*) were long considered the 'right' whales to hunt, and the data series of commercial harvests for these species are the longest of all cetaceans. COSEWIC (Committee on the Status of Endangered Wildlife in Canada) formerly considered two eastern Canadian populations (Davis Strait-Baffin Bay and Hudson Bay-Foxe Basin), both 'Threatened' (based on likely incomplete data). Recent genetic and satellite tagging data (Dueck *et al.*, 2006; Heide-Jørgensen *et al.*, 2006; 2003; Postma *et al.*, 2006) indicate that the bowhead whales in eastern Canada and West Greenland constitute a single population with considerable age and sex structuring. A single-stock hypothesis has also been tentatively endorsed by the IWC, pending genetic re-analysis (IWC, 2008). COSEWIC reassessed the status of bowhead whales in the eastern Arctic given the new information on stock structure (and abundance) and recently upgraded the eastern Canada-West Greenland (EC-WG) population to 'Special Concern' (COSEWIC, 2009). The population supports a limited subsistence hunt by Inuit in both Canada (Nunavik and Nunavut) and West Greenland.

Subsistence bowhead whaling by Thule Inuit in the central and eastern Arctic started *ca* 1200 AD following an eastward migration from Alaska originating *ca* 1000 AD. Commercial harvesting started with Basque whalers *ca* 1530 AD and ended with American and Scottish whalers in Hudson Bay in the early 1900s. This paper summarises the available harvest data for bowhead whales in the waters of eastern Canada and West Greenland. These data are mostly from published sources. Archived sources in museums will undoubtedly provide further information; however such diligent research is beyond the scope of this manuscript.

Catch series are an important component of population assessments, along with an understanding of stock structure and present abundance. In particular, they allow the estimation of the unexploited population size and thus can be used to assess the status of a population in relation to its past and present abundance. This, in turn, can affect whether and to what level catches can be allowed that meet management and conservation objectives. There have been several past attempts to estimate pre-whaling population size (reviewed by Woodby and Botkin, 1993). Mitchell (1977) used a three-step method that involved summing the number of whales killed during the peak decade, correcting upwards for struck and lost whales, and estimating the residual population after the peak decade, based on the number of whales harvested in following decades. Using this method, Mitchell (1977) estimated the Davis Strait 'stock' to be about 6,000 whales in 1729 and the Hudson Bay 'stock' about 680 in 1859. The Davis Strait estimate was subsequently revised

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to 11,000 in 1825 (Mitchell and Reeves, 1981). Woodby and Botkin (1993) used a simple population model and estimated similar pre-exploitation population sizes. The IWC Scientific Committee now uses a 'management procedure approach' (e.g. Punt and Donovan, 2007) that explicitly takes uncertainty into account. It is therefore important that catch history series are carefully reviewed and uncertainties identified. More complete harvest data will provide better assessments and ultimately management advice.

A number of different nations harvested bowhead whales, and the harvest series is far from complete with the availability of harvest records varying considerably amongst nations and eras. In addition, there are limitations associated with the available data on commercial bowhead whaling (see Ross, 1979a; 1979b). There are also a number of errors in many whaling sources, for example, see Schevill (1957) on Sanderson (1956) ('an irresponsible book… Ivan Sanderson's carelessness is evident…'), Barkham (1994) on Proulx (1993), Sanger (1985) on Jenkins (1971) and Jackson (1978) (which, despite being one of the best sources on British whaling, still contains a number of errors), and Higdon (2008a) on Romero and Kannada (2006). Ultimately, nearly all sources and most major commentaries are flawed to some extent.

A number of different native cultures have inhabited the Canadian eastern Arctic and West Greenland (e.g. McGhee, 1990; Stoker and Krupnik, 1993). The Thule, the first culture to be active bowhead whalers, migrated eastward from Alaska *ca* 1000 AD and arrived in the central and eastern Arctic *ca* 1200 AD (Friesen, 2004; Park, 2000; Savelle and McCartney, 1990). Inuit in West Greenland and eastern Canada traditionally used bowhead whales for subsistence, and bones were used in the construction of winter houses (Kaplan, 1985; Savelle and McCartney, 1990; Taylor, 1988). Blubber and baleen were also traded to Euroamerican whalers and traders. Inuit harvests themselves probably did not have significant negative effects on bowhead whale population sizes, given the small populations of hunters and the selection for young whales (McCartney and Savelle, 1985; 1993; Savelle and McCartney, 1991; 1994). However, when taken in concert with commercial whaling after *ca* 1530, subsistence removals are part of the cumulative effect on population size and should therefore be included in any harvest series. Apart from in recent years, there is little documentation of Inuit harvests, and no harvest series exist.

Research efforts on the Thule and historic Inuit cultures have seldom been designed to examine whaling in a quantitative manner, but rather have been site-specific studies designed around cultural-historic questions (Savelle and McCartney, 1990). This makes it difficult to quantify the importance of bowhead whales to the Thule and historic Inuit cultures. For the purposes of reconstructing harvests to estimate pre-commercial exploitation population size, kills during the classic Thule phase (the peak of aboriginal bowhead whaling, occurring prior to commercial exploitation) are not relevant. However, knowledge of the importance of bowhead whales to early Thule culture adds context to the estimates of harvests after 1530 AD.

The harvest data are summarised by nation and divided into two broad sections – 'Euroamerican' (c.f. Caulfield, 1993) and Inuit subsistence whaling. The first European bowhead whalers were Norse settlers in West Greenland from 986 until *ca* 1500 AD (Jones, 1986). The settlers used whales for subsistence purposes (Degerbol, 1936; Enghoff, 2003; McGovern *et al.*, 1996), but the number of animals harvested is not known. However it was probably small and occurred prior to the establishment of commercial whaling; thus no harvest data are included here. Commercial efforts of all nations were influenced by numerous political, social and economic factors that are beyond the scope of this review. A number of sources are available, including Jackson (1978), Ross (1993) and Scoresby (1820). A preliminary version of this study is available as a Canadian Science Advisory Secretariat Research Document produced by the Government of Canada (Higdon, 2008b).

EUROAMERICAN WHALING

Commercial whaling grounds

Commercial bowhead whaling in eastern Canada and West Greenland occurred on a number of different 'grounds' (see summaries by Reeves *et al.*, 1983; Ross, 1993). The geographical distribution of whaling was related to whale abundance but also changed in response to numerous socioeconomic and political factors (Ross, 1993). Nineteenth-century whalers had a detailed knowledge of bowhead distribution and migration patterns, and this knowledge allowed the fleets to establish itineraries for catching whales at different seasons and in different areas (Reeves *et al.*, 1983). The seven main grounds are shown in Fig. 1.

The first bowhead whaling ground in the western North Atlantic, the Strait of Belle Isle/Gulf of St. Lawrence area ('Grand Bay'), was used by the Basques starting *ca* 1530 and already in decline by the late 1500s (Barkham, 1984). A multi-nation fishery for bowheads on grounds along the West Greenland coast (to *ca* 73°N) was started by the Dutch and Germans in the late 1600s, although no catch data are available until 1719 (de Jong, 1978; 1983; Ross, 1979a). Shore stations were established by Danish colonists in the early 1700s, but most whales were taken in a spring and summer ship-based fishery centered near the West Greenland coast (Reeves *et al.*, 1983). This included much of the Davis Strait whaling conducted by the Dutch, Germans and British (particularly prior to 1817 when the western Baffin Bay fishery started). Many important grounds on the 'east side' (i.e. Greenland side of Davis Strait) were depleted by the early 1800s (Reeves *et al.*, 1983).

The 'south-west fishing' grounds, centered on the pack ice edge in the Resolution Island area, were an alternative to the West Greenland ('east side') grounds in the spring. The whaling occurred at the mouth of Hudson Strait, along the southeast coast of Baffin Island to Cumberland Sound, and along the northeast coast of Labrador (Reeves *et al.*, 1983). This was among the most difficult fisheries to prosecute (Scoresby, 1820), since although large numbers of whales were seen, they were hard to catch because of the weather and the ice (Gray, 1888). Whaling could start as early as April and often lasted through June (Reeves *et al.*, 1983), with whales sometimes still caught as late as July in icy conditions near the Labrador coast (Scoresby, 1820).

The 'west water' was a summer fishery conducted in the vicinity of Pond Inlet, the Lancaster Sound region, Prince Regent Inlet and the northern Gulf of Boothia. The fishery

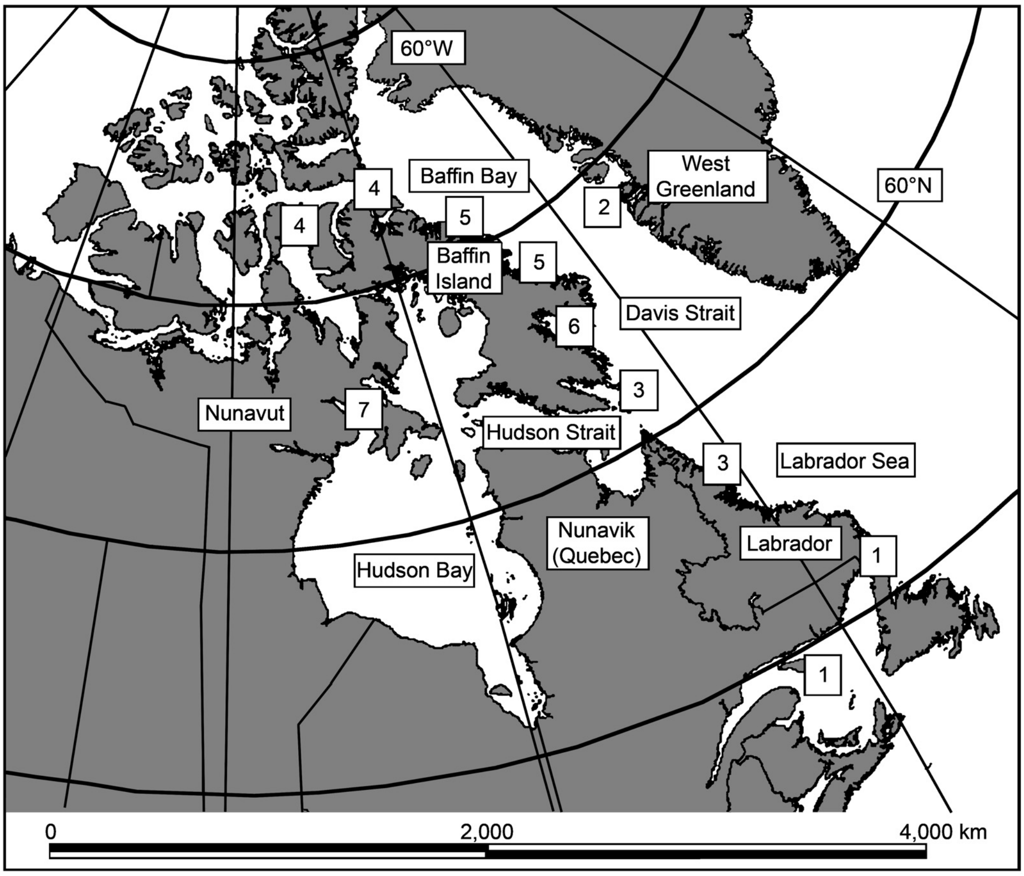

Fig. 1. Map of the eastern Arctic showing the seven main whaling grounds: 1) Strait of Belle Isle/Gulf of St. Lawrence ('Grand Bay'); 2) the West Greenland coast, or 'east side' grounds; 3) the spring 'south-west fishing' grounds, including the northeast coast of Labrador, the mouth of Hudson Strait, and southeast Baffin Island; 4) the summer 'west water' grounds, including Pond Inlet, the Lancaster Sound region, and Prince Regent Inlet; 5) the autumn 'rock-nosing' grounds along the entire east coast of Baffin Island; 6) Cumberland Sound, a spring and fall fishery; and 7) northwestern Hudson Bay.

started in 1817 when Scottish vessels first penetrated the Melville Bay ice and crossed Baffin Bay (Ross, 1979a; 1993). Large whales were often present off the mouth of Pond Inlet (Smith, 1922) and most catches were made here from early June to early September (Brown, 1868; Low, 1906). A number of authors have written about the abundance of whales in Prince Regent Inlet and the northern Gulf of Boothia during July, August and early September (reviewed by Reeves *et al.*, 1983). Some years were 'closed seasons', in which the land-floe persisted in western Baffin Bay and blocked the entrances to Pond Inlet and Lancaster Sound. Large numbers of whales would aggregate along the land-floe when their westward migration was blocked; and harvests were often high but comprised of small (young) whales (Finley and Darling, 1990; Lubbock, 1937; Reeves *et al.*, 1983).

The autumn 'rock-nosing' grounds were found along almost the entire east coast of Baffin Island. This was an inshore fishery undertaken by vessels that failed to fill their holds at the 'south-west fishing' or 'west water' grounds (Reeves *et al.*, 1983). Vessels would leave the Lancaster Sound area in late August or early September and some would remain on the grounds until November; by this time they would be rock-nosing in Cumberland Sound or south. In the late 1800s, Cumberland Sound also became an important ground for early and late-season whaling, often using shore-stations and with some overwintering (Ross, 1979a; 1993; Sanger, 2007). The last ground opened was northwest Hudson Bay, which had a short lifespan (1860–1915). American and Scottish vessels arrived in mid-August, whaled for a month before finding a winter harbour, and then started spring floe-edge whaling from whaleboats in May (Ross, 1974; 1979a).

Basque whalers

The Basques are an ethnic group who primarily inhabit an area known as the Greater Basque Country (*Euskal Herria* in the Basque language), located around the western end of the Pyrenees on the coast of the Bay of Biscay and straddling parts of northeastern Spain and southwestern France (Douglass and Bilbao, 2005). The ancestral Basque homelands encompass parts of each country, and while Basques living within Spanish borders are officially considered citizens of Spain, they consider themselves a separate group entirely (Kurlansky, 1999). The Basques first started whaling in the eastern Atlantic (Bay of Biscay) before moving to the northwest Atlantic. Basque whalers became established in the Strait of Belle Isle *ca* 1530 AD and were there on an annual basis until *ca* 1630 (Aguilar, 1986; Barkham, 1977; 1978; 1984; Cumbaa, 1986). The fishery peaked in the mid 1500s (the most productive decades were the 1560s and 1570s) and was in decline by the 1580s, with some ships returning half-empty (Aguilar, 1986; Barkham, 1984). Basque effort greatly diminished after *ca* 1590, and the north shore of the Strait of Belle Isle was abandoned by the early 1630s (Barkham, 1984). It was not until *ca* 1580 that the whalers extended their grounds west into the Gulf of St. Lawrence, an expansion that occurred after the peak whaling efforts (Barkham, 1978; McLeod *et al.*, 2008).

Basque whaling in Newfoundland and the Gulf of St. Lawrence officially ended in 1713 with the signing of the Treaty of Utrecht, although the industry had been in decline long before this time (however scattered French Basque vessels were still active along the north shore of the Gulf of St. Lawrence in the 1730s, Reeves and Mitchell, 1986). Most of the 20 known whaling stations were abandoned by the mid-1600s, but at least one station (Petit Mécatina, QC) was active into the early 1700s (McLeod *et al.*, 2008). Overhunting was one potential cause of whaling decline, but other factors such as conflict with local aboriginal peoples, rising taxes, alternative economic pursuits like cod fishing, and impressments of whaleships into naval service all played a role (reviewed by Ross, 1993). The opening of the Spitsbergen fishery in the early 1600s, with its large and previously unexploited whale stocks, was undoubtedly a major factor in the decline of Grand Bay whaling. Both English and Dutch vessels in Spitsbergen hired Basque whalers (de Jong, 1978; 1983; Jenkins, 1971).

Several authors have estimated the typical catch per year during the peak of Basque whaling. Using 12 whales per vessel and 20–30 vessels per year, Aguilar (1986) estimated a total yearly harvest of 300–500 whales (not including those struck and lost) and suggested that 25,000–40,000 whales were killed during the peak period of *ca* 1530–1610. Barkham (1984) used 15 ships per year (but acknowledged that there were likely at least 20 ships during the peak years), and an average capacity of 1,000 barrels per ship to estimate peak yields of 300 whales per year. Aguilar's (1986) fig. 4 provides a measure of Basque whaling effort, based on the number of extant manuscripts or written references as an index of activity. However, this must be used with caution as the relative abundance of documents is not necessarily correlated with whaling intensity. The number of documents written before 1530 was negligible (*ca* 3%). The proportion of written references (Aguilar, 1986) peaks from the 1550s to the 1570s, agreeing well with the peak in whaling activity as reported by Barkham (1984). Previous authors have assumed an approximate 50–50 split with bowheads and right whales, although recent evidence suggests that the harvest was in fact nearly all bowheads (see below).

Aguilar (1986) assumed an average yield of 12 whales per vessel, based on an average vessel capacity of 1,000 Spanish barrels and an average yield of 85 barrels per whale (which appears to represent an average or typical yield for both balaenid species). However he stated that 'the usual yield from a single whale was between 70 and 140 barrels of *fat*' (Aguilar, 1986, p.195), but then stated that each barrel contained '180 litres of *oil*' [my italics]. The capacity of a Spanish barrel was 180l, and a typical yield of 85 barrels would equal 15,300l of blubber or oil (range 12,600 to 25,200l for 70–140 barrels). Allen (1908) estimated the oil production for Spitsbergen bowheads as 80–100 hogsheads (hhd) per whale, a measure equivalent to 140l (or 11,200–14,000l per whale). If Aguilar (1986) was in fact referring to oil, then his estimates are much higher than Allen's. Scoresby (1820) stated that West Greenland whales delivered 14 tons or tuns (*ca* 13,350l or 95hhd) of oil on average, in agreement with Allen (1908) and considerably lower than Aguilar's (1986) estimate. It is assumed that Aguilar's (1986) typical yield of 85 Spanish barrels (or 109hhd) was in fact referring to barrels of blubber and not oil.

Table 1

Estimated Basque whale harvest (all species) in the Strait of Belle Isle and Gulf of St. Lawrence assuming the proportion of written references (Aguilar, 1986) represents actual whaling effort, with various assumptions as to the total number of whaling vessels (20, 25, or 30) during the peak harvest period 1551–75. Catch per year assumes an average vessel capacity of 12 whales (Aguilar, 1986). A small proportion of written references (*ca.* 3%) were dated pre-1530. Genetic data (McLeod *et al.*, 2008) indicate that nearly all (*ca.* 90%) whales were bowheads.

Period	Percentage of written references[1]	Harvest/year with different numbers of vessels during peak (1551–75)		
		20	25	30
1530–50	20.5	219	273	328
1551–75 (peak)	22.5	240	300	360
1576–1600	19.5	208	260	312
1601–25	10	107	133	160
1626–50	7	75	93	112
1651–75	11	117	147	176
1676–1700	4.5	48	60	72
1701–13	2	38	48	57
Total estimated harvest		**24,968**	**31,182**	**37,429**

[1] From fig. 4 of Aguilar (1986).

Basque whalers built tryworks on shore to render the oil (Aguilar, 1986) before returning to France or Spain. A 0.75 conversion factor, i.e. 3 tons of oil from 4 tons of blubber (Scoresby, 1820, see also Gad, 1973, p.221); of Aguilar's (1986) 85 barrel average results in 64 Spanish barrels (or 82hhd) of oil and is thus in closer agreement with Allen (1908) and Scoresby (1820). Assuming an average vessel capability of 1,000 Spanish barrels, as per Aguilar (1986) and Barkham (1984), a typical yield of 64 barrels of oil per whale would increase the capacity to about 16 whales per vessel. However, given the uncertainty around these estimates, Aguilar's (1986) more conservative estimate of 12 whales per ship is retained. Assuming this as a typical yield per vessel, Table 1 shows estimated Basque harvests from 1530–1713, using a range of peak vessel numbers and assuming the distribution of written records is representative of effort. An estimate of 25 vessels per year during the peak of Basque whaling effort equates to an average of 300 whales per year during the peak period. Estimates of 20 and 30 vessels results in yearly peak harvests of 260 or 360 whales per year, respectively, agreeing well with the estimates by Aguilar (Aguilar, 1986) and Barkham (1984).

Historical research has shown that there were two distinct Basque whaling periods, the summer season in June/July and the winter whaling season. During the early years of Basque whaling, the vessels generally returned to Europe after the summer season, but in the 1550s the whalers discovered an influx of whales that arrived in September/October, after which they began to stay for the winter whaling season (Huxley [Barkham] 1987 in McLeod *et al.*, 2008). The two seasons were typically interpreted as a right whale hunt in the summer and a bowhead hunt during the winter (Aguilar, 1986; Cumbaa, 1986). However given that the harvest was nearly all bowhead whales (see below), the distinct summer and winter whaling seasons likely represented sex- and/or age-based segregation and migration of the bowhead population (McLeod *et al.*, 2008). The summer seasonal hunt was largely abandoned by the mid-1570s (McLeod *et al.*, 2008).

The *San Juan* which sank in Red Bay, Labrador in autumn 1565 was discovered in the late 1970s (Barkham and Grenier, 1978). Excavation led to the recovery of a number of bones of whales that the Basques harvested in the 1500s (Barkham, 1984). Cumbaa (1986) examined humeri of 17 individuals, and osteological analysis suggested nine bowhead and eight right whales. However recent genetic analyses of these same bones have shown that the harvest was actually nearly all bowhead; Rastogi *et al.* (2004) analysed 21 humeri that had been identified using osteological analyses as eight bowheads and 13 right whales but their DNA analysis identified only one as a right whale and the remaining 20 as bowhead. The bones were from a minimum of 16 individuals – this suggests a harvest that was *ca* 94% bowhead whales. McLeod *et al.* (2006) present preliminary results of more extensive analyses than that of Rastogi *et al.* (2004). Analyses of 188 bones from 18 different sites indicate that 183 are from bowhead whales, one is from a right whale, and four are from other species (Frasier *et al.*, 2007). Additional genetic analyses have since been conducted on 218 bone samples, from 10 different sites (McLeod *et al.*, 2008). Five different species were present, and 203 of these bones (93%) were from bowhead whales. The 218 bones were from a minimum of 80 individuals, and 72 of these were bowheads (90%).

There is thus considerable evidence that the vast majority (≥90%) of Basque harvests were bowhead whales. Assuming a peak of 25 vessels (the midpoint of Table 1, also see Aguilar, 1986), 31,182 whales might have been harvested from 1530–1713, of which an estimated 28,075 were bowheads (assuming 90% of the total harvests). Assumed peak vessel numbers of 20 and 30 result in an estimated bowhead harvest of 22,454 and 33,683, respectively.

Aguilar (1986) suggested that 25,000–40,000 whales were taken from 1530–1610. In the present assessment, the harvests during this peak period are lower, with 67% of the total taken prior to 1610 (20,930 whales, 18,846 of which were bowheads). The proportion of written references per 25-year period declined after 1551–1575, which agrees with Barkham's (1984) suggestion of the peak of Basque whaling effort. However, it increased again after 1651 although Basque whaling had declined considerably by this time and most whaling stations had been abandoned (McLeod *et al.*, 2008). Much of the available written documentation may actually have been in reference to past whaling activities and may thus not be completely representative of Basque whaling effort. Nonetheless, the recent genetic analyses (McLeod *et al.*, 2008; McLeod *et al.*, 2006; Rastogi *et al.*, 2004) clearly indicate that large numbers of bowhead whales were taken by the Basque fleet. The relationship (in terms of population structure) between these whales and the current population is also unknown. They may have been a component of a wide-ranging stock such as found today, or they may have been from a geographically separate stock that was extirpated. Furthermore, at that time (the Little Ice Age, Fagan, 2000; Lamb, 1995), the climate may have been such that bowheads from Davis Strait, Baffin Bay and Hudson Bay, as found in the 1700s and later, were excluded from more northerly latitudes by heavy ice and thus had a more southerly distribution.

The harvest series estimated here ends in 1713, but both French and Spanish Basque vessels were active in Davis Strait after this time. French Basque reportedly started whaling in Davis Strait in 1719 (Du Pasquier, 1986), and both French and Spanish vessels were reported off Disko Bay, West Greenland, by the 1730s (Ciriquiain-Gaiztarro, 1961; Gad, 1973); no data was found for Spanish Basque harvests or effort in Davis Strait. Du Pasquier (1986) provides the number of French Arctic vessels known per year from 1613–1766, although the list is incomplete and the data sources available did not distinguish between grounds east and west of Greenland. French Basque vessels were also still occasionally present along the North Shore of the Gulf of St. Lawrence in the 1730s (Reeves and Mitchell, 1986). The French Basque Arctic fishery started to decline after the mid-1730s and ended in 1766 (du Pasquier, 1986). No estimate of Davis Strait harvests is included here.

Dutch whaling

Dutch whaling in Davis Strait started in the 1600s as an extension of their dominance on the Spitsbergen grounds. However harvest data are only available after 1719, when the trade became considerable enough to be distinguished from that which occurred east of Greenland (de Jong, 1978; 1983). In Davis Strait, the number of Dutch vessels peaked in 1732 (Vaughn, 1986). After this, numbers fluctuated, with a near-continuous decline after 1770 (de Jong, 1978). Both de Jong (de Jong, 1978; 1983) and Ross (Ross, 1979a) provide statistics on the number of vessels sailed and the number of whales flensed for the Davis Strait fishery. Ross (1979a) notes 3,329 voyages catching 7,644 whales from 1719–1826. De Jong's (1978; 1983) numbers are slightly higher, showing 3,348 Dutch vessels capturing 7,697 whales from 1719–1823. The harvest series used here is based on the source with the highest number of whales caught, with yearly gaps filled in from the other source where appropriate. De Jong (1978; 1983) includes more harvests than Ross (1979a), but this second source contains catch information for 1802 and 1824–1826, not included by de Jong (1978; 1983). Ross' (1979a) catches for these years were added to the de Jong (1978; 1983) series for a total Dutch catch of 7,699 whales from 1719–1826. This is an incomplete series and thus an underestimate, since, as noted above, Dutch traders and whalers were in West Greenland by the late 1600s (Kuup and Hart, 1976) but no data are available until after 1719. Additionally, Dutch whalers occasionally took right whales ('Noordkapers') in the 1700s while hunting for bowheads in Davis Strait (Reeves and Mitchell, 1986); thus estimates based on oil returns may include some unknown proportion of non-bowhead returns.

British whaling

Both England and Scotland have a long history of Arctic whaling. In the early 1600s, the English competed fiercely with the Dutch in the Spitsbergen fishery (Conway, 1904; 1906; de Jong, 1978; 1983; Ross, 1993). The Dutch eventually dominated and the English fleet essentially gave up whaling by 1650, returning in the 1700s after Davis Strait whaling had started. It is not possible to conclusively determine when the English first started Davis Strait whaling (Vaughn, 1986) but it was probably around 1750 when the British government increased the bounty for whaling vessels (Jackson, 1978; Ross, 1979a; 1993). English vessels also participated to some extent in whaling in the Strait of Belle Isle (Mitchell and Reeves, 1983). British whaling began to increase significantly in the 1770s as the Dutch fleet declined (Ross, 1993; Vaughn, 1986). In 1817, two Scottish vessels crossed to Baffin Island and caught a large number of whales, which led to the development of a new British fishery in Lancaster Sound and along the Baffin Island coast, involving a counter-clockwise circuit of Baffin Bay (Dunbar, 1972; Ross, 1979a; 1993; Vaughn, 1986; 1991). By the second half of the 19th century, the industry was dying, and only the Scots continued to outfit vessels. Scottish whalers continued to be successful because they expanded their harvest to other species such as white whales (*Delphinapterus leucas*) and seals and pioneered the use of steam-powered vessels (Jackson, 1978; Sanger, 1985).

Sanger (1985) presents harvest statistics for both Davis Strait and east of Greenland for 1750–1801, but for Scottish vessels only. In Davis Strait, 84 Scottish vessels caught 301 whales. Ross (1979a; 1993) presents British whaling data from 1814 onwards, using a variety of sources including whaling logbooks and the ‘Kinnes Lists’, a nearly continuous shipping list giving the particulars of whaling voyages, in the possession of the Dundee firm of Robert Kinnes and Sons. The Kinnes Lists begin in 1790 and end in 1911, but do not separate Davis Strait catches until 1814. Ross (1979a) included 20,043 whales harvested by 2,600 vessels (‘ship-seasons’) from 1814–1911. Ross (1979a) described the limitations in his approach, and was careful to note the provisional nature of his harvest series and that additional research was required. One source of uncertainty with these estimates is with the species composition. In the mid-1800s, some British vessels took humpback whales (*Megaptera novaeangliae*), and the practice of doing so may have occurred more frequently than is generally believed (Mitchell and Reeves, 1983). Davis Strait whalers also took right whales on occasion (Reeves and Mitchell, 1986).

Chesley Sanger (Memorial University of Newfoundland, St. John’s, NL) has provided unpublished data collected during his PhD research (Sanger, 1985) that adds to the harvest series presented by Ross (1979a). Sanger (unpublished data) includes Scottish harvests from 1751–1813 (1,519 whales, and includes the 1750–1801 data from Sanger, 1985), and both Scottish and English harvests from 1814–1910. Sanger (unpublished data) used the same Kinnes Lists as Ross (1979a) but updated this using other sources (mainly newspapers), particularly for the Scottish aspect of the fishery. Sanger (unpublished data) provides a total British harvest of 20,308 whales (12,111 by Scottish and 8,197 by English) secured by 2,607 vessels (1,659 Scottish and 948 English) from 1814–1910. This is a slight increase in terms of the number of vessels and whales taken over Ross (1979a). The biggest difference between the two series is Sanger’s inclusion of Scottish catches from land-station catches in Cumberland Sound, which Ross (1979a; 1979b) noted were missing from his compilation. From 1853–1890, a minimum of 68 overwintering Scottish voyages secured at least 346 whales (Sanger, 2007). The harvest series here therefore uses Sanger (unpublished data) as the main source for British whaling until 1910, with harvests for 1911 (four whales) from Ross (1979a), resulting in a total British harvest of 20,312 whales.

None of the aforementioned sources provide English data prior to 1814, with the exception of six whales harvested by the Hudson’s Bay Company (HBC) from 1767–1772 (Ross, 1974; 1979a). However, Jackson (1978) provides some limited information to help fill gaps for early English whaling: the number of English vessels from 1733–1785; the number of Scottish vessels from 1750–1785; yearly average oil and bone returns for 1733–1795; and the number of English and Scottish vessels clearing to, and entering from, ‘Greenland’ for 1781–1800. Jackson (1978) does not distinguish between whaling east and west of Greenland, but Sanger (1985) does for the number of Scottish vessels sailed, and whales harvested, for 1750–1801.

For the present paper, it is assumed that the English started whaling in Davis Strait in 1750 (Jackson, 1978; Ross, 1979a; 1993). This is the first year Scottish whaling data, separated into the two grounds, are available (Sanger, 1985; in 1750 there was only one Scottish vessel, which fished east of Greenland). From 1733–1749 the number of English ‘Greenland’ vessels ranged from 3–6 (Jackson, 1978). If there was any British activity in Davis Strait prior to 1750, as suggested by Jenkins (1971) and Gad (1973), it was likely of minor importance. Scottish whalers were in Davis Strait from 1751–1754, then moved all their effort to East Greenland, not returning again until 1787 (Sanger, 1985). From 1787–1814 the catch between the two grounds fluctuated, in some years more whales were harvested east of Greenland, in others the majority were taken in Davis Strait (Sanger, unpublished data).

The oil returns in Jackson (1978) for 1750 onwards were converted to number of whales using 6.8hhd (140l each) to one ton and 90hhd per whale (Allen, 1908). The number of whales harvested by English vessels was determined by subtracting the Scottish northern whale harvest from both grounds (Sanger, 1985; unpublished data). The proportion of Scottish vessels and whale harvests in Davis Strait (Sanger, 1985) was then used to estimate the proportion of total English vessels and whales (from Jackson, 1978) that were in Davis Strait. This resulted in an estimate of 1,292 whales captured by 408 vessels (Table 2). When combined with Sanger’s (1985; unpublished data) Scottish data, the total British harvest prior to the establishment of the Kinnes Lists in 1814 was estimated as 2,811 whales, with the majority (1,519) caught by the Scots, and most of these (1,245) taken from 1801 to 1813 (Sanger, unpublished data). Ross (1979a) estimated that there were over 400 British voyages to Davis Strait prior to 1814, and the estimated number of voyages here (408 English plus 84 Scottish) agrees well with this. There may have been additional English voyages, for example from 1801–1813, and also during the 1755–1786 period when the Scots fished east of Greenland only (Jackson, 1978; Sanger, 1985).

Estimating the early English harvest in this manner assumes that Scottish and English vessels were equal in their distribution on the two grounds, which may not be the case. In 1750, there was one Scottish vessel, which fished on the East Greenland grounds (Sanger, 1985), so in this estimate

Table 2

English Davis Strait whaling efforts from 1750–1800 estimated using British vessel and oil data from Jackson (1978). Oil yield converted to number of whales using Allen (1908), English whale harvest determined by subtracting Scottish harvests from Sanger (1985), and proportion of total vessels and total whale harvest in Davis Strait estimated using Scottish whaling effort (Sanger, 1985).

	English 'Greenland fishery'		Estimated English in W. Greenland			
Year	Vessels	Whales	Vessels	Whales	Whales/vessel	Notes
1750	19	27	–	–	–	Reportedly 20 English vessels in Davis Strait (Proulx, 1986 – but not a reliable source, Barkham, 1994)
1751	23	34	4	32	8.0	
1752	30	19	3	2	0.7	
1753	35	6	2	0	0.0	
1754	52	45	3	0	0.0	
1755 to 1786	1,852	3,107	0	0	–	No Scottish vessels in Davis Strait 1755–86 (Sanger, 1985). An estimated 1,852 English voyages caught 3,107 whales from 1755–86 but none assigned to West Greenland
1787	217	657	7	33	4.7	
1788	222	461	50	144	2.9	Reportedly 90 English whalers in West Greenland waters (Gad, 1982)
1789	151	336	62	183	3.0	
1790	103	264	47	71	1.5	
1791	93	212	32	108	3.4	
1792	87	170	52	27	0.5	
1793	73	226	42	101	2.4	
1794	53	190	13	92	7.1	
1795	40	194	12	62	5.2	
1796	44	278	10	73	7.3	
1797	57	354	17	66	3.9	
1798	59	359	24	114	4.8	
1799	60	366	12	96	8.0	
1800	54	345	16	88	5.5	
Total	3,324	7,650	408	1,292	–	

none of the 19 English vessels were assigned to Davis Strait (Table 2). Although Proulx (1986) stated that there were 20 English vessels in Davis Strait in that year (but see Barkham, 1994 for problems with the accuracy and reliability of Proulx [specifically Proulx 1993, but the issues are relevant to the 1986 publication as well]). In 1788, I estimate 50 English vessels in Davis Strait; however Danish sources indicated that there were 90 'English' whalers in West Greenland waters (Gad, 1982). Even when the seven Scottish vessels (Sanger, 1985; unpublished data) are added, the total number of British vessels is much lower than 90. This again suggests that Scottish whaling effort may not be representative of English effort, but detailed archival research would be required to address this.

Another source of whale products for British markets was barter between the HBC and Hudson Strait Inuit. The baleen from a minimum of 115 bowhead whales was collected between 1737 and 1800 (Barr, 1994). This excludes baleen collected by HBC supply voyages from 1670–1736 and 1801–1913 (approximately 660 trips total, Cook and Holland, 1978). Whaling in Hudson Bay was attempted by the HBC between 1767 and 1772, but was largely unsuccessful and only six whales were taken (Ross, 1974; 1979a).

The total (minimum) British whale harvest therefore includes 1,519 whales taken by the Scots from 1751–1813 (Sanger, 1985; unpublished data), 20,312 whales taken by the combined British fleet from 1814 to 1911 (Ross, 1979a; 1993; Sanger, unpublished data), six whales harvested by the HBC in Hudson Bay in the 1700s (Ross, 1974; 1979a), 115 whales secured by the HBC through trade (Barr, 1994), and an estimated 1,292 whales taken by the English fleet between 1751 and 1800 (based on data in Jackson, 1978 and the assumptions noted above, and likely incomplete). Combining all data results in a total minimum British removal of 23,244 whales from 1737–1911.

German whaling

German vessels first started whaling on the Spitsbergen grounds and were heavily involved in Arctic whaling by the late 1600s (de Jong, 1978; 1983). Ross (1979a) and de Jong (1983) provide some data on German Davis Strait whaling from 1719 to the late 1700s, although German vessels were again there prior to 1719 (Gad, 1970; Vaughn, 1986). According to Ross (1979a), the Germans caught 327 whales on 264 voyages from 1719–1792. The harvests in de Jong (1983) are lower, with 207 vessels and 277 whales from 1719–1783. For both sources the data are limited and do not include all the different whaling ports; therefore they provide underestimates of the total harvest. Data on German whaling in Davis Strait between 1792 and 1826, when the last German vessel sailed (Hacquebord, 2005), and prior to 1719, are unavailable. The harvest series, based on Ross (1979a) and updated for gaps with de Jong (1983), includes an estimated harvest of 332 whales.

Danish-Norwegian whaling in West Greenland

The Danes also first started whaling at Spitsbergen. Sporadic trips to Davis Strait were undertaken in the 1650s but no catches were apparently made (Gad, 1970). Small numbers of vessels were whaling in Davis Strait in the early 1700s (Gad, 1970; 1973), but the number of whales caught, if any, is unknown. These vessels were chiefly traders, not whalers, but they secured some whalebone from Greenland Inuit (Gad, 1973). In 1721, Danish colonies were established in West Greenland and a ship was outfitted specifically for Davis Strait whaling (Gad, 1973; Jones, 1970). Despite a trade monopoly granted in 1723, the Danes faced stiff competition from Dutch traders and were never very successful with either whaling or trading (Gad, 1973; Jones, 1970). Several West Greenland whaling stations were established in the 1770s (Gad, 1973), and up to eight stations and 12 ships were operating in the late 1780s (Gad, 1982). Local hired Inuit did the whale hunting, using European boats and tackle. War between Denmark-Norway and England starting in 1807 impacted Greenland trade (Gad, 1982), but Danish whalers were still active into the late 19th century (Vaughn, 1984).

There is no complete summary of the Danish bowhead whale harvest in Davis Strait. Gad (1973; 1982) provides some information in his narrative of the history of Greenland. Gad (1973) summarised blubber and baleen secured in trade and whales actively killed for 1721–1776. De Jong (1983) stated that adult whales typically yielded 30–40 tuns (tons, 953.9l or 252 US gallons) of blubber and calves and juveniles yielded 5–10 tuns. Scoresby (1820) gave the average yield of West Greenland bowheads as 14 tuns of oil, or 17.5 tuns of blubber using a 1.25 conversion factor. However given that the contemporary age-class structure in Disko Bay, West Greenland is nearly all (*ca* 85%) large adults >14 m in length (Heide-Jørgensen *et al.*, 2007; Laidre *et al.*, 2007, also see Eschricht and Reinhardt, 1866), I assumed a typical yield of 30 tuns of blubber per whale. Danish barrels (tønde) used to hold whale oil were equivalent to 131.5l (*ca* 34.7 US gallons), and this value was used to convert barrels to tuns. The minimum number of whales was estimated using the 30 tuns/whale conversion factor. Decreasing the estimate to 17.5 tuns of blubber per whale (Scoresby, 1820) would increase the estimated harvest, and my estimates could be considered conservative. In some years (e.g. 1755 and 1773), Gad (1973) noted that the totals included a mix of seal and whale oil; I arbitrarily assumed half of each when estimating total bowhead harvests. The estimated Danish harvest (mainly from trade with Inuit) is 95 whales from 1721 to 1776. This is a combination of both estimated numbers from blubber secured in trade and the number killed by colonists working with local Inuit. Gad (1973) reported 31 of the total estimate as actively killed by colonists and locals. These data are incomplete, with no information available for 27 of the 56 years. In addition, sometimes an entire whale harvested by the Greenlanders was shared amongst the locals, with the traders receiving none (Gad, 1973).

Cooperative shore-station whaling conducted by the Danes and West Greenland Inuit started *ca* 1777 (Vaughn, 1984). Gad (1982, p.206) provides a graph showing the production (in barrels, i.e. tøndes) of Greenland whale oil refined in Copenhagen from 1777–1807 (1785–87 missing), that provides a more comprehensive measure of whaling effort than for previous years. The oil refined for each year was estimated (to the nearest 25 barrels) from the graph and the number of whales estimated as follows: using the above 30 tuns of blubber per whale average, provides an average yield of 24 tuns of oil (conversion factor from Scoresby, 1820) or about 22,894l, or 174 tøndes per whale. The total oil yield from Gad's (1982) graph was converted to whales using the 174 conversion factor. The estimated annual number of whales ranges from 1–25 (average of 14) with a total estimated harvest of 393 whales from 1777–1807. An unknown proportion of these whales were harvested on the Spitsbergen grounds. I have assumed an even distribution between the two grounds, which results in a West Greenland harvest of 197 whales. Although this assumption may not be valid it is consistent with the limited available data; the estimated West Greenland harvest in 1798 was eight whales, and Gad (1982) reported that nine were taken, and Sandgreen (1973, in Caulfield, 1993) reported that the Disko Bay shore-stations landed six whales in 1777, compared to seven estimated here using oil returns (prior to the correction for Inuit blubber distribution as discussed below).

Harvests previous to 1777 (summarised from Gad, 1973) occurred on the West Greenland grounds only and no correction for Spitsbergen harvests is necessary. Until 1803, Greenlanders received half the blubber of whales they helped capture; after 1803 the natives received two-thirds (Gad, 1982). Estimated harvests from 1777 (establishment of shore stations) to 1803 were therefore corrected by a factor of two, and those for 1804–1807 by a factor of three, resulting in a total of 524 whales from 1721–1807 (range 1–26, with no data for 30 years). Cooperative whaling attempts occurred prior to the establishment of shore-stations in 1777, but a correction for Greenlanders receiving half the blubber of landed whales prior to this is not used in this paper as some of the blubber came from trade and not active whaling. The estimated harvest from 1721–1807 is therefore likely an underestimate.

Vaughn (1984) suggested that the average Danish catch was 20–30/year at the end of the 18th century, declining to half that in 1800–1850, with only one animal per year by 1870, when only one station was still working (also see Eschricht and Reinhardt, 1866; Rink, 1877). The yearly average compiled from Gad (1982) for 1777–1799 is 16 whales (with no data for three years), slightly under the lower limit suggested by Vaughn (1984). The estimated average harvest from Gad (1982) for 1800–1807 is 14 whales per year (range 2–22), in good agreement with Vaughn's (1984) estimate of 10–15 from 1800–1850. Caulfield (1993) reported that the Danish catch at Qeqertarsuaq in 1804 was 20 whales, compared to a total estimated catch of 21 whales here using the oil return data (and after correction for Inuit shares). The catch at Qeqertarsuaq declined to 12 whales in 1816 and was down to only 1–2 each year by the 1830s and 1840s (Amdrup *et al.*, 1921; Fisker, 1984; both in Caulfield, 1993). Whaling operations were shut down at Qeqertarsuaq in 1851 due to economic difficulties (Sveistrup and Dalgaard, 1945 in Caulfield, 1993). Danish shore-station whaling ended throughout West Greenland in the late 19th century (Vaughn, 1984). My estimated harvest of 524 whales up to 1807 (using data from Gad, 1973; 1982) was updated with an additional 14 whales per year assumed for 1808–1850 (average estimate for 1800–1807), declining to five per year for 1851–1869, and dropping again to 1 per year from 1870 to an assumed end date of 1890. For this part of the harvest series, I assume Vaughn (1984) implicitly included the fact that Inuit received a share of the blubber of harvested whales, and no correction was included. The total estimated Danish harvest is 1,242 whales from 1721–1890.

The Danish colonial records mentioned by Eschricht and Reinhardt (1866, p.4) are available on microfilm (M.

Klinowska, pers. comm. in Reeves *et al.*, 1983), and analyses of these records began in the early 1980s (Klinowska, 1982). Some information on bowhead catches is recorded in the daybooks of the shore-stations of the Royal Greenland Trading Company, and the majority survive in the State Archive in Copenhagen, running from 1774 to 1916 (Klinowska, 1982). Klinowska (1982) provides a brief description of the available data but did not conduct a full analysis. Eschricht and Reinhardt (1866) had access to the same data but unfortunately only mention it briefly. Klinowska (1982) examined bowhead movements (arrival and departure dates and length of stay at the different stations) and used a series of explanatory variables including catch per decade. However, instead of summarising the Danish shore-station catches, Klinowska (1982) used the international catches summarised by Ross (1979a). It is unfortunate that neither Eschricht and Reinhardt (1866) nor Klinowska (1982) summarised the daybook data, as these could provide additional information to the summaries and assumptions in Gad (1973; 1982) and Vaughn (1984) that were used here to estimate Danish shore-station catches.

One additional manuscript, again unpublished, contains reference to this archived data. Klinowska and Gerslund (1983), submitted as a proposal to the IWC for continued research, summarised the daybooks for November-June from four of the nine northern shore-stations for the year 1800–1801. This reportedly represented the first year of a reasonable run of records for the area. However, the proposal for continued research was not supported (M. Klinowska, pers. comm., 18 February 2008). Analyses of these archived logbooks could be undertaken, but would require time, resources, and specialised expertise. The microfilms are available from the IWC. The four daybooks examined by Klinowska and Gerslund (1983) included a total harvest of at least 50 bowhead whales in 1800–1801, including one taken by an English vessel and 17 taken at the Holsteinsborg station. The remainder were taken at four stations in Disko Bay. This represents landed whales only and is a subset of the available data. It is apparent that significant numbers of whales were taken by Danish shore-stations. In the present harvest series, I estimated Danish harvests of 22 whales in 1800 and 14 in 1801; these are thus known to be an underestimate. However without having the Daybook data summarised for other years, it is currently not possible to determine to what extent the Danish harvests may have been underestimated. While limited to one year only, the available data suggest that Vaughn (1984) (and by extension, this study) may have greatly underestimated Danish whaling effort in the early 1800s. Examination of the data may also provide guidance on species composition of the harvest. It is assumed that whale oil returns represented bowhead whales only. However West Greenlanders had a well-developed humpback whale fishery established by the late 1700s (Mitchell and Reeves, 1983; Reeves and Smith, 2002). Danish shore stations probably took humpback whales opportunistically, and some of the oil returns may represent this species (or even right whales).

French (non-Basque) whaling

French (and Spanish) Basque whaling has been discussed previously. However non-Basque French vessels were also active in the Northern whale fishery. The French Basque fishery ended in 1766, but a whaling company was established in Dunkirk (outside the Basque region) in 1784 with support from the government, and was active on both northern and southern whaling grounds until 1788, but with little success (Du Pasquier, 1986). French whaling also expanded after 1788 with a colony of Nantucketers who settled at Dunkirk. The proportion of those vessels that traveled to northern regions is unknown, but based on du Pasquier's (1986) text and Table 6 it does appear that most (if not all) harvests were of right whales in the South Atlantic. The Government of France again tried to revive the industry in 1817 with American expertise and capital. Du Pasquier's (1986) Table 8 indicates that few of these vessels went to Northern grounds, with most whaling in the Southern Hemisphere (between 1–4 vessels per year from 1817–1837 on Northern grounds, and in most years only one). Some of these vessels likely traveled to whaling grounds west of Greenland, but no data on relative proportions are available in du Pasquier (1986). Another source (Du Pasquier, 1982) may contain more information. Given the low numbers of vessels involved, I have assumed that harvests west of Greenland were negligible, and none are included here.

American whaling

Yankee whaling started in New England in the mid-1600s as a coastal, shore-based fishery similar to that of the Basques (Stackpole, 1953). In 1712, the first sperm whale (*Physeter macrocephalus*) was taken by an American vessel, launching an expansion into pelagic regions (Starbuck, 1878). The first American vessel to visit Davis Strait did so in 1732 (Starbuck, 1878 and according to Bernard, 1761 in Ross, 1979a), and by 1737 the Davis Strait fleet from Massachusetts alone consisted of 50–60 vessels (Clark, 1887; Stackpole, 1953). The main targets in this fishery were sperm and right whales, but bowhead whales were probably also taken (Jackson, 1978; Reeves *et al.*, 1983; Reeves and Mitchell, 1986). Starbuck (1878) provides some general discussion on sporadic 18th-century American voyages to Davis Strait, while Stackpole (1953) discusses some specific voyages. However, no comprehensive data on the number of voyages or the size of the catch are available, and there are no harvest records available for this aspect of the American fishery (Jenkins, 1971; Ross, 1979a). In June 1753, the sloop *Greyhound* took a whale near 60°N in Davis Strait amongst heavy ice (Stackpole, 1953: 43–44), and Reeves and Mitchell (1986) considered this to most likely be a bowhead (although it was reported as a right whale by Townsend, 1935).

The ceding of Canada to England opened up the Gulf of St. Lawrence and Strait of Belle Isle to Yankee whalers, and by the mid-1760s up to 100 New England vessels were active there (Scoresby, 1820; Starbuck, 1878). There are again no data available but it is likely that at least some bowhead whales were taken. Some American vessels in the Strait of Belle Isle attempted to overwinter or arrive early in the spring when ice was still present, suggesting active bowhead whaling (Reeves and Mitchell, 1986). The whales pursued by the *Reliance* in the Strait of Belle Isle in the 1760s were likely bowhead (Reeves and Mitchell, 1986).

In the 1840s, American whalers again started visiting Davis Strait and Baffin Bay (Clark, 1887). In the 1850s whalers from both New England and Scotland established a shore-based fishery in Cumberland Sound (Hacquebord, 2005; Ross, 1979a; 1984: 1985; Sanger, 2007). After 1860, American (and some Scottish) whalers moved into Hudson Bay, a predominantly American fishery that lasted until the early 1900s (Ross, 1979a; 1993). Ross (1979a) contains American whaling data starting in 1846, when the Americans returned to Davis Strait and Baffin Bay, and starting in 1860 for Hudson Bay. During this time, 349 vessels caught 945 whales. American Arctic whaling occurred primarily in the Pacific region, starting in the mid 1800s (Bockstoce, 1986; Bockstoce and Botkin, 1983), and only a minor proportion (< 5%) of American bowhead harvests in the mid- to late 1800s occurred in the eastern Arctic (Clark, 1887). Ross' (Ross, 1979a, also 1974) harvest reconstructions were based on oil and baleen returns, and he assumed that the returns reflected bowhead whales only. However, American vessels travelling to Hudson Bay ('Hudson's Bay') or Cumberland Sound ('Cumberland Inlet') often cruised for right whales off Greenland before reaching the bowhead whaling grounds (Reeves and Mitchell, 1986), and some of the returns included by Ross (1979a) could represent right whales. Yankee whalers in the Arctic after 1820 were also aware of the market for humpback oil and lowered their whaleboats for that species on occasion (Mitchell and Reeves, 1983). In 1878, the New Bedford brig *A.J. Ross* chased humpback whales along the Labrador coast while heading to the Hudson Bay bowhead grounds (Reeves and Smith, 2002).

Best (1987) estimated the landed catch of baleen whales made by American whalers from 1805–1909, building largely on logbook data originally presented in Townsend (1935). He estimated that American vessels took 248–291 bowhead whales from 1815–1819. However this appears to be an extrapolation from the five bowheads taken by the ship *Mars* of Nantucket in 1817, the only vessel catching bowhead whales for this time period that was listed by Townsend (1935). This was before the American expansion into the western Arctic, and these whales would thus possibly have been captured in the Strait of Belle Isle, Davis Strait or the Labrador Sea. However, the five whales taken by the *Mars* also could have been taken east of Greenland. In the absence of additional information, I consider the figure of 248–291 whales to be uncertain and have not included this in the harvest reconstruction.

The American Offshore Whaling Voyage database (Lund *et al.*, 2008) includes three voyages by the *Richmond* of New Bedford, for 'Hudson's Bay', in July 1816–May 1817 (1,700bbl oil), July 1818–19 (1,800bbl oil), and again from July 1827–28 (1800bbl oil and 12,295lbs bone). The total oil harvest from these three over-wintering voyages was 5,300 barrels. This would represent about 44 bowheads, using the average Davis Strait yield of 120bbl as reported by Best (1987), if it was assumed that all were bowheads, which probably is not the case. Whaling masters would sometimes declare a voyage to one region but then sail to another (Ross, 1979a), and these voyages occurred well-before the known start of American whaling on the Hudson Bay ground. The harvests could have occurred in southern Davis Strait or along the Labrador coast, but also possibly occurred east of Greenland. As noted, the catch was also not necessarily all bowheads.

Given this uncertainty, the only American harvests included here are the 945 from 1846–1915 estimated by Ross (1979a). No harvests from the 1700s or early 1800s are included for the reasons noted above and therefore the total catch is an underestimate to an unknown degree.

Canadian whaling

Some Canadian colonists reportedly tried to take up whaling in the Strait of Belle Isle and Gulf of St. Lawrence after the Basques left but were largely unsuccessful (Proulx, 1986). Quebec residents of the Gaspé Bay, on the south shore of the St. Lawrence, were whaling from sailing vessels throughout the 1800s (Mitchell and Reeves, 1983). During the American Revolution, some American whalers moved north and helped build whaling industries in Newfoundland and Nova Scotia (Jackson, 1978). Colonial whaling concentrated mostly on humpback whales (Clark, 1887; Mitchell and Reeves, 1983; Reeves and Smith, 2002). However in 1842, Bonnycastle wrote that whales of all species were taken in Newfoundland waters, including 'the largest mysticetus or great common oil whale of the northern oceans, which occasionally visits these waters' (Clark, 1887: 217). The Little Ice Age started in the 13th century, when pack ice began advancing southwards in the North Atlantic, and ended about 1850 when the climate again began to warm (Fagan, 2000; Lamb, 1995). With southward expansion of pack ice, it seems possible that at least some bowhead whales were taken by colonial whalers in the Strait of Belle Isle and the Gulf of St. Lawrence prior to the mid 1800s, although no harvests are known. Shore station-based 'modern' whaling began in Newfoundland in the early 1900s, but no bowhead whales were reported taken (Dickinson and Sangar, 2005).

Summary of commercial harvests (see Fig. 2 and Table 3)

For all nations combined, the estimated commercial harvest is 55,916–67,537 whales from 1530–1915 AD (61,537 whales with a peak Basque effort of 25 vessels per year). In the eastern Arctic (including the Gulf of St. Lawrence and Strait of Belle Isle), the most active whalers were the Basque and the British. There are a number of gaps in this series and the total harvest is probably underestimated. Many

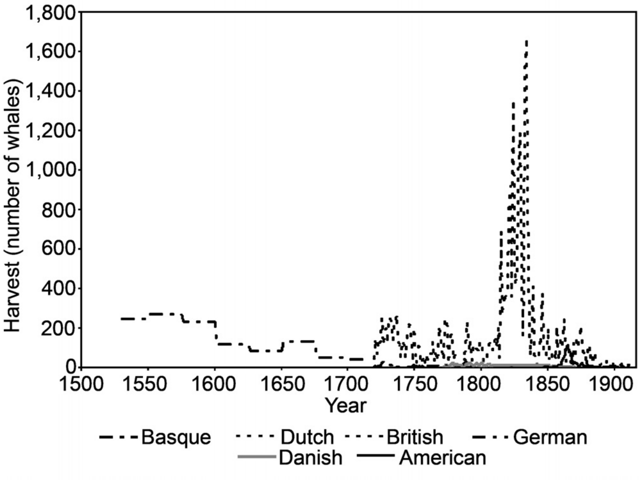

Fig. 2. Estimated commercial harvest of bowhead whales in eastern Canada and West Greenland, 1530–1915 AD, by nation. The Basque harvest is based on an assumed peak of 25 vessels per year.

Table 3

Summary of commercial bowhead whale harvests, by nation (see text for further details).

Nation	Start date	End date	Estimated bowhead harvest
Norse settlers, W. Greenland	1150	Pre-1500	Unknown but likely minor (subsistence)
Basque	1530	1713	22,454–33,683[1]
	1714	1766	Unknown
Dutch	1600s	1718	Unknown
	1719	1826	7,699
British	1737	1911	23,244[2]
German	1600s	1718	Unknown
	1719	1792	332
Danish-Norwegian	1600s	1720	Unknown
	1721	1890	1,242
French (non-Basque)	1784	1837	Unknown
American	1700s	1700s	Unknown
	1846	1915	945
Canadian	????	????	Unknown
Total estimated harvest[3]	**55,916–67,537 (61,537)**		

[1]Range of values depending on assumptions of vessels per year during peak (1551–75) (see Table 1). [2]Includes 115 whales secured by Hudson's Bay Company (HBC) through trade with Hudson Strait Inuit and six whales taken by HBC whalers in the mid-1700s, but excludes possible English Davis Strait harvests in the mid-1700s and 1801–1814. [3]Range of values depending on assumed number of Basque vessels, value in parentheses assumes a peak Basque effort of 25 vessels per year (midpoint of Table 1).

assumptions regarding the distribution of whaling effort, species composition of the catch, and average catch per vessel have been employed, and these may not be valid in many cases. Despite these uncertainties, this commercial harvest series is more complete than the previous summaries it builds upon (e.g. de Jong, 1978; 1983; Ross, 1979a; 1993).

INUIT SUBSISTENCE WHALING SINCE 1200 AD

The Thule culture

The Thule culture (Mathiassen, 1927), direct ancestors of today's Inuit, spread eastward from Alaska starting *ca* 1000 AD, arriving in the central Canadian Arctic *ca* 1200 AD, and eventually reaching the eastern Arctic, Labrador and West Greenland (Friesen, 2004; Park, 2000; Savelle and McCartney, 1990). Bowhead whales were critically important to the initial Thule expansion (McCartney, 1977; McGhee, 1969–1970; 1972; 1975). A warming trend led to a decrease in summer ice cover, and a range expansion for both whales and whalers. The decline in whaling and abandonment of the High Arctic *ca* 1500 AD was a consequence of a cooling trend that increased ice cover and decreased bowhead distribution.

McCartney (1977) distinguished between 'classic' and 'modified' Thule, where classic Thule (*ca* 1000–1300 AD, but with significant regional variation) refers to the early culture carried from the Chukchi and Beaufort Seas into the Canadian Arctic. The classic Thule culture coincided with a major warming episode when bowhead whales achieved their maximum range (McCartney and Savelle, 1985). The modified Thule culture (McCartney, 1977) refers to adaptations that corresponded with the onset of cooler temperatures, when the reduction in bowhead whale availability led to a shifting of Thule subsistence patterns. The human population largely abandoned the central and high Arctic between *ca* 1400–1600 AD, likely due to reduced whale availability. The transition from classic to modified Thule was not uniform. Schledermann (1979) noted temporal and geographic variability in Thule whaling and suggested that the 'baleen period' lasted to between 1400 and 1700 AD, with the later date corresponding to sites on more open waters where whales were still accessible.

Bowhead whale bones were used extensively in the construction of Thule winter houses. Houses were built using bones with a high 'architectural utility' such as mandibles, maxillae and premaxillae, ribs, and scapulae (Savelle, 1997). Thule winter house construction was highly variable, resulting from differing spatiotemporal availability of bowhead whales in addition to differences in whaling-related social status between households (Dawson, 2001; Whitridge, 2002).

The relative numbers of whales that were killed as opposed to scavenged is unknown. This has led to a questioning of the role of active bowhead whaling (Freeman, 1979; Yorga, 1979). However there is considerable direct and indirect evidence that bowheads were actively harvested (McCartney, 1980; McCartney and Savelle, 1985; Savelle and McCartney, 1988; Savelle and McCartney, 1990). The most convincing information comes from estimates of the size of whales, as nearly all (97%) of the remains at classic Thule sites in the central Arctic were from yearling whales (McCartney and Savelle, 1985; 1993; Savelle and McCartney, 1991; 1994). Thule whalers actively selected for immature whales between 7–10m in length (McCartney and Savelle, 1993; Savelle and McCartney, 1991; 1994), presumably related to their ease of capture.

There was significant geographic and temporal variation in Thule subsistence patterns and not all groups used bowhead whales to the same degree (Mathiassen, 1927; McCartney and Savelle, 1985; Savelle and McCartney, 1990; 1994; 1999). Quantifying the importance of bowhead whales to the classic Thule diet has proven difficult. Bones of small animals such as ringed seals (*Pusa hispida*) are generally considered to be 'diet-derived', but bowhead bones can be 'shelter-derived' as well (McCartney, 1980). Bowhead whales have thus often been excluded from many zooarchaeological studies of Thule subsistence patterns (e.g. Staab, 1979). McCartney and Savelle (1985), using data from Rick (1980) on faunal remains from Thule winter houses on Somerset Island, provide some rough estimates of the relative importance of bowhead whales during the classic Thule phase (i.e. pre-1300 AD). McCartney and Savelle (1985) used some conservative estimates to suggest that at a minimum the food value of bowheads was equal to the food from all other animals combined and that the bowhead to 'other' food ratio could be as high as 3:1–5:1. Savelle and McCartney (1990) conservatively estimated that one juvenile whale was equal to some 120 caribou (*Rangifer tarandus*) or 180 ringed seals. Whales would have also been used for fuel (i.e. oil), and this may have been just as important as the food value, if not more so.

Harvest series for the Thule culture pre-1500 AD

Stoker and Krupnik (1993) summarised data from McCartney (1979), who examined whale bone winter houses at Thule sites throughout the central Arctic region (excluding Labrador and the Ungava Peninsula) and estimated that

Table 4

Estimated bowhead whale use by classic Thule culture (*ca.* 1200–1500 AD) in the central and eastern Canadian Arctic (columns 1–4 from McCartney, 1979 as summarised by Stoker and Krupnik, 1993).

Region	No. houses	Avg. whales per house	Min. no. whales	Median total whales	Whales per year (300 years)	Nunavut region
Somerset Island	183	10–15	1,830–2,745	2,288	8	Qikiqtaaluk
Boothia Peninsula	50	4–5	200–250	225	1	Kitikmeot
Admiralty Inlet	93	3	279	279	1	Qikiqtaaluk
Navy Board-Pond inlets	161	3	483	483	2	Qikiqtaaluk
Clyde area	140	2–3	280–420	350	2	Qikiqtaaluk
Broughton area	303	1	303	303	1	Qikiqtaaluk
Cumberland Sound	389	3	1,167	1,167	4	Qikiqtaaluk
Frobisher Bay-Hudson Strait-Foxe Peninsula	155	2–3	310–465	388	2	Qikiqtaaluk
Western H. Bay-Repulse Bay-Southampton Island	300	1	300	300	1	Kivalliq
Western Melville Pen. and adj. islands	103	3	309	309	1	Qikiqtaaluk
Ellesmere-Northern Devon islands	186	2–3	372–558	465	2	Qikiqtaaluk
Lancaster Sound-Barrow Strait	131	1–2	131–262	197	1	Qikiqtaaluk

6,301–8,215 individual whales were used. It seems reasonable to assume that nearly all whales were actively harvested given the preponderance of young whales (McCartney and Savelle, 1985; 1993; Savelle and McCartney, 1991; 1994), as Holocene stranding (mortality) profiles are similar to live population profiles (Savelle *et al.*, 2000), i.e. younger whales were not more likely to strand. McCartney's (1979) data, as shown by Stoker and Krupnik (1993), are included in Table 4. The average number of whales used per year (i.e. harvested) was determined using the median total whale estimate and a 300 year time period (Stoker and Krupnik, 1993); each site was assigned to one of the three current Government of Nunavut regions and all estimates were rounded up to whole animals.

The Kitikmeot Region is poorly represented in Table 4, with only one location (Boothia Peninsula). However this region historically did not contain large numbers of whales and Thule Inuit there depended mostly on ringed seals and caribou (Mathiassen, 1927; McCartney and Savelle, 1985; Savelle and McCartney, 1990). The Kivalliq Region also has poor coverage, with the only surveys in western Hudson Bay. However this area would represent the most productive whaling zone in the region (Ross, 1974). Ungava Bay, Labrador and Greenland are also excluded (see below). Most data are for the Qikiqtaaluk Region, but this is reasonable as most early Thule whaling would have occurred in the central Arctic islands.

The classic Thule period for the different regions was defined based on Schledermann (1979) (Table 5). For Repulse Bay the baleen period as reported by Schledermann (1979) occurred from 1000–1100 to 1400 AD, but the period is started here at 1200 AD (Friesen, 2004; Park, 2000). An average harvest of one whale per year in western Hudson Bay-Repulse Bay-Southampton Island (Table 4) over this period would result in 201 whales (Table 6). The baleen period in Cumberland Sound was from 1250–1650 AD (Table 5). A harvest of four whales per year (Table 4) until 1500 AD results in a total harvest of 1,004 whales. For the remaining regions in Table 4 the total harvest was 21 whales per year. It is assumed that the abandonment of the central and high Arctic Islands, or at least a shifting of subsistence strategies, was complete by 1500 AD. This, combined with establishment by 1200 AD, would result in a further Thule harvest of 6,321 whales. For Labrador, no harvests are added before 1500, following Schledermann (1979). For West Greenland, Schledermann (1979) (Table 5) dated the start of the baleen period as 1200 AD (although this may be too early, Friesen, 2004; Park, 2000). A West Greenland harvest of ten whales per year (Vaughn, 1984) results in an estimated harvest of 3,010 whales pre-1500. The total estimated harvest is thus 10,536 whales pre-1500 AD, peaking from 1250–1400 with an estimated average of 36 per year (Table 6).

Quality of harvest estimates

There are several lines of evidence to suggest that harvests may be underestimated. The harvest per region is based on McCartney's (1979) whalebone winter house data (as summarised by Stoker and Krupnik, 1993). For at least some regions the minimum numbers of individuals (MNI) calculations in McCartney (1979) are negatively biased because large numbers of buried bones were not included (McCartney and Savelle, 1985). This, combined with significant bone removal by prehistoric and historic Inuit, in addition to contemporary Inuit for whalebone carvings (McCartney, 1979), significantly reduced the amount of bone counted at some sites. In addition, not all whale crania or mandibles ended up in winter houses, with many left on beach processing sites or stockpiled in caches for future architectural use (Savelle, 1997). The estimated yearly harvest for Somerset Island is only eight whales (Table 4), yet the caches there could have stored the meat and blubber of 15–25 animals (Savelle and McCartney, 1990). In comparison to most commercial data, the Inuit harvest estimates are the least reliable of this summary (see

Table 5

Approximate dates of the 'baleen period' as defined by Schledermann (1979). In this assessment the start of the baleen period for Repulse Bay was changed to 1200 AD (see text).

Site	Approximate time period (AD)
Naujan (Repulse Bay)	1000–1100 to 1400
Cumberland Sound	1250 to 1650
Labrador	1500 to 1700
Comer's Midden (Northwest Greenland)	1200–1300 to 1550
Sermermiut (Disko Bay, Greenland)	1200–1300 to 1650

Table 6

Summary of estimated Thule/Inuit bowhead whale harvests in eastern Canada and West Greenland between 1200 and 2009 AD. Estimated average yearly harvest provided, except for Labrador 1771–1849 and all regions post-1917, where annual harvest statistics (with an unknown level of completeness) are available.

Location	Period (AD)	Yearly harvest	Total whales
Pre-1500			
Repulse Bay (Naujan)	1200–1400	1	201
Cumberland Sound	1250–1500	4	1,004
Remainder of Canadian Arctic	1200–1500	21	6,321
West Greenland	1200–1500	10	3,010
Total			10,536
Peak harvest	1250–1400	36	
1501 – ‘historic’			
Western Baffin Island	1501–1650	11	1,650
Labrador	1501–1700	5	1,000
Hudson Bay/Nunavik	1501–1700	5	1,000
Northwest Greenland	1501–1550	5	250
Southwest Greenland	1501–1650	5	750
Total			4,650
Peak harvest	1501–1550	31	
‘Historic’ period			
Cumberland Sound	1651–1860	10	2,100
Northern Hudson Strait (southern Baffin Island)	1651–1860	3	630
Southwest Hudson Bay (Marble Island south)	1701–1860	1	160
Repulse Bay (and Foxe Basin)	1701–1860	2	320
Nunavik	1701–1860	2	320
Labrador	1701–1770	5	350
	1771–1849	Variable	143*
West Greenland	1651–1721	5	355
	1722–1770	3	147
	1771–1900	1	130
Total			4,655
Peak harvests	1793	34	
	1781	32	
	1651–1721	28	
Post-commercial whaling period			
All regions	1918–2009	Variable	65**
Totals			
Total harvest 1200–2009 AD			19,906
Harvest 1530–2009 AD			8,471

*Includes 36 struck/lost. **Includes 14 struck/lost.

below). Savelle (in review) has incorporated additional archaeological data (revised bone counts, additional sites) than that available in Stoker and Krupnik (1993), and classic Thule harvests may have been considerably higher than that estimated here.

Harvest series for the Thule culture post 1500 AD (pre-‘historic’)

Thule whaling declined in the central Arctic after *ca* 1500 AD, before the start of widespread commercial whaling. Bowhead whaling survived only on the western coast of Baffin Island, Hudson Bay, West Greenland and Labrador (Stoker and Krupnik, 1993). Schledermann (1979) suggested that deteriorating climate conditions in the central Arctic resulting in population movement into regions where open water conditions allowed continued hunting of bowhead whales. For the post-1500 AD Thule harvest it is assumed that bowhead hunting continued only in the locations noted above and again used the ‘baleen period’ dates in Table 5. For western Baffin Island, the five locations in Table 4 (Navy Board and Pond inlets, Clyde area, Broughton area, Cumberland Sound and Frobisher Bay-Hudson Strait-Foxe Peninsula) have a combined total of 11 whales per year. Assuming the baleen period ended at 1650 AD (Table 5), the total harvest of whales from 1501–1650 AD for all these regions is 1,650.

For Labrador, the ‘baleen period’ ended in 1700 AD (Table 5). Assuming a harvest of five whales per year, (average harvest at the time of initial Moravian contact, Taylor, 1988 – see below) results in 1,000 whales 1501–1700 AD. According to Schledermann (1979) the Thule site at Repulse Bay (Naujan) was occupied until 1400 AD (Table 5). However after *ca* 1500–1600 AD whaling again occurred in western Hudson Bay (Stoker and Krupnik, 1993). Assuming a harvest of five whales per year (see below) results in a total western Hudson Bay harvest of 1,000 whales 1501–1700 AD. For West Greenland a harvest of ten whales per year (Vaughn, 1984), or five each in the northwest and southwest, is again assumed. The baleen period lasted until 1550 AD in northwest Greenland and 1650 AD in southwest Greenland (Table 5), for an estimate of 1,000 whales from 1501–1650 AD. The combined estimated harvest for 1501–1650/1700 AD is 4,650 whales, peaking early (1501–1550) with an average of 31 whales per year (Table 6).

Historic Inuit bowhead whaling

The Historic Inuit period also exhibits significant geographic variation, with definitions largely dependent on the time of first European contact. For example, McCartney (1977) defined the historic period in Hudson Bay as starting in 1610. In West Greenland, the first extensive European contact did not begin until Danish-Norwegian colonisation in 1721 (Gad, 1973; Rink, 1877), although there was limited contact with European traders and whalers before this time. A similar situation occurred in Labrador where there was only limited contact until the late 18th century when Moravian mission stations were established. Inuit on Baffin Island were in contact with European explorers starting in the 1600s (in addition to possible contact with the Norse before this, Fitzhugh, 1985). European (and American) contact in the Canadian eastern Arctic culminated in the mid-1800s with the presence of many commercial whalers, which had a profound effect on local Inuit (Ross, 1974; Ross, 1979b). In this summary, all dates begin, somewhat arbitrarily, to bridge the gap between Schledermann's (1979) 'baleen period' dates (Table 5) and those discussed in this section.

A large body of literature exists from whalers, explorers and missionaries, and some early ethnographic accounts of native whaling are available (Boas, 1888; Cranz, 1820; Egede, 1745; Oswalt, 1979; Parry, 1824; 1826; Ross, 1819). These accounts, while clearly indicating that early historic period native whaling occurred, are brief and of little value in reconstructing harvest numbers. In most cases the authors were less concerned with describing Inuit harvesting practices than they were with general ethno-cultural observations or notations of discoveries.

Many of these ethnographic accounts also described situations in which early European whalers had already reduced whale populations and had a significant effect on Inuit culture, thus impacting the very lifestyles they described (Taylor, 1979). The presence of Euroamerican whalers in places such as Pond Inlet, Cumberland Sound and northwest Hudson Bay may have had a significant effect on the native harvest of bowheads. Both Clark (1979) and Freeman (1979) suggest that trade with Euroamericans may have created renewed interest in bowhead whaling among Inuit. In many cases, some of the whales harvested by Inuit may be included in the commercial totals through trade of baleen and blubber. Despite these shortcomings, historic ethnographic accounts are of some value in reconstructing Inuit bowhead harvests during the early contact period, although a number of assumptions are necessary, which may or may not be valid.

Historic whaling in Nunavut and Nunavik waters

Some limited data are available for three areas in Nunavut: Cumberland Sound, southeastern Baffin Island on Hudson Strait, and northwest Hudson Bay.

Cumberland Sound

Some data on contact-period Inuit whaling are available for Cumberland Sound, which commercial whalers first entered in 1839 (Haller, 1966, in Taylor, 1979). In 1840 Penny observed freshly killed whales in Cumberland Sound (M'Donald, 1841), and stated that Inuit there killed 'annually from 8 to 12 whales', something worth noting as it was 'peculiar to these Esquimaux' (Penny, 1840, in Stevenson, 1997: 40). Captain Penny travelled extensively in the region and was very familiar with eastern Baffin Island, and his statement suggests that by the mid-1800s bowhead whaling in this area was largely limited to Cumberland Sound. Inuit oral history on North Baffin Island indicates that bowhead whaling declined in the historic period prior to the arrival of Scottish whalers, who then hired local Inuit hunters (J. Alooloo, Pond Inlet Hunters and Trappers Organisation, pers. comm., 18 April 2007).

However Penny's statement is contradictory to both Schledermann's (1979) 'baleen period' end of 1650 AD (Table 5) and the estimated annual harvests from archaeological evidence (Table 4). Two possibilities may explain the discrepancy in dates. First, the presence of foreign whalers and traders, and thus foreign trade items, prompted the Inuit to increase bowhead harvests strictly as a trade item (Clark, 1979; Freeman, 1979). The second possibility, and the one preferred by Stevenson (1997), is that Schledermann's (1979) stratigraphic sequence was correct but that his chronological and cultural interpretations were not (also see Friesen, 2004; Park, 2000). Regardless of the reason, the available ethnographic evidence suggests that in the early to mid-1800s Cumberland Sound Inuit took an average of ten whales per year, a high harvest level unique to this region. For the discrepancy in annual harvest numbers, it is worth noting the earlier discussion regarding the likely underestimates of pre-contact harvest due to the limitation of using whalebone houses only (also see Savelle, in review). Another possibility is increased human population size in Cumberland Sound due to migration from central and high Arctic regions with cooling climatic conditions (Schledermann, 1979).

Hudson Strait

Barr (1994) presented data on baleen secured by HBC ships in Hudson Strait and Hudson Bay (here included with British whaling harvests). Most baleen came from Hudson Strait (78% of the total from 1737–1778), and then mainly from the Kimmirut area. Barr (1994) estimated that from 1737–1800, the products of 65 average-sized bowhead whales (i.e. one per year) were traded by Inuit of southern Baffin Island. In some years the equivalent of three to five average-sized whales was traded (Barr, 1994). In Labrador, only 24 of 63 whales (38%) killed from 1771–1784 had marketable baleen over 1.8m long (Taylor, 1988). Given this information, along with the cultural (i.e. Thule) tradition of selection for small whales, it seems likely that during the mid through late-1700s, an average of three whales per year was being harvested by Inuit along the northern side of Hudson Strait, with harvests in some exceptional years possibly exceeding ten whales.

Ross (1974) presents evidence that the Inuit harvest decreased by the late-1800s. In 1880, Inuit took three whales under contract to an American whaling firm, and a whaling/trading station was established in central Hudson Strait shortly after. By this time commercial whaling had already reduced whale numbers in Hudson Bay. Inuit occasionally took whales using boats supplied by the station but numbers were not large. In 1886, local Inuit stated that no whales had been taken in three years (Ross, 1974). Maxwell (1979) summarised archaeological and ethnographic information for the Kimmirut region and suggested that small numbers of bowhead whales may have been harvested up until 70 years ago (i.e. the early 1900s). Much of the baleen was probably traded and is thus likely included in the harvest series for American and Scottish whalers (Ross, 1974; 1979a; Sanger, unpublished data).

Western Hudson Bay

The Hudson's Bay Company also secured baleen along the western Hudson Bay coast, although amounts were much lower than in Hudson Strait (Barr, 1994). From 1737–88 Barr's (1994, p.242) table 2 includes only 7,058lbs of baleen traded at Churchill and another 7,032lbs secured by expeditions north to Marble Island. This equals a total of *ca* 10 average-sized bowhead whales over the 42 year period, or an average of one whale every four years. Ross (1974) also summarised HBC trade between Churchill and Marble Island and gave similar numbers. Hearne (1795) witnessed three whales harvested near Churchill in a 20-year period prior to 1795, and Hudson Bay Inuit killed one whale, and struck and lost two, in 1828 (Reeves *et al.*, 1983; Reeves and Mitchell, 1990). Given the suggestions above for Hudson Strait harvests, an average of one whale per year may have been taken in Hudson Bay from Marble Island south.

The presence of whale bone on eastern Melville Peninsula suggests a long history of bowhead harvesting in Foxe Basin continuing into the historic period (Stoker and Krupnik, 1993). However, Parry (1824) was informed by local Inuit that most whales were found in the Repulse Bay area. The estimates above based on the baleen trade do not include the Repulse Bay region, which would have been the most productive area for bowhead whaling in Hudson Bay. It may be reasonable to assume that an average of one to two bowhead whales was taken in the area every year. Inuit harvests likely declined in the later 1800s as they did in Hudson Strait (Ross, 1974).

Total estimated Nunavut and Nunavik harvest, 'historic' period

For the 'historic' period, my estimated Inuit harvests in Nunavut and Nunavik end in 1860. This date corresponds to the initiation of commercial whaling in Hudson Bay and occurs just after the establishment of shore stations in Cumberland Sound in the mid-1850s. Some whales were probably harvested after 1860 (e.g. Maxwell, 1979; Ross, 1974), but most whale products would have been traded to American and Scottish whalers and thus included in the commercial harvest series for those countries. Assuming Penny's estimation of 8–12 whales per year (Stevenson, 1997) is correct, this would result in a total Cumberland Sound harvest of 2,100 whales (i.e. 10 per year) from 1650–1860. However the discrepancy between the harvest levels in Table 4 and Penny's statement is still unresolved. In addition, the commercial harvests off West Greenland in the 1700s reduced the bowhead population, and may have negatively impacted Inuit harvest levels. For northern Hudson Strait (southern Baffin Island), an average of three whales per year is assumed for 1701–1860, for a total of 480 whales.

For southwestern Hudson Bay (south of Marble Island), an average harvest of one whale per year is assumed, for a total of 160 whales from 1701–1860. Assuming a combined average yearly harvest of two whales in Repulse Bay and Foxe Basin results in an additional 320 whales from 1701–1860. No bowhead harvest data are available for Nunavik (eastern Hudson Bay and southern Hudson Strait). McCartney (1979) excluded the Ungava Bay region, so there is no archaeological data and any harvests in this region were thus excluded from the pre-contact harvest series. There are also no ethnographic accounts for harvests, but contemporary Inuit have suggested that Nunavimmiut may have traditionally harvested a maximum of 3–4 bowheads per year (A. Kullula and J. Peters, Makivik Corp., pers. comm., 14 March 2007). A possibly conservative estimate of two whales per year results in another 320 whales from 1701–1860. The majority of Nunavik harvests would have occurred in northeast Hudson Bay and Hudson Strait, however Inuit have reported bowhead occurrence during winter at some of the more southern islands on the east side of Hudson Bay (Low, 1906). Inuit on the Belcher Islands, in southeast Hudson Bay, reportedly have a historic tradition of bowhead whale hunting (L. Arragutainaq, Sanikiluaq Hunters and Trappers Organisation, pers. comm., 7 September 2007). Harvests in this region of Hudson Bay may thus have been higher than assumed here.

The total estimated harvest in Nunavut and Nunavik for the period 1651/1701 (depending on region) to 1860 is 3,530 whales (Table 6). The harvest series is based on scattered ethnographic accounts and a number of untestable assumptions. While these estimates are based on the best data available there is unfortunately no way to determine the level of bias. One source of negative bias is the at least occasional harvests in other regions. For example, in 1869 Inuit in Admiralty Inlet killed five large whales (Hall, 1876). It is unknown whether historic Inuit in this or other excluded regions harvested whales on a regular basis.

Labrador

Bowhead whaling was introduced to Labrador by Thule migrants at least by 1500 AD (Kaplan, 1985) and possibly as early as 1350 AD (Jordan, 1978). The estimated harvest between 1501 and 1700 AD was 1,000 whales (five per year), based on Taylor's (1988) data that showed an average of 4–5 whales per year were harvested during the early contact period (1771–84). Direct contact with Europeans before this time was minimal, and the early Moravian mission records used by Taylor (1988) represent a whaling complex that was aboriginal in all but a small number of technical adaptations (Taylor, 1979). A number of historical sources are available starting in the late-1700s, and these provide information on bowhead harvests during the historic period. In 1771, Moravian missionaries encountered Inuit who wanted to barter baleen (Hillier, 1967 in Schledermann, 1979), signifying a long-standing tradition of trade with Europeans. This suggests a continuation of active bowhead whaling between 1700 and the establishment of the Moravian missions in 1771. My estimated Labrador harvest for 1701–70 is thus 350 whales (i.e. five per year).

Labrador is unique relative to other eastern Arctic regions in that there are detailed historical accounts of native bowhead whaling. Taylor (1974; 1988) summarised known harvests in Labrador using Moravian mission documents; these data were updated with Brice-Bennett (1978) and Reeves et al. (1983). From 1771–1849 Labrador Inuit harvested a minimum of 107 bowhead whales (plus another 36 struck and lost), and found 56 drift whales (which were likely struck and lost in Davis Strait before drifting to the Labrador coast) (Table 6).

West Greenland

Extensive contact between West Greenland Inuit and Europeans started with Danish-Norwegian colonisation in 1721 (Gad, 1973). For the harvest series, a harvest of five whales per year (Vaughn, 1984) for southwest Greenland is assumed for 1651–1721, for an estimated 355 whales. After colonisation some whale products were traded and therefore included in Danish-Norwegian commercial harvests. However, in many cases Inuit harvested whales and kept all products for their own use, so an average of three whales per year was assumed for the period 1722–70 (before the establishment of Danish shore stations, Gad, 1973). The total estimated West Greenland harvest for this 49-year period is 147 whales.

The Greenlandic hunt for bowhead whales lost its importance in the late 18th or early 19th century due to declining stocks, which prompted a shift to other large whales such as humpback whales (Caulfield, 1993; Kapel, 1979; Kapel and Petersen, 1982; Rink, 1877). In the mid- to late-1800s West Greenlanders averaged one bowhead whale per season (Rink, 1877), supplemented by several drift whale carcasses and one or two humpback whales. Assuming an average harvest of one bowhead per year from 1771–1900, results in an additional 130 whales taken, in addition to the cooperative harvests made with Danish shore-stations discussed previously.

Summary of historic period whaling

In summary, an estimated total of 4,655 whales were taken by Inuit in eastern Canada and West Greenland during the historic whaling period (Table 6).

Inuit harvests post-commercial whaling

In many areas, a tradition of native bowhead whaling that existed as recently as the late-1800s did not persist into the 20th century (Caulfield, 1993; Kapel, 1979; Kapel and Petersen, 1982; Reeves and Mitchell, 1985). Commercial overexploitation was undoubtedly a major factor in this discontinuation. However, after commercial whaling ended there were continued but sporadic Inuit harvests throughout the 20th century, often using equipment left by commercial whalers.

Mitchell and Reeves (1982) and Reeves *et al.* (1983) summarised known harvests and whales struck and lost after 1915. Additional records are available in Gaston and Ouellet (1997, 2000), and Richard (2000) containing comments by R.R. Reeves. In 1985 hunters shot a whale near Arviat in western Hudson Bay; it is unknown whether they killed the animal, but a carcass washed ashore nearby soon after (Stewart *et al.*, 1991). Only three whales were reported harvested in West Greenland during the 20th century (Kapel, 1979; Kapel and Petersen, 1982; Reeves and Heide-Jørgensen, 1996). One young (9–10m) bowhead whale was killed in a white whale net in northwest Greenland in autumn 1980 (Kapel, 1985), for a total known West Greenland kill of four whales post-commercial whaling. Nunavik Inuit reportedly captured a whale in 1979, but it was not killed and subsequently escaped, even after having some skin and blubber removed (A. Kullula and J. Peters, Makivik Corp., pers. comm., 14 March 2007), that was not included in the sources above. Other local Inuit have also reported that this event actually occurred in the 1960s, not the 1970s (Noble, 2008). In total, a minimum of 36 whales were killed, with another 14 struck and lost and three drift whales utilised, by Canadian and Greenland Inuit from 1918–1988. Documentation is sporadic and opportunistic, and these harvests represent minimum values. Most reports summarised by Mitchell and Reeves (1982) came from published sources (e.g. Degerbol and Freuchen, 1935; Sutton and Hamilton, 1932) or HBC post journals, and all are limited in time and space. Mitchell and Reeves (1982) suspected that considerably more whaling had taken place than was reported.

In recent years Canadian Inuit have been issued licenses to conduct subsistence harvests (DFO, unpublished data). In 1994 there was an unlicensed kill in northern Foxe Basin, and there have been licensed harvests since 1996. One whale was taken in each of 1996, 1998, 2000, 2003, and 2005. Three bowheads (two in Nunavut and one in Nunavik) were harvested in each of 2008 and 2009. West Greenland has recently obtained a quota of two strikes per year for the five years 2008–2012, with carry-over (IWC, 2008), and three whales were landed in 2009. In 2004 another bowhead was caught in a net in West Greenland; a kill was attempted but the whale escaped after being injured with rifles (Siku Circumpolar News Service, 2004). Prior to 2003 eight bowhead whales were reported entangled in nets in eastern Canada and West Greenland (DFO, unpublished data). Since that time an additional four whales have been reported to be entangled – two in 2005 and one in 2006 in Nunavut, and one in Disko Bay in 2003 (DFO, unpublished data). It is unknown if this 2003 report from West Greenland represents confusion with the whale that was reportedly entangled and then shot (but escaped) in 2004 (Siku Circumpolar News Service, 2004). The fates of these whales are unknown, but all reportedly disappeared with at least part of the net. However given that they were not shot at (except the 2003 or 2004 whale in West Greenland), they were not included as harvested whales in the catch series. Thus, the total (minimum) harvest between 1918 and 2009, for both eastern Canada (with no known harvests in Labrador) and Greenland combined, is 65 whales, including 14 struck and lost* (Table 6).

Summary of Inuit subsistence harvests

In total, an estimated 19,906 bowhead whales may have been harvested by Inuit in eastern Canada and West Greenland since 1200 AD (Table 6). Most (11,435 whales, 57%) were taken before commercial whaling became established *ca* 1530 AD. There are a number of assumptions included, based on limited and sometimes contradictory data, and unfortunately testing of these assumptions will be difficult. Inuit harvest levels post-1530 AD are small in relation to commercial harvests (Fig. 4), and harvests at these levels would have remained sustainable had commercial

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*2010 harvests: two in Canada (DFO, unpublished data) and three in West Greenland (Heide-Jørgensen *et al.,* 2010).

overexploitation not significantly reduced the whale population.

TECHNOLOGICAL ADVANCES IN WHALING

The entire history of Arctic bowhead whaling can be considered 'traditional' whaling, in contrast to the 'modern' whaling of the late 1800s and 1900s. The technological differences between the two eras are profound. Modern whaling employed numerous technological advances including floating factories, harpoon cannons, and fast steam-powered catcher boats, enabling the capture of the fastest baleen whales. Bowhead whaling in the eastern Arctic utilised mainly hand harpoons from small man-rowed whaleboats, and, for almost its entire history, depended on sailing vessels to make their way through Arctic ice fields. Nonetheless, there were some technological advances throughout the history of bowhead whaling.

In the early years, vessels were usually multipurpose ships (de Jong, 1978). When ice fishing started off Spitsbergen in 1660, the Dutch and Germans started fortifying vessels with an extra layer of planks and extra beams and knees to resist the pressure of ice floes (de Jong, 1978). The British first tried fortifying a ship against the ice in 1790, but it was a failure as the ship was crushed (Jackson, 1978). The biggest technological advance in Arctic whaling vessels was the use of steam power to easier penetrate the Arctic ice. The first steam whaler sailed from Hull in 1857 (Jackson, 1978). Scotland had better luck with steamers than the English ports, and their whaling and sealing fleets quickly became dominated by steam-powered vessels. Between 1861 and 1881, the Scottish fleet changed from 13% to 95% steamers (Jackson 1978), including the entire Dundee fleet by 1873 (Clark, 1887; Jackson, 1978). During the second half of the 19th century, a small fleet of Scottish steamers regularly voyaged through the North Water (Dunbar, 1972; Vaughn, 1991). By the 1870s, Scottish vessels were predominately steam powered, and their catch rates were almost always higher than sailing vessels (Table 7). However, they did not consistently outperform sailing vessels and in some years sailing vessels caught more whales on average. That being said, even when the average catch per vessel was higher for sailing vessels, steam-powered vessels caught larger whales (Sanger, 1991). The large technological advances provided by steam vessels (chiefly the opportunity to penetrate further into the Canadian Arctic) occurred during the final days of the eastern Arctic bowhead hunt, when bowhead numbers were low. The vast majority of Arctic bowhead whales were taken by sailing vessels.

Most bowhead whales taken in eastern Arctic waters were caught using hand harpoons; harpoon cannons were never successfully used in this fishery. However, there were attempts by several nations to invent a suitable cannon. The Danes attempted to build their own several times from the 1760s to 1780s, and experimented with an English-built canon in the 1790s (Gad, 1982). Some British whalers had reportedly experimented with harpoon guns in the 1730s (Sanderson, 1956), again in the 1790s (Gad, 1982), and yet again in 1821 (Jenkins, 1971). Over time, the inventions improved in quality, but whalers generally preferred to use a hand harpoon. The harpoon cannon never became popular until the 'modern' whaling era (the modern harpoon gun, invented in 1860 by the Norwegian sailor Sven Foyn, came into popular use in the 1880s).

Table 7

Numbers of sail and steam powered vessels in British Davis Strait and East Greenland whaling 1865–1876, with total whale harvest and average catch per vessel, by vessel type (data from Clark, 1887).

	Number of vessels		Number of whales		Catch per vessel	
Year	Sail	Steam	Sail	Steam	Sail	Steam
1865	15	11	5	62	0.3	5.6
1866	13	15	42	37	3.2	2.5
1867	11	30	16	8	1.5	0.3
1868	12	18	23	111	1.9	6.2
1869	10	16	8	14	0.8	0.9
1870	8	14	18	61	2.3	4.4
1871	6	15	11	141	1.8	9.4
1872	5	17	9	125	1.8	7.4
1873	4	18	12	160	3.0	8.9
1874	3	16	0	190	0.0	11.9
1875	2	18	13	85	6.5	4.7
1876	3	17	5	77	1.7	4.5

Another whaling invention that improved catch efficiency was the tail knife. It came into use with both Danish and British whalers in the early nineteenth century (Gad, 1982; Scoresby, 1820). It was created to cut the whale's tendons and muscles, preventing it from using its tail. Greenland Inuit were reported to be extremely pleased with its efficiency (Gad, 1982).

STRUCK AND LOST RATES

All of the harvest estimates presented here are of the number of landed whales only, with no accounting for whales which were struck and lost (except for the recent Inuit harvests for which information is reported). Struck and lost animals include those which were harpooned and escaped (to presumably die), those that were killed but lost due to bad weather, breaking lines, etc, and those products that were on ships which sunk or burned. For population modelling, it is necessary to estimate the percentage of whales that were killed but not retrieved. Woodby and Botkin (1993) reported a 24% loss rate for the Bering Sea stock during the nineteenth century (i.e. 24% of the total struck not captured or about 1 in 4 whales struck but not landed). Mitchell (1977) used a 15% loss rate for Hudson Bay and a 20% loss rate for Davis Strait in his calculations of pre-exploitation bowhead population sizes. Mitchell and Reeves (1981) and Woodby and Botkin (1993) used similar values (also see IWC, 1992). In modelling the Spitsbergen bowhead stock, Allen and Keay (2006) used a loss rate of 20%. Those authors tested the sensitivity of their model, and an increase in loss rate to 25% or a decrease to 15% resulted in only slight changes (about 4%) to the pristine stock size estimate.

In the 1780s, the Danish Greenland colonists made a concerted effort to get the Greenlanders to stop whaling from umiaks due to high struck and loss rates (Gad, 1982). By 1788, Greenland Inuit employed in Danish whaling were all using the new 'European' methods with Danish sloops, ropes and tackle. Even with improved equipment, colony whalers lost a large number of whales. For example between December 1779 and mid-May 1780 whalers at Godhavn caught two whales but lost five (Gad, 1973). Klinowska and

Gerslund (1983) summarised struck and lost rates at three Danish shore stations for 1800–1801, and loss rates ranged from 21% to 75% (eight landed and six lost at the Vester Eiland station). For the three stations combined, a total of 28 whales were landed and 13 were struck and lost (overall loss rate 46%). Of these 13 whales, two were definitely dead; and a third was lost with five harpoons and four lines attached and assumed moribund (Klinowska and Gerslund, 1983). Two additional whales were reported lost at Ritenbank (a secondary report from the Godhavn daybook). In recent years (since the mid-1990s) about 80% of the bowheads struck by Alaskan subsistence whalers are landed (Suydam *et al.*, 2007), although in the past up to half those struck were lost (Hess, 1998). Technological and methodological improvements have resulted in this increase in the proportion of whales landed, but the majority of struck but lost whales are considered to have a poor chance of survival (Suydam *et al.*, 2006; 2007).

In the 1700s and 1800s, French whalers targeting Southern right whales (*Eubalaena australis*), a closely related species with similar characteristics and behaviour lost 30–40% of the whales struck (Du Pasquier, 1986). Reeves and Mitchell (1986) used loss rate factors of 1.25–1.57 for American pelagic whaling for North Atlantic right whales. The factor of 1.57 was calculated for the northern Cape Farewell Ground, which would be most similar in environmental conditions to the bowhead whaling grounds, but this was based on few data (13 whales captured, six killed but lost, and one struck but lost). The IWC has used correction factors of 1.2–1.6 for assessments of global right whale populations (IWC, 1986; 2001). These correction factors may be too low, given that Scarff (2001) estimated a struck-lost correction factor of 2.4 for pre-modern ship-based whaling for Pacific right whales (*Eubalaena japonica*). Hacquebord (2005) suggested that the Basques caught approximately 300 whales per year in Grand Bay, but struck and lost another 150 (i.e. a correction factor of 1.5). Bad weather was a factor in the loss of killed whales. In 1852, a British whaler caught four whales along the northwest Baffin Island coast, but severe weather caused three to break adrift from the boat and be lost (Reeves *et al.*, 1983). In some years large numbers of ships were lost, often with cargoes on board. At least 82 ships were lost in Davis Strait from 1819–1843 (Mitchell and Reeves, 1981). The population modelling exercises undertaken as part of the IWC's AWMP consider the sensitivity of varying struck and lost rates; it should be noted that it is likely that they were higher than the 15–20% used previously (Mitchell and Reeves, 1981; Mitchell, 1977; Woodby and Botkin, 1993), at least for some nations and eras.

AGE AND SEX SEGREGATION OF HARVESTS

Bowhead whales exhibit considerable age- and sex-based segregation in their spatiotemporal distribution (Dueck *et al.*, 2006; Finley, 1990; Heide-Jørgensen *et al.*, 2006). In Disko Bay, West Greenland, few calves or juvenile whales have been observed in recent decades, and this pattern is consistent with observations made during the commercial whaling period (Eschricht and Reinhardt, 1866; Heide-Jørgensen *et al.*, 2007). Most (85%) bowhead whales in Disko Bay in spring are large adult females >14m long that are unaccompanied by calves (Heide-Jørgensen *et al.*, 2007; Laidre *et al.*, 2007). Foxe Basin is an important nursery area and is characterised by a large proportion of juvenile whales and cows with calves (Cosens and Blouw, 2003). Commercial whalers did not enter Foxe Basin so it is unknown whether this population structure was the same historically.

Klinowska and Gerslund (1983) suggested that the Disko Bay region was a calving ground, based on the catch of a pregnant female in April 1801 (also see Eschricht and Reinhardt, 1866) in addition to the catch of a very small calf in May of the same year. This animal was reportedly *ca* 3.8m long (12 Danish feet, or 'fod'), with baleen 0.9m long (3 fod). The foetus from the pregnant female was reported to be 4.7m long (Eschricht and Reinhardt, 1866; Klinowska and Gerslund, 1983), considerably larger than the young calf. The baleen plates were also significantly longer than reported for bowhead calves from Alaska (60cm, George and Suydam, 2006). However, the Danish logs gave measurements to the nearest 10 fod (3.14m) (Klinowska and Gerslund, 1983) and the length was probably overestimated. Historical body length data are also difficult to compare with modern data due to differences in the way measurements were taken. Until the modern era, length was typically measured along the body contour rather than in a straight line. Given the gestation lengths of bowhead whales (Koski *et al.*, 1993) and the fact that most bowhead whales currently observed in West Greenland are large adult females (Heide-Jørgensen *et al.*, 2007; Laidre *et al.*, 2007), it is not surprising that pregnant females were found there in spring. Alaskan bowhead calves are usually born between early April and early June (Koski *et al.*, 1993) and births have been observed in Foxe Basin as late as June (NWMB, 2000). However, most calves are born before the females arrive in the Foxe Basin nursery.

There are limited data available on the sex and age composition of commercial bowhead whale harvests in Hudson Bay. Reeves and Cosens (2003) summarised data from logbooks of American whalers from 1862–1905 and provided the age and sex of 164 whales that were struck, killed or sighted. All age classes were represented, with calves making up *ca* 16%, subadults 32% and adults 52% of the harvests. Sex was not reported for the majority of adult whales (64 of 85), but most with data were females (17 of 21 adult whales). Northwestern Hudson Bay may have been a historically important nursery area.

Some data are also available on British catches in Baffin Bay. On the 'south-west fishing' ground whales of both sexes were taken and they were usually large (Duncan, 1827; Lubbock, 1937; Reeves *et al.*, 1983). Finley and Darling (1990) analysed data from the logbook from the whaling vessel *Cumbrian* in 1823 (also in Lubbock, 1937; Reeves *et al.*, 1983). This vessel took adult whales of both sexes (at a near 50:50 ratio) in addition to calves. Excluding calves (known by whalers as 'suckers'), males ranged in size from 9.1 to 16.2m, and females were generally larger (12.8–17.1m). Reeves *et al.* (1983) summarised data from the *Abram* in 1839, which took large whales up to 18m long (Finley and Darling, 1990) on the rock-nosing grounds along the east coast of Baffin Island. This 'rock-nosing' was a specialised bowhead whale fishery that occurred along the east Baffin coast in the autumn and was directed at large whales. In 1827, the *Cumbrian* took 18 whales which were all adults (> 13.7m), and these whales may have been taken along the east coast of Baffin Island (Finley and Darling, 1990). In 'close-seasons' heavy ice conditions excluded whales and whalers from Lancaster Sound. In these years whalers typically encountered large numbers of small whales along the Lancaster Sound ice edge, and total yields were lower due to the prevalence of small whales (Finley and Darling, 1990; Lubbock, 1937; Reeves *et al.*, 1983). Spring whales taken at the floe edge in Cumberland Sound were generally small, but those taken in the fall were usually large (Reeves *et al.*, 1983).

Klinowska and Gerslund (1983) provide total length data for nine whales harvested in Disko Bay (the 'east side' grounds) in 1800–1801, including the calf noted above. The other eight whales were all large adults ranging in size from 15.7 to over 25m. This 25m animal is considerably larger than contemporary adult whales and most likely represents an overestimation due to rounding up and/or different measurement techniques. Two additional whales had baleen lengths over 2.51m (8 fod), and two had baleen lengths over 3.14m (10 fod); thus also representing adult whales. The calf noted above was captured at the same time as an adult whale over 18m long (but again note the potential for significant rounding errors and differences in the way measurements were taken). These limited data suggest that the historical bowhead population in West Greenland was similar to that observed there today, i.e. mostly large adult females (Heide-Jørgensen *et al.*, 2007; Laidre *et al.*, 2007).

The average yields recorded during the later stages of the Baffin Bay fishery (post-1860), after the introduction of steam power, suggest that the industry was processing smaller whales, a similar pattern to that observed on the Spitsbergen grounds (Finley, 1990; Finley and Darling, 1990). During the 1870s, steam-powered vessels were able to penetrate the 'nursery grounds' in Prince Regent Inlet (Ross, 1985). Markham (1874) presented baleen length data on whales taken by the *Arctic* in 1873, mostly from Prince Regent Inlet (also in Finley and Darling, 1990; Sanger, 1991). The harvest again comprised calves and large whales, with a sex ratio of non-calves approaching 50:50. Total whale length was estimated using baleen length data and the regression equation of Lowry (1993). Females taken ranged from *ca* 6m to over 16m in length, while males were slightly smaller, up to *ca* 15.8m. Sanger (1991: Table 2) summarised the baleen lengths of 31 whales harvested by 16 Scottish steam voyages to Davis Strait between 1885 and 1890, of which 29 were adults. Most whales currently observed during autumn in Isabella Bay (Baffin Bay) are large adults >13m long (Finley, 1990), suggesting that current segregation patterns are similar to those historically.

Cumbaa (1986) examined bones from the Basque whaling station at Red Bay and nearly all were from adult whales. Only one young animal (8–9m total length) was found in 17 individual whales assessed but there was a large range in size. One or two bones may have come from a foetal whale, suggesting that pregnant females may have been harvested. The two distinct whaling seasons of the Basques, which were historically thought to refer to right whales (summer) and bowhead whales (autumn), may have resulted from sex- and/or age-based segregation and migration of the bowhead population (McLeod *et al.*, 2008).

Sex ratios in the Baffin Bay fishery approached 50:50, and the size of whales harvested declined towards the end of the commercial whaling period. The use of steam-powered vessels (chiefly by the Scottish fleet) in the late 1800s allowed whalers to penetrate further into the Canadian Arctic and enter the Prince Regent Inlet nursery grounds, which may have resulted in an increased harvests of calves and juveniles towards the later stages of the fishery. A higher proportion of calves were taken in Hudson Bay, with a higher proportion of subadults taken in Baffin Bay and a similar proportion of adults taken on both grounds. This pattern is possibly due to northwest Hudson Bay being an important historical nursery ground. Basque harvests in Labrador require further study, but limited evidence suggests that mostly adult whales were taken. Early Thule whalers took mostly juvenile and subadult whales (McCartney and Savelle, 1985; 1993; Savelle and McCartney, 1991; 1994), but the size of whales taken by Inuit hunters after *ca* 1500 AD has not been well documented. In Labrador during the late 1700s a variety of age classes were taken, ranging from juveniles to large adults (Taylor, 1974; 1988). Inuit hunters in the High Arctic also appear to have at least occasionally taken larger whales (e.g. five large whales in Admiralty Inlet in 1869; Hall, 1876).

DATA QUALITY

The harvest data included here are compiled from a variety of sources, and there is considerable variation in the quality and availability of harvest data. For certain nations and eras (e.g. Dutch after 1719, English after 1814) harvests are based on 'hard data' on the number of vessels and whale yield (oil and/or baleen or actual number taken). These harvests can be considered the most accurate and reliable, but even with these data there are a number of assumptions and uncertainties. Harvest estimates are often based on assumptions of typical whale yield and the number of whales is estimated based on oil and/or baleen data. In his summary of whale catches, Ross (Ross, 1979a: 118) was careful to note that '[p]rinted figures tend to possess an air of unassailable reliability. The impressive columns of numbers …by their smug, self-confident appearance, may suggest a degree of accuracy that is in fact entirely unwarranted'.

For many nations and eras, time series data of vessel numbers and whale products obtained are not available. For these harvests it was necessary to employ a number of assumptions that may not be accurate. Harvest data was therefore scored for data quality and reliability on a three-point scale as follows:

(1) Most reliable, harvest data from published peer-reviewed studies with annual data on harvests (either number of whales or yield in oil and/or baleen) and number of vessels if applicable (commercial harvests), with harvests west of Greenland explicitly separated from those on the Spitsbergen grounds. Examples of 'most reliable' harvest data include those made by American whalers after 1846 (Ross, 1979a), Dutch after 1719 (de Jong, 1978; Ross, 1979a), English after 1814 (Ross, 1979a; Sanger, unpublished data), Scottish after 1750 (Sanger, 1985), German harvests after 1719 (de Jong, 1978; Ross, 1979a), and Inuit harvests in Labrador from

1771–1849 (Brice-Bennett, 1978; Reeves *et al.*, 1983; Taylor, 1974; 1988) and those during the 1900s after commercial whaling ended (DFO, unpublished data; Gaston and Ouellet, 1997 J. Peters and A. Kulula pers. comm; Kapel, 1979; 1985; Kapel and Petersen, 1982; Mitchell and Reeves, 1982; NWMB, 2000; Reeves *et al.*, 1983; Reeves and Heide-Jørgensen, 1996; Richard, 2000; Siku Circumpolar News Service, 2004; Stewart *et al.*, 1991).

These Inuit harvests should not be considered 'complete', but they are based on actual documentation and are thus 'more reliable' than the estimates made in this paper for other regions and eras using average harvests based on bone availability. Additionally, despite the commercial data generally being considered 'most reliable', a number of uncertainties exist as discussed previously (e.g. assuming oil or bone came exclusively from bowheads and not also humpbacks or right whales, incomplete records, limited temporal or port coverage, etc).

(2) Moderately reliable, some data available on either whale yields or vessel numbers, but not separated into the Davis Strait and Spitsbergen grounds or with no catch/vessel data. Harvests were assigned to the Davis Strait fishery based on assumptions on effort and harvest efficiency (catch/vessel) from other nations or using an even 50:50 split. Examples of 'moderately reliable' harvest data include early English harvests (estimated using vessel and product data from Jackson, 1978 and a number of assumptions), and Danish shore-station whaling in West Greenland between 1721 and 1807 (using data from Gad, 1973; 1982 and a number of assumptions).

(3) Least reliable, harvests estimated using a variety of disparate data sources and assumptions, and not based on any actual time series data of vessel numbers or whale products. The 'least reliable' harvest data here include those of the Basques in the Strait of Belle Isle and Gulf of St. Lawrence, all Inuit harvests excluding those noted above, and Danish catches in West Greenland from 1808 to the late 1800s (using assumed average harvests from Vaughn, 1984).

Table 8 summarises the estimated harvests by era and nation and the reliability of the data. The 'most reliable' data (score = 1) include a total estimated harvest of 31,136 whales between 1719 and 1915. Over half of the total compiled harvests (31,435–42,664 whales, depending on estimated Basque harvest) are based on a number of assumptions and are considered the 'least reliable'.

SUMMARY, CONCLUSIONS AND DIRECTIONS FOR FURTHER RESEARCH

The history of bowhead whaling in the waters of eastern Canada and West Greenland is long and varied, and I have attempted to compile all readily available harvest data. However this compilation was limited mainly to published sources (the exception being some of C. Sanger's British data), and no archival material was examined. There is additional information available in museums and archives (e.g. the daybooks of the Royal Greenland Trade, Eschricht and Reinhardt, 1866; Klinowska, 1982; Klinowska and Gerslund, 1983). However, such detailed historical research was beyond the scope of this project and much painstaking research will be needed to fill gaps in the harvest series, which will never be truly complete. Nonetheless, the harvest data presented here (Figs 2–5, Tables 4, 6, 8) represent an improvement over de Jong (1978) and Ross (1979a), which were previously the most complete harvest series available. Using this revised harvest series will improve estimates of pre-exploitation population size over previous attempts (Mitchell and Reeves, 1981; Mitchell, 1977; Woodby and Botkin, 1993).

The quality of catch reporting varies considerably between different nations and eras. Dutch data are among the most extensive and accurate; however there are differences between the harvest series provided by different sources (de Jong, 1978; 1983 vs.; Ross, 1979a). Similar situations exist for both British (Ross, 1979a vs.; Sanger, unpublished) and German (de Jong, 1983 *vs*. Ross, 1979a) whaling. The differences are small and mostly reflect varying assumptions about the oil and baleen yield of an average bowhead and differences in deciphering historical documents. In Table 3,

Table 8

Summary of commercial and Inuit subsistence harvests of bowhead whales in eastern Canada and West Greenland since 1530 AD, with estimates of data quality.

Nation	Era	Harvest	Data quality	Source(s)
Basque	1530–1713	22,454–33,683	3	Numerous assumptions (see text)
Dutch	1719–1826	7,699	1	de Jong (1983); Ross (1979a)
Scottish	1750–1813	1,519	1	Sanger (1985; unpublished data)
English	1750–1800	1,292	2	Jackson (1978) and assumptions
English (HBC)	1767–1772	6	1	Ross (1979a)
British (Scottish and English)	1814–1911	20,312	1	Ross (1979a); Sanger (unpublished data)
English (HBC trade)	1737–1800	115	1	Barr (1994)
German	1719–1792	332	1	de Jong (1983); Ross (1979a)
Danish-Norwegian	1721–1776	95	2	Gad (1973)
	1777–1807	429	2	Gad (1982)
	1808–1890	718	3	Vaughn (1984) and assumptions
American	1846–1915	945	1	Ross (1979a)
Inuit (excl. Labrador 1771–1849)	1530–1917	8,263	3	Numerous assumptions (see text)
Labrador Inuit	1771–1849	143	1	Brice-Bennett (1978); Reeves *et al.* (1983); Taylor (1974; 1988)
Inuit post-commercial whaling	1918–2009	65	1	DFO (unpublished data); Gaston and Ouellet (1997); Kapel (1979; 1985); Kapel and Peterson (1982); Mitchell and Reeves (1982); NWMB (2000); J. Peters and A. Kulula (pers. comm.); Reeves *et al.* (1983); Reeves and Heide-Jørgensen (1996); Richard (2000); Siku Circumpolar News Service (2004); Stewart *et al.* (1991)

the total commercial harvest estimate is based on the source with the highest recorded harvest, with yearly gaps filled in using other sources where appropriate.

For Basque whaling, a complete catch series is unavailable, although some relevant information undoubtedly exists in French-language materials (Du Pasquier, 2000; 1982). The Basques were active in the Strait of Belle Isle and Gulf of St. Lawrence from *ca* 1530 AD and the fishery peaked in the mid-1500s (Barkham, 1984). The vast majority of harvested whales were bowheads (McLeod *et al.*, 2008; 2006; Rastogi *et al.*, 2004). Peak harvests in the range of 300–500 whales per year have been estimated (Aguilar, 1986; Barkham, 1984; this study). Basque whalers also fished in Davis Strait in the 1700s, at least sporadically, but harvests are unknown. There are no data concerning Dutch Davis Strait whaling prior to 1719 (de Jong, 1978; 1983; Ross, 1979a). A similar situation exists with the German harvest series (de Jong, 1983; Ross, 1979a), which is not only limited in temporal coverage but also with incomplete port coverage. No complete history of Danish whaling at the West Greenland colonies has been written. The summaries of Gad (1973; 1982) and Vaughn (1984) presented here are only an initial step towards establishing a catch history for this phase of whaling.

Data on British harvests in Davis Strait for 1750–1801 are available for Scottish harvests only (Sanger, 1985) and after 1814 for both English and Scottish harvests (Ross, 1979a; 1993; Sanger, unpublished data). Data on vessels and whales harvested are also available for Scottish whaling only from 1802–1813 (Sanger, unpublished data). Jackson (1978) provides limited data on English harvests from 1750–1800. A number of assumptions resulted in the estimated English whale kill for those years (Table 2). This is a slight improvement over previous compilations containing no estimates, but it is no substitute for detailed historical research. Another source of British whale products was trade between Inuit and the HBC. Barr (1994) summarised data for 1737–1800, which included the baleen from *ca* 115 whales. While these data assist in providing a more complete harvest series, they again do not summarise the entire trade.

Ross (1979a) provides American Davis Strait whaling after 1846 and in Hudson Bay from 1860. However, this series is missing harvests from the first American whaling trips to Davis Strait in the 1700s. Best (1987) provides an estimate of 248–291 bowheads taken by American whalers from 1815–19. This occurred previous to the American expansion into the Pacific grounds, so these whales were possibly harvested in Davis Strait by right and sperm whaling vessels. However they could have been taken east of Greenland as well, and given this uncertainty they have not been included in my harvest series. After the Basques left the Strait of Belle Isle and Gulf of St. Lawrence Canadian colonists conducted sporadic whaling there (Reeves and Mitchell, 1986). At least some bowheads may have been taken (Bonnycastle's 1842 statement that whales taken in Newfoundland waters included 'the largest mysticetus or great common oil whale of the northern oceans, which occasionally visits these waters', Clark, 1887: 217).

Inuit throughout eastern Canada and West Greenland have harvested bowhead whales for centuries. Knowledge of the total Inuit harvest will always be elusive but there are some data. The total estimated Inuit harvest from 1200–2009 AD is 19,906 whales (Fig. 3, Table 6 but see Savelle (in review) for higher estimated Classic Thule harvests). The majority (57%) were harvested prior to the start of commercial whaling *ca* 1530 AD. Low numbers were reported harvested after the cessation of commercial whaling in the early 1900s, but additional unreported Inuit whaling likely took place (Mitchell and Reeves, 1982; see NWMB, 2000).

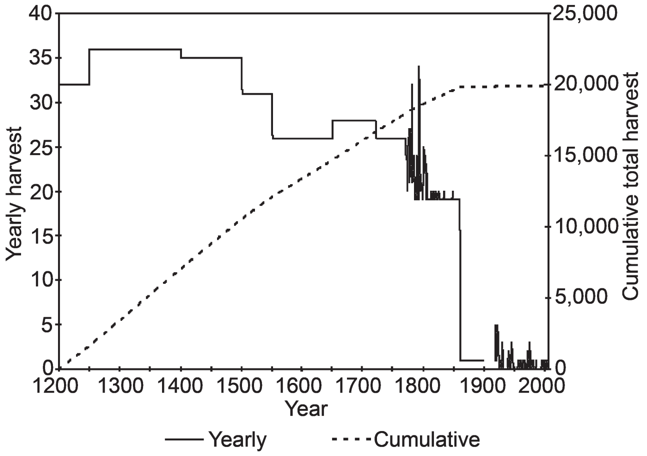

Fig. 3. Estimated yearly and cumulative Inuit harvests of bowhead whales in the eastern Canadian Arctic and West Greenland from 1200–2009 AD. Pre-1500 harvests represent the classic Thule culture, and the majority of Inuit harvests occurred during this time, prior to the establishment of commercial whaling *ca* 1530 AD.

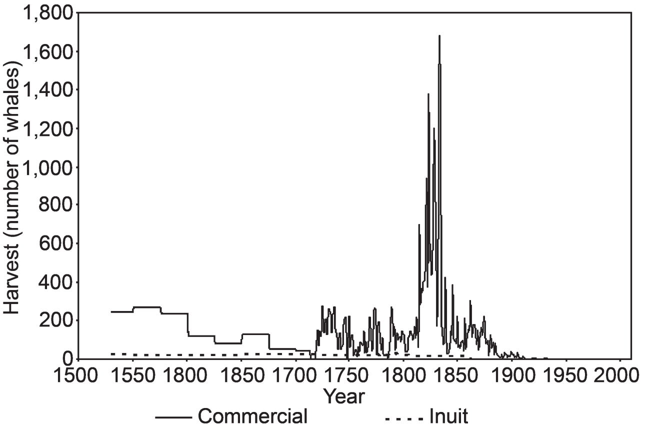

Fig. 4. Comparison of commercial and Inuit subsistence harvest levels of bowhead whales in the eastern Arctic, 1530–2009 AD. Commercial harvests assume peak Basque whaling effort of 25 vessels per year.

An estimated harvest of almost 20,000 animals may sound unreasonably high; however this took place over *ca* 800 years and never exceeded an estimated 36 whales per year (during the peak of the classic Thule period). In most years, harvests were considerably lower, and even during peak years Inuit harvests paled in comparison to those made by commercial whalers (Fig. 4). Inuit harvests alone would not have negatively impacted a healthy bowhead population and would have remained sustainable if commercial whalers had not reduced the species to such low numbers. With an annual growth rate of 3–4% (George *et al.*, 2004), a pristine population of 10,000 whales (likely an underestimate; Woodby and Botkin, 1993) would produce far more calves per year than the number of young whales taken for subsistence purposes. Even if this harvest series significantly underestimates true harvest levels (Savelle, in review), there would likely have been little effect on bowhead population size in the absence of commercial harvests.

Estimated Inuit harvests, as summarised in Fig. 3, show little annual variation, except for Labrador harvests during the early contact period (when Moravian missionaries kept detailed records). The Inuit harvest series for the remaining regions and time periods (and also for Basque whaling) is based on estimated average yearly harvests and ignore the variability that undoubtedly occurred.

The Inuit harvest series is based on limited data and a number of assumptions which will be extremely hard to test. One method which may be used to better quantify the importance of bowhead whales over time is the use of stable isotopes. Coltrain *et al.* (2004) used stable isotope signatures of skeletal remains to measure the importance of different species to modified Thule whalers in Hudson Bay. Bowhead whales accounted for approximately 12% of the total dietary intake. Without similar data from other regions and time periods it is difficult to convert this to an estimate of the number of whales used or how the importance of bowhead whales changed over time. Analyses of isotopic signatures of classic Thule remains, perhaps from Somerset Island, would assist in quantifying the importance of bowhead whales over time. Another pertinent research avenue would be examination of skeletal remains from Labrador Inuit. Analysis of remains from *ca* 1500 to the mid-1800s could be used in conjunction with the detailed harvest series in the Moravian mission documents (Taylor, 1974; 1988) to better assess the importance of bowhead whales over time. However an assessment such as this still would not incorporate the importance of bowhead whale oil as fuel.

Overall, the combined commercial and Inuit harvests in eastern Canada and West Greenland since 1530 AD was estimated at 70,008 whales (Fig. 5, Tables 3, 6, also Appendix 1). The manuscript includes little information on the numbers of vessels and/or catch per vessel. Catch per voyage data are available for some whaling nations and/or periods (see Appendix 1), but not all (and those with said data are considered the 'most reliable', Table 8). This harvest series can now be used with a population model to improve past estimates of pre-exploitation population size. All whale harvests reported here are landed whales only, with no accounting for struck and lost whales (with the exception of recent Inuit harvests as discussed above). During population modelling and assessment it will be necessary to explore various assumptions regarding struck and loss rates, noting that rates of 15–20% used previously (Mitchell, 1977) may be too conservative. Overall, the use of this expanded harvest series and more detailed modelling techniques, will provide more accurate estimates of pre-whaling population size and improve conservation and recovery planning for eastern Canada-West Greenland bowhead whales.

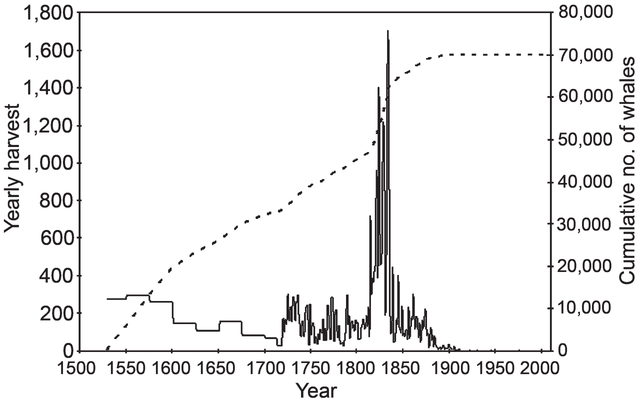

Fig. 5. Total yearly and cumulative harvest of bowhead whales in eastern Canada and West Greenland, 1530–2009 AD, combining commercial and Inuit harvests (assuming 25 Basque vessels per year during peak).

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Appendix 1

Harvest series for bowhead whales in eastern Canada and West Greenland, from 1530 to 2009 AD, assuming 25 Basque vessels per year at the peak of their whaling activities in the Gulf of St. Lawrence/Strait of Belle Isle. Catch per vessel (CPV) data is provided where available. The summary is known to be incomplete in many cases and is based on a number of assumptions and disparate data sources, as discussed in the text.

		Dutch		Scottish		English		Hudson's Bay Company		German			American			
Year	Basque	Whales	CPV	Whales	CPV	Whales	CPV	Whaling	Trade	Whales	CPV	Danish	Whales	CPV	Inuit	Total
1530	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1531	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1532	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1533	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1534	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1535	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1536	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1537	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1538	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1539	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1540	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1541	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1542	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1543	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1544	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1545	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1546	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1547	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1548	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1549	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1550	246	–	–	–	–	–	–	–	–	–	–	–	–	–	31	277
1551	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1552	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1553	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1554	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1555	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1556	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1557	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1558	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1559	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1560	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1561	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1562	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1563	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296

Cont.

		Dutch		Scottish		English		Hudson's Bay Company		German			American			
Year	Basque	Whales	CPV	Whales	CPV	Whales	CPV	Whaling	Trade	Whales	CPV	Danish	Whales	CPV	Inuit	Total
1564	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1565	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1566	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1567	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1568	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1569	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1570	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1571	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1572	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1573	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1574	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1575	270	–	–	–	–	–	–	–	–	–	–	–	–	–	26	296
1576	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1577	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1578	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1579	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1580	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1581	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1582	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1583	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1584	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1585	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1586	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1587	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1588	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1589	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1590	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1591	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1592	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1593	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1594	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1595	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1596	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1597	234														26	260
1598	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1599	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1600	234	–	–	–	–	–	–	–	–	–	–	–	–	–	26	260
1601	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1602	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1603	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1604	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1605	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1606	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1607	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1608	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1609	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1610	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1611	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1612	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1613	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1614	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1615	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1616	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1617	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1618	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1619	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1620	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1621	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1622	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1623	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1624	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1625	120	–	–	–	–	–	–	–	–	–	–	–	–	–	26	146
1626	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1627	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1628	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1629	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1630	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1631	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1632	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1633	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1634	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1635	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1636	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1637	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110

Cont.

		Dutch		Scottish		English		Hudson's Bay Company		German			American			
Year	Basque	Whales	CPV	Whales	CPV	Whales	CPV	Whaling	Trade	Whales	CPV	Danish	Whales	CPV	Inuit	Total
1638	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	116
1639	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1640	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1641	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1642	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1643	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1644	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1645	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1646	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1647	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1648	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1649	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1650	84	–	–	–	–	–	–	–	–	–	–	–	–	–	26	110
1651	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1652	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1653	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1654	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1655	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1656	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1657	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1658	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1659	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1660	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1661	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1662	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1663	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1664	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1665	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1666	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1667	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1668	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1669	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1670	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1671	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1672	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1673	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1674	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1675	132	–	–	–	–	–	–	–	–	–	–	–	–	–	28	160
1676	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1677	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1678	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1679	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1680	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1681	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1682	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1683	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1684	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1685	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1686	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1687	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1688	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1689	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1690	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1691	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1692	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1693	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1694	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1695	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1696	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1697	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1698	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1699	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1700	54	–	–	–	–	–	–	–	–	–	–	–	–	–	28	82
1701	43	–	–	–	–	–	–	–	–	–	–	–	–	–	28	71
1702	43	–	–	–	–	–	–	–	–	–	–	–	–	–	28	71
1703	43	–	–	–	–	–	–	–	–	–	–	–	–	–	28	71
1704	43	–	–	–	–	–	–	–	–	–	–	–	–	–	28	71
1705	43	–	–	–	–	–	–	–	–	–	–	–	–	–	28	71
1706	43	–	–	–	–	–	–	–	–	–	–	–	–	–	28	71
1707	43	–	–	–	–	–	–	–	–	–	–	–	–	–	28	71
1708	43	–	–	–	–	–	–	–	–	–	–	–	–	–	28	71
1709	43	–	–	–	–	–	–	–	–	–	–	–	–	–	28	71
1710	43	–	–	–	–	–	–	–	–	–	–	–	–	–	28	71
1711	43	–	–	–	–	–	–	–	–	–	–	–	–	–	28	71

Cont.

		Dutch		Scottish		English		Hudson's Bay Company		German			American			
Year	Basque	Whales	CPV	Whales	CPV	Whales	CPV	Whaling	Trade	Whales	CPV	Danish	Whales	CPV	Inuit	Total
1712	43	–	–	–	–	–	–	–	–	–	–	–	–	–	28	71
1713	43	–	–	–	–	–	–	–	–	–	–	–	–	–	28	71
1714	–	–	–	–	–	–	–	–	–	–	–	–	–	–	28	28
1715	–	–	–	–	–	–	–	–	–	–	–	–	–	–	28	28
1716	–	–	–	–	–	–	–	–	–	–	–	–	–	–	28	28
1717	–	–	–	–	–	–	–	–	–	–	–	–	–	–	28	28
1718	–	–	–	–	–	–	–	–	–	–	–	–	–	–	28	28
1719	–	43	1.5	–	–	–	–	–	–	1	0.3	–	–	–	28	72
1720	–	145	2.3	–	–	–	–	–	–	7	1.2	–	–	–	28	180
1721	–	65	0.6	–	–	–	–	–	–	8	0.5	1	–	–	28	102
1722	–	136	2	–	–	–	–	–	–	11	1.8	1	–	–	26	174
1723	–	113	2.5	–	–	–	–	–	–	5	1.3	1	–	–	26	145
1724	–	135	2.3	–	–	–	–	–	–	6	3	3	–	–	26	170
1725	–	251	3.1	–	–	–	–	–	–	27	3	1	–	–	26	305
1726	–	114	1	–	–	–	–	–	–	23	1	0	–	–	26	163
1727	–	179	1.8	–	–	–	–	–	–	14	0.7	1	–	–	26	220
1728	–	199	2.2	–	–	–	–	–	–	14	1.6	0	–	–	26	239
1729	–	122	1.3	–	–	–	–	–	–	9	1.1	0	–	–	26	157
1730	–	214	2.6	–	–	–	–	–	–	8	1	1	–	–	26	249
1731	–	255	2.6	–	–	–	–	–	–	6	0.5	2	–	–	26	289
1732	–	219	1.6	–	–	–	–	–	–	15	0.8	1	–	–	26	261
1733	–	136	1.2	–	–	–	–	–	–	1	0.2	1	–	–	26	164
1734	–	230	2.5	–	–	–	–	–	–	6	0.8	1	–	–	26	263
1735	–	226	2.2	–	–	–	–	–	–	6	1.5	2	–	–	26	260
1736	–	269	2.9	–	–	–	–	–	–	1	1	3	–	–	26	299
1737	–	151	1.7	–	–	–	–	–	1	4	1	4	–	–	26	186
1738	–	115	1.6	–	–	–	–	–	1	–	–	0	–	–	26	142
1739	–	52	0.9	–	–	–	–	–	1	–	–	0	–	–	26	79
1740	–	114	3.5	–	–	–	–	–	1	–	–	0	–	–	26	141
1741	–	137	4	–	–	–	–	–	1	1	1	0	–	–	26	165
1742	–	50	1	–	–	–	–	–	1	2	2	0	–	–	26	79
1743	–	76	1.5	–	–	–	–	–	1	–	–	2	–	–	26	105
1744	–	183	4.7	–	–	–	–	–	1	–	–	0	–	–	26	210
1745	–	207	6.7	–	–	–	–	–	1	–	–	4	–	–	26	238
1746	–	217	5.4	–	–	–	–	–	1	–	–	5	–	–	26	249
1747	–	132	3.6	–	–	–	–	–	1	4	4	4	–	–	26	167
1748	–	0	0	–	–	–	–	–	1	–	–	6	–	–	26	33
1749	–	206	5	–	–	–	–	–	3	16	4	0	–	–	26	251
1750	–	58	1.3	–	–	–	–	–	2	2	0.5	2	–	–	26	90
1751	–	67	1.5	5	5	32	–	–	1	5	1	0	–	–	26	136
1752	–	108	2.6	4	4	2	–	–	1	9	1.8	4	–	–	26	154
1753	–	100	2.1	2	2	0	–	–	2	3	1	0	–	–	26	133
1754	–	18	0.5	0	0	0	–	–	1	0	0	0	–	–	26	45
1755	–	41	1.4	0	0	0	–	–	1	–	–	9	–	–	26	77
1756	–	40	1.5	–	–	0	–	–	1	–	–	0	–	–	26	67
1757	–	10	0.5	–	–	0	–	–	5	–	–	0	–	–	26	41
1758	–	66	8.3	–	–	0	–	–	1	–	–	0	–	–	26	93
1759	–	39	1.8	–	–	0	–	–	1	0	0	0	–	–	26	66
1760	–	78	5.2	–	–	0	–	–	2	10	3.3	0	–	–	26	116
1761	–	70	3	–	–	0	–	–	2	7	2.3	0	–	–	26	105
1762	–	66	2.4	–	–	0	–	–	1	4	1.3	0	–	–	26	97
1763	–	132	3.8	–	–	0	–	–	1	8	4	6	–	–	26	173
1764	–	31	0.8	–	–	0	–	–	3	1	0.5	0	–	–	26	61
1765	–	82	2.3	–	–	0	–	0	1	11	3.7	1	–	–	26	121
1766	–	33	1	–	–	0	–	0	1	0	0	0	–	–	26	60
1767	–	80	2.4	–	–	0	–	1	2	3	1	0	–	–	26	112
1768	–	208	5.8	–	–	0	–	1	2	9	3	2	–	–	26	248
1769	–	159	3.8	–	–	0	–	0	1	7	1.8	0	–	–	26	193
1770	–	86	1.9	–	–	0	–	0	5	6	1.5	0	–	–	26	123
1771	–	38	1	–	–	0	–	3	1	0	0	0	–	–	24	66
1772	–	240	6.3	–	–	0	–	1	2	12	6	5	–	–	24	284
1773	–	250	5.8	–	–	0	–	–	1	9	4.5	7	–	–	20	287
1774	–	179	3.7	–	–	0	–	–	2	5	1.7	1	–	–	25	212
1775	–	19	0.4	–	–	0	–	–	6	1	0.3	0	–	–	26	52
1776	–	145	3.7	–	–	0	–	–	6	7	2.3	14	–	–	27	199
1777	–	178	4	–	–	0	–	–	2	5	1.7	14	–	–	21	220
1778	–	55	1.2	–	–	0	–	–	4	1	0.3	22	–	–	26	108
1779	–	36	0.8	–	–	0	–	–	–	0	0	10	–	–	27	73
1780	–	91	2.5	–	–	0	–	–	6	2	2	14	–	–	23	136
1781	–	–	–	–	–	0	–	–	6	1	1	20	–	–	32	59
1782	–	–	–	–	–	0	–	–	1	3	3	14	–	–	21	39
1783	–	2	0.2	–	–	0	–	–	3	0	0	16	–	–	22	43
1784	–	8	1.3	–	–	0	–	–	1	–	–	14	–	–	24	47
1785	–	5	5	–	–	0	–	–	2	–	–	0	–	–	22	29

Cont.

		Dutch		Scottish		English		Hudson's Bay Company		German			American			
Year	Basque	Whales	CPV	Whales	CPV	Whales	CPV	Whaling	Trade	Whales	CPV	Danish	Whales	CPV	Inuit	Total
1786	–	39	5.6	–	–	0	–	–	–	–	–	0	–	–	19	58
1787	–	41	5.9	5	5	33	–	–	1	–	–	0	–	–	19	99
1788	–	21	1.9	25	3.6	144	–	–	2	0	0	18	–	–	19	229
1789	–	23	2.9	48	4.4	183	–	–	–	6	3	16	–	–	24	300
1790	–	10	0.7	16	1.6	71	–	–	–	0	0	22	–	–	23	142
1791	–	18	1.4	25	3.1	108	–	–	–	0	0	24	–	–	19	194
1792	–	2	0.2	6	0.5	27	–	–	–	0	0	14	–	–	19	68
1793	–	–	0	13	1.6	101	–	–	–	–	–	6	–	–	34	154
1794	–	14	4.7	21	7	92	–	–	–	–	–	12	–	–	22	161
1795	–	–	–	24	8	62	–	–	4	–	–	12	–	–	21	123
1796	–	–	–	17	8.5	73	–	–	5	–	–	26	–	–	20	141
1797	–	1	1	12	4	66	–	–	–	–	–	10	–	–	21	110
1798	–	–	–	13	3.3	114	–	–	4	–	–	16	–	–	19	166
1799	–	–	–	17	8.5	96	–	–	2	–	–	14	–	–	20	149
1800	–	–	–	21	7	88	–	–	2	–	–	22	–	–	25	158
1801	–	–	–	26	8.7	–	–	–	–	–	–	14	–	–	23	63
1802	–	0	0	30	10	–	–	–	–	–	–	14	–	–	22	66
1803	–	–	–	36	5.1	–	–	–	–	–	–	2	–	–	24	62
1804	–	–	–	89	9.9	–	–	–	–	–	–	21	–	–	19	129
1805	–	–	–	101	6.7	–	–	–	–	–	–	18	–	–	21	140
1806	–	–	–	133	9.5	–	–	–	–	–	–	18	–	–	22	173
1807	–	–	–	119	9.2	–	–	–	–	–	–	6	–	–	19	144
1808	–	–	–	86	6.6	–	–	–	–	–	–	14	–	–	19	119
1809	–	–	–	116	12.9	–	–	–	–	–	–	14	–	–	19	149
1810	–	–	–	158	14.4	–	–	–	–	–	–	14	–	–	19	191
1811	–	–	–	98	8.9	–	–	–	–	–	–	14	–	–	19	131
1812	–	–	–	206	12.9	–	–	–	–	–	–	14	–	–	19	239
1813	–	–	–	47	2.1	–	–	–	–	–	–	14	–	–	20	81
1814	–	–	–	150	6.8	538	12	–	–	–	–	14	–	–	19	721
1815	–	–	–	92	5.4	175	5.3	–	–	–	–	14	–	–	19	300
1816	–	–	–	134	8.4	223	8	–	–	–	–	14	–	–	20	391
1817	–	–	–	144	7.6	188	5.5	–	–	–	–	14	–	–	19	365
1818	–	–	–	104	5.2	285	6.6	–	–	–	–	14	–	–	20	423
1819	–	–	–	119	5.7	275	6.5	–	–	–	–	14	–	–	19	427
1820	–	–	–	307	14	463	13.2	–	–	–	–	14	–	–	20	804
1821	–	6	6	478	13.7	445	10.1	–	–	–	–	14	–	–	20	963
1822	–	2	2	226	6.3	131	5	–	–	–	–	14	–	–	19	392
1823	–	11	11	974	26.3	381	15.2	–	–	–	–	14	–	–	19	1399
1824	–	0	0	318	6.8	278	7.9	–	–	–	–	14	–	–	19	629
1825	–	2	1	206	4.1	217	5.7	–	–	–	–	14	–	–	20	459
1826	–	0	0	245	5.3	212	5.3	–	–	–	–	14	–	–	19	490
1827	–	–	–	562	16.5	396	12.4	–	–	–	–	14	–	–	19	991
1828	–	–	–	662	14.1	525	14.6	–	–	–	–	14	–	–	19	1220
1829	–	–	–	436	9.5	431	10.3	–	–	–	–	14	–	–	19	900
1830	–	–	–	56	1.2	104	2.5	–	–	–	–	14	–	–	19	193
1831	–	–	–	195	4.8	215	5.5	–	–	–	–	14	–	–	19	443
1832	–	–	–	784	23.1	699	25	–	–	–	–	14	–	–	19	1516
1833	–	–	–	844	21.6	824	22.9	–	–	–	–	14	–	–	19	1701
1834	–	–	–	498	14.2	373	11	–	–	–	–	14	–	–	20	905
1835	–	–	–	117	2.9	49	1.6	–	–	–	–	14	–	–	19	199
1836	–	–	–	44	1.2	18	0.9	–	–	–	–	14	–	–	19	95
1837	–	–	–	69	2.9	20	2.9	–	–	–	–	14	–	–	19	122
1838	–	–	–	255	11.6	160	20	–	–	–	–	14	–	–	19	448
1839	–	–	–	44	2.2	40	4.4	–	–	–	–	14	–	–	19	117
1840	–	–	–	9	0.7	6	0.9	–	–	–	–	14	–	–	19	48
1841	–	–	–	10	2.5	5	1.3	–	–	–	–	14	–	–	19	48
1842	–	–	–	44	14.7	11	11	–	–	–	–	14	–	–	19	88
1843	–	–	–	101	7.8	34	8.5	–	–	–	–	14	–	–	19	168
1844	–	–	–	72	4.5	37	5.3	–	–	–	–	14	–	–	19	142
1845	–	–	–	278	21.4	95	19	–	–	–	–	14	–	–	19	406
1846	–	–	–	71	4.7	23	4.6	–	–	–	–	14	0	0	19	127
1847	–	–	–	49	3.3	22	4.4	–	–	–	–	14	9	9	19	113
1848	–	–	–	35	3.9	24	4.8	–	–	–	–	14	8	8	20	101
1849	–	–	–	178	17.8	23	2.1	–	–	–	–	14	9	9	19	243
1850	–	–	–	37	3.7	7	0.9	–	–	–	–	14	5	5	19	82
1851	–	–	–	52	4.7	18	6	–	–	–	–	5	4	4	19	98
1852	–	–	–	41	4.6	12	3	–	–	–	–	5	0	0	19	77
1853	–	–	–	58	6.4	21	4.2	–	–	–	–	5	9	4.5	19	112
1854	–	–	–	81	6.8	3	1.5	–	–	–	–	5	9	4.5	19	117
1855	–	–	–	38	2.9	2	1	–	–	–	–	5	0	0	19	64
1856	–	–	–	178	11.9	32	16	–	–	–	–	5	1	0.3	19	235
1857	–	–	–	37	1.9	1	0.5	–	–	–	–	5	8	2	19	70
1858	–	–	–	59	3	28	4.7	–	–	–	–	5	14	4.7	19	125
1859	–	–	–	113	6.6	29	7.3	–	–	–	–	5	12	3	19	178

Cont.

		Dutch		Scottish		English		Hudson's Bay Company		German			American			
Year	Basque	Whales	CPV	Whales	CPV	Whales	CPV	Whaling	Trade	Whales	CPV	Danish	Whales	CPV	Inuit	Total
1860	–	–	–	98	4.7	13	1.9	–	–	–	–	5	33	3	19	168
1861	–	–	–	188	7	61	10.2	–	–	–	–	5	52	5.2	1	307
1862	–	–	–	100	4.3	12	2.4	–	–	–	–	5	61	6.1	1	179
1863	–	–	–	25	1.9	3	1	–	–	–	–	5	84	4.9	1	118
1864	–	–	–	65	3.8	–	–	–	–	–	–	5	114	4.2	1	185
1865	–	–	–	81	7.4	5	2.5	–	–	–	–	5	89	3.9	1	181
1866	–	–	–	44	2.8	2	2	–	–	–	–	5	69	3.1	1	121
1867	–	–	–	16	1.1	2	2	–	–	–	–	5	52	2.2	1	76
1868	–	–	–	126	7.4	–	–	–	–	–	–	5	20	1.7	1	152
1869	–	–	–	17	1.4	1	1	–	–	–	–	5	27	2.5	1	51
1870	–	–	–	80	8.9	–	–	–	–	–	–	1	24	2.7	1	106
1871	–	–	–	147	12.3	–	–	–	–	–	–	1	19	2.4	1	168
1872	–	–	–	114	8.8	–	–	–	–	–	–	1	9	1.1	1	125
1873	–	–	–	170	14.2	–	–	–	–	–	–	1	11	2.2	1	183
1874	–	–	–	212	15.1	–	–	–	–	–	–	1	13	3.3	1	227
1875	–	–	–	96	6	–	–	–	–	–	–	1	23	4.6	1	121
1876	–	–	–	71	4.4	–	–	–	–	–	–	1	9	2.3	1	82
1877	–	–	–	87	5.4	–	–	–	–	–	–	1	8	1.1	1	97
1878	–	–	–	10	0.6	–	–	–	–	–	–	1	6	0.6	1	18
1879	–	–	–	74	4.6	–	–	–	–	–	–	1	15	2.1	1	91
1880	–	–	–	117	8.4	–	–	–	–	–	–	1	7	1.2	1	126
1881	–	–	–	48	4	–	–	–	–	–	–	1	8	0.9	1	58
1882	–	–	–	79	6.6	–	–	–	–	–	–	1	8	1.6	1	89
1883	–	–	–	18	2	–	–	–	–	–	–	1	5	1	1	25
1884	–	–	–	79	7.9	–	–	–	–	–	–	1	3	0.8	1	84
1885	–	–	–	29	2.2	–	–	–	–	–	–	1	2	0.5	1	33
1886	–	–	–	19	1.4	–	–	–	–	–	–	1	3	0.6	1	24
1887	–	–	–	14	1.6	–	–	–	–	–	–	1	6	2	1	22
1888	–	–	–	8	0.9	–	–	–	–	–	–	1	0	0	1	10
1889	–	–	–	11	2.8	–	–	–	–	–	–	1	0	0	1	13
1890	–	–	–	20	2.5	–	–	–	–	–	–	1	2	2	1	24
1891	–	–	–	6	1	–	–	–	–	–	–	–	1	0.5	1	8
1892	–	–	–	8	1.3	–	–	–	–	–	–	–	4	2	1	13
1893	–	–	–	32	6.4	–	–	–	–	–	–	–	1	0.5	1	34
1894	–	–	–	16	2.7	–	–	–	–	–	–	–	6	3	1	23
1895	–	–	–	6	1	–	–	–	–	–	–	–	2	0.7	1	9
1896	–	–	–	6	1.5	–	–	–	–	–	–	–	11	2.2	1	18
1897	–	–	–	12	2.4	–	–	–	–	–	–	–	3	0.8	1	16
1898	–	–	–	6	1.5	–	–	–	–	–	–	–	10	3.3	1	17
1899	–	–	–	28	3.5	–	–	–	–	–	–	–	9	4.5	1	38
1900	–	–	–	18	2.6	–	–	–	–	–	–	–	6	3	1	25
1901	–	–	–	15	2.5	–	–	–	–	–	–	–	7	3.5	0	22
1902	–	–	–	12	2	–	–	–	–	–	–	–	0	0	0	12
1903	–	–	–	14	2	–	–	–	–	–	–	–	2	2	0	16
1904	–	–	–	11	1.6	–	–	–	–	–	–	–	1	1	0	12
1905	–	–	–	23	2.3	–	–	–	–	–	–	–	9	9	0	32
1906	–	–	–	7	0.8	–	–	–	–	–	–	–	0	–	0	7
1907	–	–	–	3	0.3	–	–	–	–	–	–	–	0	0	0	3
1908	–	–	–	5	0.8	–	–	–	–	–	–	–	0	0	0	5
1909	–	–	–	3	0.8	–	–	–	–	–	–	–	0	0	0	3
1910	–	–	–	13	1.4	–	–	–	–	–	–	–	0	0	0	13
1911	–	–	–	4	0.7	–	–	–	–	–	–	–	2	2	0	6
1912	–	–	–	–	–	–	–	–	–	–	–	–	1	1	0	1
1913	–	–	–	–	–	–	–	–	–	–	–	–	0	0	0	0
1914	–	–	–	–	–	–	–	–	–	–	–	–	0	0	0	0
1915	–	–	–	–	–	–	–	–	–	–	–	–	0	0	0	0
1916	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1917	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1918	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1919	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	5
1920	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1921	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	3
1922	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	5
1923	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2
1924	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1925	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1926	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1927	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1928	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1929	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1930	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	3
1931	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1932	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1933	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0

Cont.

		Dutch		Scottish		English		Hudson's Bay Company		German			American			
Year	Basque	Whales	CPV	Whales	CPV	Whales	CPV	Whaling	Trade	Whales	CPV	Danish	Whales	CPV	Inuit	Total
1934	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1935	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1936	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1937	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1938	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1939	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1940	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2
1941	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1942	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1943	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1944	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1945	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	3
1946	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1947	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1948	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1949	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1950	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1951	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1952	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1953	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1954	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1955	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1956	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1957	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1958	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1959	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1960	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1961	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1962	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1963	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1964	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1965	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1966	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1967	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1968	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1969	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1970	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1971	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2
1972	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1973	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1974	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1975	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	3
1976	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1977	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1978	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1979	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1980	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1981	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1982	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1983	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1984	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1985	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1986	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1987	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1988	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1989	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1990	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1991	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1992	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1993	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1994	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1995	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1996	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1997	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
1998	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
1999	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
2000	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
2001	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
2002	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
2003	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
2004	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
2005	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
2006	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
2007	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
2008	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	3
2009	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	6
Total	**28,075**	**7,699**	**0**	**13,634**	**0**	**9,489**	**0**	**6**	**115**	**332**	**0**	**1,242**	**945**	**0**	**8,471**	**70,008**